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Conditional same/different discrimination learning in the short-beaked echidna (*Tachyglossus aculeatus*)

Fiona Allison Russell
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Department of Psychology

**CONDITIONAL SAME/DIFFERENT DISCRIMINATION
LEARNING IN THE SHORT-BEAKED ECHIDNA
(*Tachyglossus aculeatus*)**

Fiona Allison Russell (B.A., G.B.Sc.)

**This thesis is presented as part of the requirements for the
award of the Degree of Doctor of Philosophy of the
University of Wollongong**

2014

Certification

I, Fiona A. Russell, declare that this thesis, submitted in fulfilment of the requirements for the award of Doctor of Philosophy, in the Department of Psychology, University of Wollongong, is wholly my own work unless otherwise referenced or acknowledged. The document has not been submitted for qualifications at any other academic institution.

Fiona A. Russell

25th February, 2014

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Last, but not least, thanks to Pitpa for being such a willing participant and helping to shed some light on one of Australia's most fascinating animals.

Abstract

Echidnas have evolved separately from other mammalian groups for more than 200 million years and incorporate a mixture of reptilian and mammalian features. Because of these factors, they have historically been considered ‘primitive’ animals. However they have successfully adapted to a wide variety of ecological niches and their neurophysiology demonstrates a number of unusual and apparently advanced characteristics, including a relatively large brain and cerebral cortex and a comparatively massive frontal cortex. These attributes make the echidna an intrinsically compelling subject for cognitive testing.

Studies of learning in the echidna have thus far been limited to only a handful of experiments. These have demonstrated that echidnas are capable of easily forming a position habit in a T-maze, show rapid improvement across a series of successive habit-reversals, are capable of learning visual discriminations and perform well in instrumental discrimination tests.

This study aims to expand on these results by conducting a number of cognitive tests of the echidna’s learning abilities, specifically its’ ability to learn colour, shape and conditional discriminations, as well as the presumptively ‘high-level’ relationally based tasks of same/different and conditional same/different categorisation. This thesis also examines the ongoing debate about the mental processes involved in relational categorisation and how commonly they occur in non-human animals.

In a wider context, echidnas are an ideal candidate to explore competing theories of cognitive evolution by examining whether a phylogenetically and physiologically ‘primitive’ species can perform what are generally considered to be ‘advanced’ cognitive tasks and what role ecological factors might play in the development of those abilities. Using an echidna as a subject also increases the comparatively small number of species used for cognitive testing and its’ distinct evolutionary history means these results provide a valuable comparison to the cognitive development of more commonly studied species.



Frontispiece: Pitpa in the Taronga Zoo enclosure

“Further studies of learning will undoubtedly disclose important facts about the intelligence of these remarkable animals and modify the quaint, explicitly and tacitly-held views that echidnas are little more than animated pin-cushions or, at best, glorified reptiles.”

– Buchmann and Rhodes (1978, p. 144)

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CHAPTER 1

INTRODUCTION

*Cognition and cognitive ability are terms whose meanings are usefully
vague and which must be defined in each context that they are used.*
(Thomas 1996, p. 157)

Researchers have been trying to assess the cognitive capacities of animals for more than a century (see Romanes 1883). This series of experiments aims to contribute to the continually growing field of the scientific study of animal cognition and, as Thomas points out above, it is important to clarify the theoretical framework within which this study has been placed. Terms such as ‘cognition’ and ‘intelligence’ are problematic even when applied to humans and debate continues both about what constitutes human intelligence and how to measure it. The issue becomes even more contentious when applied to non-human animals (McFarland 1989; Toates 1995; Wynne 2001). There are a number of competing views as to what constitutes animal cognition, or the even more contentious term ‘intelligence’, and the best ways in which to make relative assessments of different species.

The differing approaches to studying animal cognition can be broadly separated into two schools – the “anthropocentric” method of examining: “Can animals do what people do, and if so how?” and the “ecological” approach of asking: “How and why do animals do what they do in the wild?” (Shettleworth 1998, p. 17) Traditionally, the anthropocentric approach of psychologists, often described as comparative cognition, focuses on animal cognition with reference to the type of cognitive processes seen in humans. Broadly speaking, this approach uses a small number of laboratory species (such as pigeons, rats and non-human primates) and artificially designed experiments to closely examine the inner workings of cognitive mechanisms. The ecological approach of biologists, on the other hand, is generally only interested in animal cognition as it relates to species-specific activities. This approach focuses less on the “how” of cognition; rather it examines both the “why” of naturally observed cognitive processes by relating them to an animal’s ecology and the “who” by studying a wide range of species (see discussion in Shettleworth 1998).

Historically, there have been four major schools of thought in the study of animal cognition – anthropomorphism, general process learning theory, linear progression (all of which would be placed under the anthropocentric banner) and the more biologically based mosaic evolution (also known as cognitive modularity).

1.1 Anthropomorphism

Let man visit Ourang-outang in domestication, hear expressive whine, see its intelligence when spoken [to]; as if it understood every word said – see its affection – to those it knew – see its passion and rage, sulkiness, and very actions of despair; and then let him dare to boast of his proud pre-eminence.

(Darwin 1987, p. 79)

The idea that animals are essentially “little people” is a very ancient one. Some of the world’s earliest artworks depict human bodies with animal heads, suggesting a belief that animals have human qualities (Wynne 2001). In 1883 Romanes argued parrots knew what they were saying, rooks had a sense of justice and dogs enjoyed a joke. However, the first widespread attempt to scientifically demonstrate human-like mental abilities in animals was born out of Darwin’s theory of evolution and his revolutionary claims that animals are related to humans mentally as well as physically (Shettleworth 1998). According to Darwin (1871, p. 62), “... there is no fundamental difference between men and the higher mammals in their mental faculties”.

Hundreds of observations of animal behaviour were collected by various authors with the aim of proving animals were on an intellectual par with man. Many of these observations did indeed seem to show animals displaying great feats of reasoning and even morality. However, these examples were generally little more than anecdotes and when scientists such as C. Lloyd Morgan (1894) and Thorndike (1898) began to conduct systematic experiments the results fell far short of the anecdotal evidence. The idea soon fell out of favour and is now generally discounted in the scientific community (Grindley 1950).

1.2 General process learning theory

The moral and higher intellectual nature of man is as unique a phenomenon as was conscious life on its first appearance in the world ...

(Wallace 1869, p. 391)

Despite the somewhat misleading label, general process learning theory is the opposite of anthropomorphism in that it is based on the idea that human intelligence is unique.

Historically this idea was widely accepted. In the 18th century Descartes drew a sharp distinction between “rational man and dumb brutes” (cited in Mackintosh 1988) and in the 19th century this view was even held by one of the earliest exponents of evolutionary theory A. R. Wallace (see quote above).

Even in more recent times, some authors continue to espouse this idea (e.g. Lieberman 1991; Pinker 1994). Lachman, Lachman and Butterfield (1979), for example, claim: “Whenever higher mental processes are involved, we heartily disagree that human and animal behaviour are necessarily governed by the same principles. We regard the human as a specialised product of evolution, as an animal whose cognition is also specialised” (p. 211), while Curruthers (1989) speculated that it was all “darkness” in the animal mind. Others claim that some capacities, such as tool-making, symbolism, syntax, culture, self-awareness, consciousness, imitation, deception, theory of mind and morality, are exclusively human (see references in Gibson 2002). These authors dismiss evidence from other scientists that purports to demonstrate capacities in animals once thought unique to humans (e.g. self-recognition, deception, imitation, culture, theory of mind, tool-use) which supports the opposing view that the cognitive differences between animals and humans are matters of degree, rather than of kind (see references in Gibson 2002).

1.2.1 Argument for general process learning theory

One of the most well-known champions of general process learning theory is Macphail (1982, 1985, 1987), who argues that not only is man “intellectually superior”, based on his language capabilities, but that there is essentially no difference in the intelligence of non-human vertebrates. Macphail’s “null hypothesis” is that “there are no differences, either quantitative or qualitative, among the mechanisms of intelligence of non-human vertebrates” (Macphail 1982, p. 330). According to authors such as Macphail, all animal learning (and hence animal intelligence) can be accounted for using the same set of principles – an approach known as general process learning theory (Seligman 1970). These general principles encompass only the most basic forms of learning – habituation and associative learning – and it is worth outlining them here as they form the building blocks of animal learning on which experiments such as this one are based.

1.2.1.1 Habituation

One of the simplest forms of learning is habituation. This occurs when repeated exposure to a stimulus results in decreased responsiveness, such as when territorial male songbirds reduce their aggression toward familiar neighbours during the breeding season and only react to new arrivals, thus giving them more time and energy for attracting mates (Falls 1982). Habituation shows that animals can learn to recognise stimuli and is found in a broad range of species from one-celled organisms to humans (Lea 1984a; Macphail 1993).

1.2.1.2 Associative learning

Animals are continuously learning associations in the world around them and adjusting their behaviour accordingly. For example, eating certain flavours will lead to illness while others are beneficial, so an animal that is able to learn this relationship will live a longer and healthier life. Similarly, an animal that can distinguish the sound of an approaching predator from that of prey is more likely to survive to leave offspring to the next generation than one that cannot. The process whereby animals generally learn these kinds of relationships between signals and consequences is called associative learning. (See Pearce 1997; Wynne 2001).

Associative learning (or conditioning) occurs when one event becomes paired with another resulting in a change in an animal's behaviour (Pearce 1997). The processes of associative learning are traditionally split into two classes – classical and operant conditioning.

1.2.1.2.1 *Classical conditioning*

While conducting experiments on the physiology of digestion, Pavlov (1927) obtained results that led him to develop one of the basic theories of learning. He discovered that dogs would salivate when presented with a signal that had previously been paired with food. The signal (for example, ringing a bell), which was neutral and did not produce a response by itself, was called the “conditioned stimulus” (CS). The significant event (in this case food), which already produced a response, was called the “unconditioned

stimulus” (US). While initially the dogs showed little reaction to the signal, with continual pairing of the CS (sound) with the US (food), they eventually began to salivate during the CS even before the food was delivered. The response to the stimulus (in this case salivation) was defined as the “conditioned response” (CR). (See Pearce 1997; Wynne 2001).

While subsequent research has both refined and modified Pavlov’s early principles (e.g. Gallistel 1990, 1992; Rescorla and Wagner 1972), its general precepts still form the basis of classical conditioning. Classical conditioning (also called Pavlovian, respondent or type I conditioning) is the process of training an animal to associate a signal with an event. If the anticipated event is a desirable one, the response to the signal will likely be preparation for such an event, such as salivation for food or sexual arousal for the arrival of a mate. If the anticipated event is an aversive one there will generally be some form of protective or aggressive response, such as running away or cowering, or adopting an aggressive posture. This ability to use one stimulus as the predictor of the occurrence of another has been demonstrated in a wide variety of species, from simple marine snails to humans. (See Lea 1984a; Wynne 2001).

1.2.1.2.2 Operant conditioning

In classical conditioning there is a relationship between a CS and a reinforcer regardless of the subject’s behaviour, in operant conditioning (also known as instrumental or type II conditioning) there is a relationship between the subject’s behaviour and the occurrence of the reinforcer. This relationship is often called contingency – the delivery of reinforcement is contingent on the performance of a behaviour in response to the presentation of a CS. (See Mackintosh 1983).

Operant conditioning was first described by Thorndike (1911). Thorndike’s best-known studies involved cats and puzzle boxes – cages which could be opened from the inside by some kind of latch mechanism. A cat was placed in the box with food outside. Initially, the cat would flail around randomly in the cage until it chanced upon the action that would release the latch. It was then allowed access to the food for a short period, and then placed back in the puzzle box. Thorndike found that, over successive trials, the time it took for the cat to escape from the box gradually decreased. He

regarded this as merely blind trial and error learning, with the food serving to strengthen the hypothetical connection between the perception of the stimuli and the response. This approach is now considered too simplistic. However the proposal that reward is essential for learning became the basis of operant conditioning where the experimenter delivers a reward (such as food) after the animal has responded in a certain way. (See Pearce 1997; Wynne 2001).

Operant conditioning shows animals can learn what responses produce particular outcomes and has been demonstrated in a large number of animal groups including amphibians (tadpoles), lizards (anoles, collared lizards, iguanas), fish (goldfish, koi carp, queen triggerfish), birds (pigeons, doves, chickens, gulls, quail) and mammals (marsupials, rodents, rabbits, cats, dogs, raccoons, skunks, ferrets, minks, some farm animals, several primates) (Wynne 2001).

1.2.1.3 Evidence for general process learning

There is considerable evidence to support the general process view, particularly in the research of Bitterman and colleagues with honeybees (e.g. Abramson and Bitterman 1986; Bitterman, Menzel, Fietz and Schafer 1983; Couvillon and Bitterman 1984) which demonstrated the similarity in basic associative learning among species as diverse as honeybees and mammals (Kamil 1994).

Gould and Gould (1986) point out that many seemingly highly complex behaviours are in fact the result of innate “programs” and “subroutines” that require no conscious awareness. Even the famous dance “language” of bees (von Frisch 1953), in which foragers return to the hive and communicate the distance, direction and quality of the food source via a series of body movements, is wholly innate and can be performed and understood by bees with no prior experience (Gould and Gould 1986). However, despite the widespread use of programmed learning in the animal world, Gould and Gould (1986) contend that not all learning can be explained through simple programs based on trial and error and associative learning. One such example is the use of cognitive maps, in which animals as diverse as rats and bees have demonstrated the ability to utilise mental maps to determine locations and then use that information to direct their behaviour.

Gould and Gould (1986) further contend that much of the intellectual accomplishments of humans – such as language acquisition, Aristotelian logic, categorisation, pattern recognition etc. – are also based on pre-existing wiring and storage. According to the authors: “The more we look at the behaviour of insects, birds and mammals, including man, the more we see a continuum of complexity rather than any dramatic difference in kind that might separate the intellectual Valhalla of our species from the apparently mindless computations of insects” (p. 35).

In addition, as Kamil (1994) points out, “the demonstration of a general learning process present in many species does not rule out the possibility of important, significant species differences, both qualitative and quantitative” (p. 24).

1.2.2 Argument against general process learning theory

1.2.2.1 Species differences

While the principles of associative learning found in classical and operant conditioning have been extremely successful in explaining numerous instances of learning, many scientists believe it is not possible to account for all learning using these principles, as Macphail (1987) claims. Critics of Macphail argue he bases his assertions about animal learning on a very narrow definition of intelligence supported by performance on general problem-solving tests in arbitrary environments and specifically excludes specialised species adaptations, such as song learning in songbirds (Roitblat and von Fersen 1992).

Roitblat and von Fersen (1992) argue that this approach seems to arbitrarily define species differences in intelligence out of existence. They and many other authors continue to argue that the biological context of learning must be considered and that adaptive pressures have led to different kinds of learning within individuals and species (e.g. Bolles 1970; Garcia, McGowan and Green 1972; Huber 1995; Lea 1984a; Rozin and Kalat 1971; Tolman 1949) (see Shettleworth 1998). Examples of the types of species-based learning in which associative learning theories cannot be generally applied include adaptive specialisations, species-specific behaviours and special learning, and these will be explored in section 1.4.

1.2.2.2 Task differences

In addition to species-specific adaptations, other authors claim rigorous animal research has demonstrated a number of cognitive capabilities that cannot be explained by traditional associative learning theories. Zentall (1999) cites a number of examples of more ‘advanced’ cognition that have been demonstrated in animals – such as the symbolic representation of stimuli (in which two arbitrary stimuli are associated with a third event and emergent relations develop) and the ability to plan ahead, and to choose whether to plan ahead or not. Other examples of more complex learning in animals that cannot be easily accounted for by simple associative learning include those based on relational learning such as relative numerosity (Jaakkola, Fellner, Erb, Rodriguez and Guarino 2005) and transitive inference (Gillan 1981) (see section 3.6 for more examples) as well as more socially based abilities such as imitation (Akins and Zentall 1996). According to Zentall (1999), experiments like those above are providing “increasing evidence that the boundary between the mental capacities of humans and those of other animals is not nearly so clear as was once thought” (p. 208).

1.2.3 Limited general process theory

Despite the opposition to general process learning theory, it is worth noting that there are “different degrees of generality” (Wright, Rivera, Katz and Bachevalier 2003, p. 195). Some authors, such as Wright et al. (2003), support a general process account of certain cognitive abilities without explicitly rejecting the idea that other abilities might be specific to certain species. According to Kamil (1994): “It is quite conceivable, perhaps even likely, that some mechanisms of intelligence are widespread throughout broad segments of the animal kingdom while others are not” (p. 35).

For example, Wright et al. (2003) favour a type of general process account of same/different categorisation. Their theory holds that same/different categorisation is common among virtually all vertebrates. According to this theory, while there is no qualitative difference between species for this task, i.e. they can all do it, there are quantitative differences in performance between species, such as the stimulus set size required to achieve criterion performance.

1.3 Linear progression

1.3.1 Species hierarchy

... most people have a vague idea of the relative intelligence of animals. As a general rule, those species that are more like us physically are judged to be more intelligent.

(Zentall 2000b, p. 198)

The idea that intelligence is distributed in a linear progression based on a phylogenetic scale from simplest (and hence least intelligent) to most complex (and hence most intelligent, i.e. man) has existed since Aristotle (Hodos and Campbell 1969) and was widespread in the 19th century (Mackintosh 1988). Even in more recent times, there is still support for this viewpoint. Jensen (1980), for example, a well-known authority on intelligence ranking in humans, has stated that he believes there is an ascending scale of intelligence that accords with an animal's "phylogenetic status" and position on the "phylogenetic hierarchy": "Single-cell protozoans (e.g. the amoeba) rank at the bottom of the scale, followed in order by the invertebrates, the lower vertebrates, the lower mammals, the primates and man" (p. 175).

The views of Jensen (1980), and others, were based in Darwinian Theory, however many believe this a misinterpretation of Darwin's ideas. While Darwin's (1859) theory that all existing species are descended from different, earlier species is now generally accepted, it is considered erroneously simplistic to view evolution as a linear progression in which one species evolves from another in strict sequence. Instead, it is now believed that animals are related via a family tree structure, in which different species branch off from common ancestors (Shettleworth 1993). Phylogeny cannot be used to organise animals into a linear scale based on evolutionary relationships, let alone intelligence. Furthermore, Darwinian Theory is about adaptation to the environment, which does not necessarily involve progress or increasing complexity – or increasing intelligence (Mackintosh 1988).

Evidence against a linear progression of intelligence began to be produced during the late 19th century consisting of numerous field-based observations and anecdotal reports of evolutionarily 'primitive' animals performing seemingly complex behaviours.

However, some of these early reports were criticised as being unscientific, in particular Romanes' *Animal Intelligence* (1883). By the early 20th century, the introduction of more rigorous scientific standards to the study of animal behaviour by authors such as Thorndike (1898) led to the production of more reputable studies demonstrating relatively complicated behaviour in supposedly simple animals (see Wynne 2001).

More recently, tests involving the ability to acquire a learning set – that is, how long it takes a subject to learn the underlying discrimination principle when exposed to successive non-repeating discriminations – injected new life into the linear progression camp. Harlow (1949) was the first to study this phenomenon and concluded that the ability to form learning sets was related to phylogenetic position, with species closest to man being most efficient. Initial results from mammals showed performance consistent with a single ladder of intellectual improvement in line with their evolutionary position, with rhesus monkeys performing better than New World squirrel monkeys, followed in descending order by cats, rats and squirrels (Shettleworth 1998). However, further experiments showed other animals did not fall where expected on the ladder (review in Macphail 1982). For example, blue jays perform in a qualitatively similar way to rhesus monkeys (Kamil 1985), while the marsupial dunnart has demonstrated a better learning set performance than rhesus monkeys (Bonney 2001).

Aside from the contrary results, one of the problems with proposing a “‘magic bullet’ task” (Wynne 2001, p. 187) such as learning set to enable animals to be ranked by ‘intelligence’ is that factors other than ‘intelligence’ can account for the poor performance of some species (Wynne 2001). Comparisons between species based on laboratory experiments generally ignore the fact that different species have evolved in different ecological and social environments, meaning there are numerous contextual features that might favour or disadvantage one species over another (Cheney and Seyfarth 1990). As Tinbergen (1951, p. 12) remarked: “One should *not* use identical experimental techniques to compare two species, because they would almost certainly not be the same to *them*.”

A number of experimental variables have been shown to have a negative impact on different species' performance. One example is stimulus modality. Rats perform well in learning set tasks using olfactory cues (Eichenbaum, Fagan and Cohen 1986; Slotnick

and Katz 1974), but performance deteriorates when spatial cues are used (Zeldin and Olton 1986) and barely rises above chance when visual cues are employed (Warren 1965) (see Shettleworth 1998). Dolphins have so far proved incapable of mastering the learning set problem using visual stimuli, but do so easily when auditory stimuli are used (Herman and Arbeit 1973; see also Herman 1980); while monkeys have the reverse proclivity, showing far greater proficiency in visually based tasks than in comparable studies conducted using auditory stimuli (see D'Amato and Salmon 1984).

The experimental apparatus itself may be unsuitable; for example, rats can learn a shape discrimination in a jumping stand (Lashley 1938a) but not in a modified Yerkes test apparatus (Munn 1930a, 1930b). Dolphins also fare better with dynamic rather than static visual cues (Herman, Richards and Wolz 1984). Factors such as motor and motivation inequalities can also have an overwhelming effect on the performance of some species (Thomas 1986). (For more examples of inhibitory procedural factors see section 3.7.3).

Along with the discrediting of learning set as an intelligence ranking task, there has been widespread criticism of an intelligence hierarchy based on a phylogenetic ranking (Deacon 1990; Hodos and Campbell 1969; Mackintosh 1988; Pearce 1997; Rowe 1990; Salas, Broglio and Rodriguez 2003; Shettleworth 1998; Thomas 1980, 1986; Tomasello and Call 1997; Wynne 2001). Oakley and Plotkin (1979) even went so far as to argue that labelling animals according to a supposed directional progress in evolutionary change from simple to increasingly complex was “one of the great myths of modern science” (p xiv) which was flawed in both a taxonomic and functional sense while Tomasello and Call (1997) described it as “medieval” (p. 430) (see also Campbell and Hodos 1991; Hodos and Campbell 1969; Lockard 1971).

Despite this overt criticism, there still seems to be a tacit belief that some animals are more ‘primitive’ or ‘simple’ than others based on their evolutionary history. In 1977 Banks and Flora conducted a survey of college students asking them to rank the intelligence of a variety of animals out of 10, which they duly did with apes at the top with 9.2 and fish at the bottom with 1.7. The actual rankings were not the aim of the study but it revealed what is seemingly still a widespread assumption – that there is a progressive development of intelligence in the animal kingdom, culminating in humans

(Pearce 1997). According to Salas et al. (2003), “although misleading and anachronistic, this common sense conception of vertebrate evolution is widespread in different fields of neurosciences and psychology, even today” (p. 73). Similarly, Deacon (1990, p. 193-194) claimed: “Despite enormous advances in the fields of evolutionary biology and neurobiology in recent decades, we are still struggling to escape 19th century preconceptions about brain evolution. Although most of us would disavow these ideas, many contemporary theories of human brain evolution tacitly assume a *scala naturae* perspective.”

While there is little explicit support for the linear progression theory, its precepts are implicit in many animal cognition books and journal articles. Animals such as primates are generally viewed as ‘advanced’ and there is a presumption in the literature of comparative cognition that they will be able to perform relatively complex cognitive tasks while much less is expected of more ‘primitive’ species. Recent examples of this view include: “Such emergent relations can also be demonstrated in learning tasks with simpler organisms (e.g. rats and pigeons)” (Nakagawa 2003, p. 487) and “... domesticated animals ... in common with other higher animals” (Lomas, Piggins and Phillips 1998, p. 250).

1.3.2 Task hierarchy

Not all concepts are equal.

(Flemming, Beran and Washburn 2007, p. 55)

While overt support for the idea of a phylogenetic intelligence ranking of species has largely fallen out of favour, a separate concept of a hierarchy of cognitive processes is still held by many authors. This idea of ranking cognitive tasks takes a number of forms.

At one end of the spectrum is the seemingly common sense perception that some tasks are inherently more difficult than others. For example, in examining same/different categorisation (see section 3.7) Premack (1983a, 1983b) and Thompson (1995) point out that one type of task (physical matching or paired comparison same/different – S/D) required only a single comparison between two physical stimuli to determine the correct response while another type of task (second-order same/different judgments) required that three separate comparisons be made before the correct response could be selected.

The greater number of within-task activities led the authors to claim that second-order same/different tasks were “fundamentally more complex than either physical matching or paired comparison S/D tasks” (Thompson 1995, p. 211).

Similarly, Wright et al. (2003, p. 184) claim that: “Judgments of relationships that transcend individual features of the stimuli can be considered higher order learning, and therefore abstract-concept learning can be considered higher order”, Tavares and Tomaz (2002) referred to certain tasks constituting “high-cognitive abilities” (p. 132) and Vonk (2003, p 77) said: “An understanding of second-order relations ... demonstrates an even more complex cognitive skill”.

Tomasello and Call (1997), while being fervent critics of species ‘intelligence’ ranking, maintain that cognitive adaptations can be referred to as “more or less complex, depending on such things as the number of elements that must be perceptually monitored and behaviorally controlled” (p. 431).

1.3.2.1 Hierarchical models

Some authors have formalised these ideas by creating hierarchical models of task difficulty of varying levels of complexity. Huber (2001), for example, argues that animal categorisation falls into a “middle” range between simple discrimination and the formation of symbolic representations, while Herrnstein (1990) divides discrimination in non-humans into five functional levels ranging from the lowest to the highest level of abstraction – discrimination (identifying and responding to stimuli), categorisation by rote (memorisation of stimuli), open-ended categories (categorising stimuli based on some principle of perceptual similarity), concepts (categorising stimuli based on criteria other than perceptual similarity) and abstract relations (categorisation based on the relationship between stimuli). Zayan and Vauclair (1998) proposed a similar classificatory scheme broadly based on Herrnstein’s (1990) levels – categorisation by rote, open-ended categorisation, conceptual categorisation and categorisation of abstract relations.

One of the best-known models was created by Thomas (1980, 1986, 1996), which involved an eight-level task hierarchy. While the system is hierarchical (because lower

levels are generally prerequisites for higher levels), it does not mean an animal will use the processes serially. Instead, an animal would use all the processes in its repertoire as needed, either serially or in parallel.

LEVEL	CATEGORY
8	Bi-conditional concepts: Using class concepts in bi-conditional relationships, e.g. “A if and only if B”. This involves two conditionals: “if A, then B” and “if B then A”. To be a conceptual bi-conditional, A, B or both must involve class concepts. For example: relational matching to sample “if AA, choose BB, not CD” (see section 3.7.5).
7	Conjunctive, disjunctive and conditional concepts: Using class concepts in conjunctive (“and-therefore” reasoning e.g. “A and B go together, therefore choose B when you see A”), disjunctive (opposite of conjunctive, e.g. “A and B don’t go together so don’t choose B when you see A”) or conditional (“if-then” reasoning, e.g. “if A then choose B”) relationships (see section 3.7.4).
6	Absolute or relative class concepts Stimuli comparison leading to the adoption of a generalised response rule based on inherent stimulus features (absolute, e.g. perceptual categorisation, section 3.4) or relational similarity (relative, e.g. relational categorisation, section 3.6 and 3.7).
5	Concurrent discriminations: Learning to make an operant response to only one of a set of stimuli for more than one set of stimuli concurrently.
4	Chaining operant responses: Learning a connected sequence of operant responses to obtain reinforcement.
3	Simple operant conditioning: Learning to repeat a voluntary response to obtain reinforcement (see section 1.2.1.2.2).
2	Classical conditioning: Making reflex responses to a new stimulus that has been repeatedly paired with the original innate stimulus (see section 1.2.1.2.1).
1	Habituation: Learning not to respond to a repeated stimulus that has no consequences (see section 1.2.1.1).

**Thomas’ hierarchy of learning abilities
(Thomas 1996; Sappington and Goldman 1994)**

It has even been suggested that Thomas’ (1996) model should be broken down even further. Many authors consider relative class concepts to be ‘higher-level’ learning than absolute class concepts (e.g. Herrnstein 1990; Wasserman, Hugart and Kirkpatrick-Steger 1995; Wright et al. 2003; Zayan and Vauclair 1998). Although Thomas (1996) places them both on level 6 of his hierarchy, even he acknowledges an “operational difference” between the two abilities in that relative tasks require comparison between

stimuli whereas absolute tasks do not. Thompson (1995) suggests that a special class within the absolute class concept be created to encompass performance on a familiarisation/novelty procedure because it is based on relational and not physical features.

1.3.2.2 Task hierarchy as intelligence index

A number of authors have gone further and stated that an animal's intelligence can be quantified in terms of its ability to learn particular tasks (e.g. Bitterman 1965; Corning, Dyal and Lahue 1976; Harlow 1958; Mackintosh 1994; Macphail 1996; Masterton and Skeen 1972; Passingham 1975; Povinelli 1994; Razran 1971; Rumbaugh and Gill 1974; Thomas 1996; Viaud 1960). Thomas (1996) proposed that "... cognitive ability is synonymous with learning ability, and learning ability is a fundamental and defining aspect of intelligence" (p.157) that can be measured using his hierarchical system of eight fundamental processes (see above). According to Thomas (1996), all measures of cognitive ability involve one or more of these eight levels and that use of his hierarchy could "meaningfully reflect an animal's general intelligence" (Thomas 1980, p. 454).

Using Thomas' (1980, 1986, 1996) system, an animal's general cognitive ability, or 'intelligence', is determined by how many of the eight fundamental processes it can use. According to Thomas (1996), levels 1-5 can be performed using rote learning and all vertebrates may be capable of using level-five processes. Rensch (1967) cited data demonstrating some degree of concurrent discrimination learning (level 5) in fish, reptiles, birds and mammals (amphibians and monotremes are not mentioned).

Levels 6-8 involve so-called 'concept' learning (see section 3.8) and while Thomas (1996) concedes that several avian and mammalian species have demonstrated a level 6 class concept according to his criteria, he claims only non-human primates have been satisfactorily shown to use level 7 processes. However, Thomas' (1996) objections to non-primates demonstrating level 7 processes appears to be procedural and he concedes that it is reasonable that some non-primate species may succeed at level 7. According to the author, level 8 (using class concept in bi-conditional relationships) has yet to be successfully tested in animals.

The problem with using the relative difficulty of a task to create an intelligence hierarchy is that it runs into the same objections as the learning set-based hierarchy mentioned above. While not specifically linked to the discredited phylogenetic rankings, in practical terms it still uses a fairly narrow range of artificially created tasks to make a very broad assessment of overall intelligence. It is also susceptible to the problem of procedural unsuitability impairing the performance of some species.

1.4 Mosaic evolution

As evolutionary psychologists are fond of saying, the mind is like a Swiss Army knife, a general-purpose tool made of many specialised parts.

(Shettleworth 1998, p. 566-567)

Another of the prevailing views of the extent and distribution of cognitive abilities is based on viewing ‘intelligence’ in its ecological context, rather than making arbitrary comparisons between species based on artificial tests. According to this more biologically based approach, each species has evolved cognitive abilities in response to its particular ecological niche and comparisons between species that have adapted to different environments are meaningless. In this sense if two species are both equally well adapted to their environments, they can be argued to be equally ‘intelligent’.

This idea was put forward by authors such as Seligman and Hager (1972) and Hinde and Stevenson-Hinde (1973). They argued that since the intellectual processes of animals are shaped by evolution, if different species inhabit radically different environments, it would be expected that the nature of their intelligence would also be radically different (see Pearce 1997). Jerison (1990) echoed that idea, arguing that intelligence in the evolutionary sense is “multidimensional” (p. 361), suggesting that there must be many varieties of intelligence due to the many places in the evolutionary tree where encephalisation appears. He also holds that encephalisation is due to adaptations, which require greater brain tissue for their control, and that those adaptations can be called intelligent – “Many and various intelligences (in the plural) must have evolved in conjunction with evolving environments and with brains and behaviours adapted to those environments” (Jerison 1985, p. 29). He qualifies this by

saying that, except for information-processing capacity, those adaptations are likely to be “quite different from those involved in human intelligence” (Jerison 1990, p. 361).

One theory about how these adaptive intelligences may function is mosaic evolution, in which each ecological problem leads to the evolution of a distinct cognitive mechanism (Fodor 1983). The ideas behind this type of modular intelligence have been around for some time. In 1966 Jolly described different types of intelligence (e.g. “social intelligence” and “intelligence with respect to objects”), while Washburn, Jay and Lancaster (1965, p. 1546) concluded “learning ... is not a generalised ability; animals are able to learn some things with great ease and other things only with the greatest difficulty. Learning is ... the process of acquiring skills and attitudes that are of evolutionary significance to a species when living in the environment to which it is adapted.”

This concept has gained increasing support in recent years (e.g. Barton and Harvey 2000; Falk and Dudek 1993; Musser 2003; Northcutt and Kaas 1995; Rehkämper, Frahm and Cnotka 2008; Rowe 1990; Salas et al. 2003; Shettleworth 1998, Wynne 2001). According to Musser (2003): “Mosaic evolution describes a phenomenon seen in many organisms: archaic features occur alongside highly specialised or advanced features in the same plant or animal” (p. 928). One of the champions of mosaic evolution is Shettleworth (1998), who proposes that the animal mind is made up of a variety of adaptively specialised cognitive modules (see also Cosmides and Tooby 1994; Geary and Huffman 2002; Gigerenzer 1995, 1997; Hermer and Spelke 1996; Wagner and Wagner 2003; Wright and Katz 2006). Each ecologically distinct group will have evolved those modules that are required by the demands of its environment.

While taking the opposing view of the distribution of animal intelligence to that of linear hierarchy, the biological approach can be described as more accurately Darwinian in its origins as it reflects the adaptive process of physical evolution. According to Jerison (1985): “That intelligences would be of various kinds is almost an axiom of evolutionary analysis, since adaptations evolve in the contexts of the environments in which they are effective, and species never occupy identical niches” (p. 29).

Some examples of the way in which adaptation in response to ecological demands affects the development of cognitive abilities include adaptive specialisations, species-specific behaviours and special learning. All these phenomena meet a reasonable definition of learning – changes in behaviour based on experience – and demonstrate that contrary to the general process view, there are important differences between species which can often be related to their natural history (Kamil 1994).

1.4.1 Adaptive specialisations

According to Salas et al. (2003): “The vertebrate brain shows a remarkable range of diversity and specialised adaptations” (p. 73). A good example of an adaptive specialisation is found in the way that rats (and other vertebrates) learn to avoid painful and dangerous stimuli. Garcia and Koelling (1966) conducted an experiment using rats in which two conditioned stimuli (CS), a flavour and an audio-visual cue, were each paired with two unconditioned stimuli (US), illness and an electric shock, to see if the rats would learn to avoid the CS. The experiment showed this type of aversive learning has two features that distinguish it from traditional associative learning. Firstly, it can take place even with long delays between the presentation of the CS and the US, while in traditional conditioning experiments the reinforcers lose their effectiveness with even short delays. Secondly, it showed that learning only occurred when the CS and the US were in seemingly biologically relevant combinations. When illness was used as a US, aversive learning was found to be specific to flavours and not audio-visual cues; with electric shock as a US, learning was specific to audio-visual cues and not flavours. (See Lea 1984a; Shettleworth 1998).

The idea that the biological relevance of CS-US combinations influences learning is not only found in aversive conditioning. A similar phenomenon was demonstrated by Shettleworth (1975), who rewarded hamsters with food whenever they demonstrated one of six behaviours. She found the three behaviours that had a plausible association with food (rearing up, digging and scrabbling) increased in frequency but the three others (scratching, face-washing and scent-marking) were largely unaffected by reward (see Lea 1984a).

Adaptive specialisations have also been demonstrated that are specific to certain biologically relevant stimuli. Advances in neurological studies have revealed that monkeys and sheep, like people, have a special neurological face-processing module (Kendrick et al. 1995; Phelps and Roberts 1994).

1.4.2 Species-specific behaviours

Another example of the influence of biology on learning is found in species-specific behaviours. One such behaviour is autoshaping (Brown and Jenkins 1968), in which pigeons are placed in an operant chamber and a circle on the wall is lit before food is presented. Pigeons will reliably start pecking at the circle, even though it has no effect on the delivery of food. The finding that animals sometimes engage in species-specific, food-related behaviours that are irrelevant or counterproductive to the experimental paradigm has also been demonstrated elsewhere. For example, in one experiment raccoons being reinforced for putting coins in a bank started delaying reinforcement by 'washing' the coins (rubbing them together in their paws) (Breland and Breland 1961) and rats have shown difficulty learning to perform behaviours other than defensive ones in response to an electric shock (Bolles 1970). (See Shettleworth 1998).

Important species differences in learning can be found even between closely related species (Kamil 1994). Naturalistic studies of nest and egg recognition have found that royal terns (who nest in dense colonies where it is difficult to discriminate nest sites) learn to recognise their own eggs while herring gulls (who build elaborate nests spaced further apart) learn to recognise their nests but not their eggs (Shettleworth 1984). Herring gulls learn to recognise their chicks by the time they are old enough to wander from the nest (Tinbergen 1953). In contrast, kittiwakes (who nest on cliff edges and whose chicks cannot wander) recognise only their nest sites and not their own eggs or chicks (Cullen 1957).

While further study needs to be carried out to determine whether these types of species differences in behaviour also reflect differences in learning *ability*, other types of special learning have been tested for such differences.

1.4.3 Special learning

Further evidence of the way biological context influences learning is found in the area of special learning abilities, that is, abilities that seem to be acquired through slightly different processes than those described in associative learning theories. These special abilities seem to have an instinctual component that may operate independently or in tandem with more traditional types of learning. One of the best-known special learning abilities is imprinting, in which a newly hatched chick rapidly learns the mother's appearance (Lea 1984a). Other examples of special learning include song acquisition in birds (Konishi and Nottebohm 1969) and homing and migration in birds (Matthews 1968) and other animals.

Controlled experiments have been conducted to determine whether species-specific song learning reflects differences in actual learning ability rather than just behaviour (Kamil 1994). In one such study, Kroodsma and Canady (1985) raised eastern and western marsh wrens in identical conditions and exposed them to the same number of tutor songs. The authors found the western wrens learned significantly more songs than the eastern wrens. Interestingly, the authors also found neuroanatomical and ecological differences between the populations that correlated with the difference in song learning ability.

1.5 CONCLUSIONS

As discussed earlier in this chapter, animal intelligence has often been defined by comparing it to human intelligence – either that they are essentially the same (anthropomorphism) or completely different (general process learning theory), both of which theories have largely fallen from favour.

More contentious is the idea of a species hierarchy of intelligence, with an evolutionary progression from least to most intelligent. As discussed above, the idea of a rigid 'top to bottom' ranking of animals by intelligence is no longer explicitly accepted; however the tacit assumptions based on this idea continue to pervade animal cognition research.

How much influence these assumptions have on which animals are tested on complex cognitive problems, and the results of such tests, is open to conjecture. However, one of the underlying principles of this study is the rejection of a species intelligence hierarchy based on evolutionary position and the consequent importance of not making assumptions about which animals can perform certain tasks based on their phylogenetic relatedness to humans. In this sense, the study is also underpinned by the ideas of mosaic evolution – that animals have evolved particular skills and abilities to deal with the cognitive demands of their particular ecological niches, not become progressively more ‘intelligent’ throughout evolution.

However, while the present study attempts to discredit the concept of a species intelligence hierarchy, it does not reject the idea of some type of legitimate task hierarchy based on varying levels of complexity – an idea that has come under fire from some exponents of mosaic evolution. One of the major critics is Shettleworth (1998), who explicitly links task hierarchies with species hierarchies. She dismisses the idea of a hierarchy of learning processes as having an “unjustifiably narrow behavioural and phylogenetic base” because it sees animal intelligence as “consisting of learning, primarily learning to solve problems said to require intelligence in people rather than problems that occur in the species own environment, and it focuses on data from socially isolated individuals of a few species solving problems about physical causation in the laboratory” (p. 569-570).

There is certainly merit in these criticisms. It can be argued that cognitive tests should be devised with greater consideration for individual species’ ecology; that they should try and replicate more naturalistic social and physical environments; and that a greater variety of species should be tested (one area this study attempts to address). However, in some senses this is an argument about semantics. Authors such as Shettleworth (1998), Mackintosh (1988) and Tomasello and Call (1997) claim that rank order presupposes a single dimension of intelligence, a criticism also levelled at I.Q. testing in humans, and that instead scientists should focus on the efficiency of different species at solving ecologically relevant tasks. It is true that the use of task hierarchies by authors such as Thomas to rank species’ intelligence is based on a limited definition of ‘intelligence’ as learning ability. In fact, Thomas (1980) acknowledges that intelligence cannot be considered apart from an animal’s “biological equipment”. In this category he

includes features such as motor, sensory and motivational aspects. Relatively independent of these, he considers that aspect of intelligence related to how an animal ‘knows’ and responds to its environment – which can either be inherent or learned. It is this learning aspect of intelligence that he ranks on his hierarchy.

While agreeing with the basic principle of mosaic evolution – that all species, in an adaptive sense, are equally intelligent in their own ways – this study takes the view that not all comparison between species and cognitive tasks is meaningless. Furthermore, a hierarchy of cognitive processes is not the same thing as, and does not automatically lead to, the idea of phylogenetic hierarchy and the two ideas must be dealt with separately.

What Shettleworth (1998) defines as intelligence, i.e. “solving problems of ecological relevance” (p. 570) has variously been defined as the “synthetic approach” (Kamil 1988), the adaptive-evolutionary point of view (Rozin and Schull 1988) and evolutionary psychology (Barkow, Cosmides and Tooby 1992). While this approach is valuable, it often dismisses other approaches to studying animal cognition as “anthropocentric” (Shettleworth 1993, p. 179). However, defining intelligence only as it relates to solving everyday ecological problems goes against the generally understood meaning of intelligence and its common definition in both human and animal intelligence literature – that it encompasses both a set of specific cognitive skills and the more general problem-solving ability that adapts to novel environments and situations (Tomasello and Call 1997; Myers 1986; Wilson, Mackintosh and Boakes 1985b; review in Thomas 1980). According to Pearce (1997): “Many authors consider that the defining characteristic of intelligence is that it enables animals to behave adaptively” (p. 11).

Testing animals only on tasks they would naturally encounter rules out the fact that at least some animals do appear to have general, flexible learning abilities, which may have evolved to deal with ecologically complex and dynamic environments and social systems. In a broader sense, these types of flexible learning abilities could also be viewed as the cognitive component of the evolutionary process – the ability to adapt. That is, not only what *do* they do, but also what *can* they do. Wynne (2001), another supporter of the mosaic account, takes a similar position to Shettleworth on the issue of species hierarchy, yet allows for a broader view of intelligence: “... as long as we stay

away from attempts to rank the ‘intelligence’ of different species, the term might still be a useful one ... as a short-hand term for ‘wide-ranging problem-solving abilities’” (p. 4). Tomasello and Call (1997), also critics of species intelligence ranking, allow that species may solve adaptive problems with either “narrowly crafted special-purpose cognitive mechanisms (modules)” or “more domain-general general-purpose cognitive mechanisms” (p. 431).

Furthermore, rejecting the idea of task hierarchies out of hand also leads to the inevitable conclusion that all tasks are equal. While it is important to try and avoid an anthropocentric view of how animals perform various tasks, it seems self-evident that some cognitive abilities are inherently more complex than others, irrespective of how they evolved. It is possible to agree with Shettleworth’s (1998) modular theory of the distribution of cognitive abilities and still argue that the ‘modules’ vary in complexity.

Even Shettleworth (1998) seems to acknowledge this in a roundabout fashion. In discussing this topic, she refers to a study in which a one-celled organism performs a task in an evolutionarily successful yet “extremely simple” manner (p. 570). An even clearer example is seen in Shettleworth’s analysis of degrees of numerical competence: “Counting is near the top end of a continuum of abilities collectively termed numerical competence ... near the bottom end in terms of apparent cognitive complexity and resemblance to what people do when they count is numerosity discrimination ...” (p. 365). Similarly, while Wynne (2001) claims the “whole notion of a psychological scale is now considered outdated” (p. 12), he too refers to some behaviours as being “complex” or having explanations that are more or less “complicated” (p. 4).

Interestingly, some authors have explicitly linked the mosaic account and the task hierarchy models. Wright et al. (2003, p. 195) claim that studies focused on which animals can perform “abstract-concept” learning take a “decidedly modular approach ... sometimes taking the form of a hierarchy beginning with simple associative (item-specific) learning through category (natural-concept) learning, and ending with relational (abstract-concept) learning or analogical (relations-among-relations) learning. A species that fails to pass the test for the next higher level is thought to not have this specialised function or cognitive module”.

If intelligence is seen to include the ability to solve problems in a dynamic and flexible manner, then testing animals using stimuli and situations which are *not* part of their natural ecology is also important. An artificial task, in addition to being easier to control and analyse, examines an animal's ability to deal with unpredictable environments – that is, its ability to learn. And because tasks do vary in complexity, they allow scientists to determine how complex a problem an animal might be able to solve and examine the means by which that solution is found. This type of testing can also be used to examine more biologically based questions such as – do some physical and social environments encourage generalist problem-solving ability, do animals from different ecologies use different means to solve the same problems etc.

This study combines aspects of both the first approach, by examining the ability of an animal to perform a complex, artificially constructed cognitive task, and the second, by using a non-traditional, phylogenetically 'primitive' species and contextualising the results in terms of that species' unique physiology and ecology.

Finally, while championing the value of artificial testing of general cognitive abilities, it is important to acknowledge its limitations, particularly in terms of species comparison. These types of experiments are not exhaustive tests of general 'intelligence' and, in isolation, can really only shed light on a particular animal's ability to perform a specific task under specific conditions. Making comparisons between species' ability to perform a particular task is problematic. Firstly, as discussed earlier, an animal's inability to perform a task may be due to procedural incompatibilities such as modality (Macphail 1982; Thomas 1986; Wright et al. 2003); secondly, it is impossible to exactly reproduce the conditions of stimulus, response, reinforcer and motivation (Bitterman 1975; Wasserman 1993a) and thirdly, the ability of different species to perform a particular task does not mean that the same cognitive processes are at work (Wasserman 1993a).

However, that does not mean the 'comparative' should be removed from comparative cognition. Wasserman (1993a) argues that it is possible to provide animals with an essentially equivalent experience, "to have the critical features of the experimental design or paradigm effectively operative and suitable for each species under consideration" (p. 156). Once a substantial body of experimental literature has been amassed, these types of results might cautiously be used to make comments about

comparative ‘intelligence’ in terms of generalised adaptiveness or, more simply, learning ability based on the number, variety and complexity of tasks a species can perform. This type of comparative cognition should not be aimed at creating some sort of species’ intelligence ranking; rather it can be used to examine the similarities and differences in the processes of cognition and how those processes have evolved in different species (Cook 1993; Shettleworth 1993; Wasserman 1993a).

1.6 RATIONALE

The cognitive capacities of animals remain a relatively unexplored research area.

(Zentall 2000a, p. 122)

In summary, this study has been designed to contribute to the ongoing debate about comparative animal cognition by setting these experiments in the intellectual framework of both the task hierarchy and mosaic approaches.

While the idea of a species hierarchy of intelligence based on phylogenetic position is not generally explicitly supported, an implicit belief in this type of cognitive ranking still pervades animal cognition literature. This study uses a fairly extreme case to test this belief by examining the ability of a member of one of the most evolutionarily ‘primitive’ mammalian species, the echidna, to perform what is considered a relatively ‘advanced’ cognitive task, conditional same/different categorisation.

The mosaic perspective argues that species evolve particular abilities to adapt to their particular ecological niches. This paper seeks to expand on this idea and examine whether a species with a varied ecology, such as the echidna, might evolve the ability to adapt to novel learning situations such as those found in artificial discrimination testing and perform complex cognitive tasks. It also attempts to examine what role a varied ecology might play in the development of ‘advanced’ mental abilities.

CHAPTER 2

**THE SUBJECT – *THE ECHIDNA*
(*TACHYGLOSSUS ACULEATUS*)**

The selection of the species to be used in these experiments was subject to a number of criteria. As outlined in the introduction, one of the goals of this study was to examine the validity of the idea of a phylogenetic hierarchy of intelligence – whether explicitly expressed or implied by the language and expectations of a segment of animal cognition literature. To accomplish this it was decided to select a subject that has been regarded as phylogenetically ‘primitive’ – a word which often seems to be used to delineate species which are evolutionarily far removed from humans as well as to those that emerged early in evolutionary terms.

One of the theories opposed to a phylogenetically based intelligence hierarchy is that of mosaic evolution, which asserts that different species have developed specific cognitive abilities in response to differing ecological pressures rather than become progressively more generally ‘intelligent’ over time. Because of this, it was important that the subject had a varied ecology that might lead to the evolution of relatively complex problem-solving abilities.

The Australian short-beaked echidna, *Tachyglossus aculeatus*, fulfilled both these criteria. Because of the theoretical goals of this experiment it is important to review what is known about the subject’s evolutionary history, ecology, biology, environment and cognitive ability. For the sake of brevity, this information has been limited to those characteristics of the echidna that are relevant to this study.

2.1 Biology, evolution and behaviour

2.1.1 Taxonomy, classification and distribution

Tachyglossus aculeatus (the common or short-beaked echidna) is one of three extant species of monotreme mammals. The others are the long-beaked echidna (*Zaglossus* spp.), found only in Papua New Guinea, and the platypus (*Ornithorhynchus anatinus*), found in Eastern Australia and Tasmania. Monotremes display numerous plesiomorphic reptilian characteristics; the most obvious being that they are oviparous (egg-laying) and the eggs are covered with keratin that forms the covering of most reptile eggs. Other anatomical features with reptilian characteristics include: formation of an egg ‘tooth’ in the embryo; a single cloacal outlet; structure of the reproductive organs; bones in the

skull and shoulder girdle and some features of the eyes and ears. However, echidnas are classified as mammals and belong to the subclass Prototheria of the class Mammalia. This is because they also possess mammalian characteristics – they are covered in hair; suckle their young with milk secreted from mammary glands; are able to generate body heat internally (endothermy); possess three ossicles in the middle ear; have only one bone in the lower jaw; have a false palate and a diaphragm separating chest from abdomen (Abensperg-Traun 1990; Augee, Gooden and Musser 2006; Australian Wildlife Series 1981; Gates 1973; Griffiths 1978, 1989; Musser 2003). This mixture of mammalian and reptilian characteristics is reflected in the name “echidna”, which is derived from the Greek goddess Ekhidna who was half woman, half serpent (Augee et al. 2006).

Five subspecies of *Tachyglossus aculeatus* have been described – *aculeatus*, *setosus*, *acanthion*, *multiaculeatus* and *lawesii*. The main criteria of differentiation are: fur length and colour; spine length and thickness and the length of the claw on digit two on the hind limb relative to that on digit three (Augee et al. 2006; Griffiths 1978, 1989). In general, the subspecies can be related to habitat (Augee et al. 2006); however no major behavioural differences have been described.

The echidna has a geographical range from close to the equator in Papua New Guinea to 43°S in Tasmania (Augee and Gooden 1993). The echidna is the most widely distributed native mammal in Australia (Morrow, Andersen and Nicol 2009; Strahan 1984), occurring in all major habitats in mainland Australia and Tasmania (Nicol 2003). Indeed, apart from the house mouse, no other mammal can be found in so many divergent ecologies (Augee et al. 2006). It has been recorded in habitats as diverse as the Simpson Desert (Griffiths 1978), the tropical grasslands of the Northern Territory (Augee et al. 2006) and the Southern Alps (Griffiths 1968), as well as a variety of altitudes from the lowland eucalyptus woodland around Port Moresby to altitudes of up to 1600 metres in the central highlands of New Guinea (Augee et al. 2006). *Tachyglossus aculeatus aculeatus*, the subject of this study, is found mainly in southeastern Australia (Abensperg-Traun 1990).

2.1.2 Evolution

It is widely accepted that mammals developed during the Mesozoic era more than 200 million years ago from mammal-like reptiles known as synapsids (Augee et al. 2006; Divac 1995). They are generally recognised as having branched into three main lines: prototherians (monotremes), metatherians (marsupials) and eutherians (placentals) (Divac 1995); although there is still some debate about these classifications (Watson 1990). The point of divergence of the monotremes from modern therians (marsupials and placentals) is uncertain.

The orthodox view is that monotreme ancestors represent the earliest mammalian lineage, predating the lineage that became the therian ancestor of modern placentals and marsupials (Dorit, Walker and Barnes 1991; Graves 1991; Musser 2003; Rowe 1990). The idea that the therians (marsupials and eutherians) are more closely related to each other than to prototherians (monotremes) – the so-called “Theria hypothesis” (Huxley 1880) – is based on a wide range of anatomical and physiological features, such as the numerous plesiomorphic features retained by monotremes, and recent fossil material (Kirsch and Mayer 1998; Musser 2003). This theory has also received the majority of support from nuclear gene sequence data and immunological gene studies (Killian, Buckley, Stewart, Munday and Jirtle 2001; reviews in Belov and Hellman 2003; Madsen 2009; Musser 2003).

A secondary theory, the “Marsupionta hypothesis” (Gregory 1934, 1947; Kirsch and Mayer 1998; Kühne 1973, 1977), suggests that monotremes and marsupials are more closely related to each other than either is to eutherians. The idea that monotremes and marsupials evolved from the same ancestor is supported by mitochondrial genome sequencing and DNA hybridisation analyses (reviews in Belov and Hellman 2003; Madsen 2009; Musser 2003).

While these are the two main theories, some palaeontologists believe that, despite their many plesiomorphies, monotremes share a close relationship to therians. This idea has found support in some reworked mitochondrial DNA experiments, despite the fact that previous mtDNA studies had been found to support Marsupionta. Another theory, that a

split between monotremes, marsupials and eutherians happened almost simultaneously, receives more support from geneticists than palaeontologists (Musser 2003).

Whichever theory is correct, fossil records and genetic studies indicate monotremes have evolved independently from all other mammals for at least 120 million years and more likely more than 200 million years (Clemens 1979; Dawson 1983; Griffiths 1968, 1978; Krubitzer and Campi 2009; Madsen 2009; Musser 2003; O'Brien and Graves 1990; Phillips, Bennett and Lee 2009; Rismiller 1999). The fossil record shows a platypus-like monotreme that is about 120 million years old (Archer, Flannery, Ritchie and Molnar 1985) and new fragmented fossil remains suggest monotremes have evolved independently for more than 200 million years (Woodburne, Rich and Springer 2003). The results of a number of genetic studies indicate monotremes split from therians between 204 and 237 million years ago (reviews in Grützner, Deakin, Rens, El-Mogharbel and Graves 2003; Madsen 2009). Echidnas are often thought to have evolved separately from platypus for between 35 million and 65 million years (Abensperg-Traun 1990; Dawson 1983; Griffiths 1978; Griffiths, Wells and Barrie 1991; Musser 2003; Richardson 1987; Westerman and Edwards 1992). Phillips et al. (2009) combined genetic and fossil evidence to estimate the divergence at between 19 and 48 million years while molecular dating studies place the split variously between 17 and 57 million years (review in Belov and Hellman 2003), 17 and 80 million years (references in Rowe, Rich, Vickers-Rich, Springer and Woodburne 2008) and 17 and 35 million years (references in Phillips et al. 2009).

2.1.2.1 Echidnas as 'primitive' mammals

The evolutionary history of monotremes has influenced how they are viewed in the wider scientific community, particularly as they are generally considered to be the mammals most distantly related to humans (Krubitzer, Manger, Pettigrew and Calford 1995), and they are often referred to as the "oldest living mammals" (e.g. Rismiller 1999; Rismiller and McKelvey 2003) and "living fossils" (Phillips et al. 2009). Graves, Hope and Cooper (1990) point out that one of the difficulties faced in studying monotremes is the array of entrenched misconceptions about them, such as the idea that they are atypical, aberrant animals who only survived because they were geographically isolated and did not face competition from more 'advanced' eutherians.

T. H. Huxley, an evolutionary biologist writing in the late nineteenth century, believed that monotremes “represent earlier, and serial stages in the evolution of true viviparous mammals” (from Graves et al. 1990, p. 144) and incorporated this idea into his nomenclature. The placentals were classified as eutherians (“true beasts”) and marsupials as metatherians (“other beasts”), while monotremes were placed in the subclass prototherians (“first beasts”) and were considered even less “true beasts” than marsupials because they laid eggs (Graves et al. 1990). The lesser status of monotremes as “almost mammals” (Augee et al. 2006, p. 1) was further stressed by the grouping of eutherians and metatherians into the separate subclass therians. According to Augee et al. (2006), the view of echidnas as “some sort of early test model that wasn’t quite right has tarnished them for two centuries” (p. 1).

The impact of Huxley’s theories was described by Tyndale-Biscoe in 1973:

Huxley’s idea has had a long and baneful influence on the understanding of marsupials and monotremes; it encouraged people to think that by studying these mammals they could ride a sort of Wellsian Time Machine back to the origin of mammals. Even more, that this was the only proper purpose in studying these animals, notwithstanding the clear evidence of convergence to show that they are marvellously adapted to their present environment. Huxley’s grandson, Julian, began to redress the balance by emphasising in his “*Evolution: the modern synthesis*”, that all living animals must be viewed in the context of their adaptations to the present environment, but the old idea dies hard.

(cited in Graves et al. 1990, p. 144)

Huxley’s influence can be seen almost a century later in MacIntyre’s (1967) proposition that monotremes be studied not as mammals but as living therapsid reptiles (one of the synapsids, a subgroup of which were the ancestors of mammals) and be referred to as “quasi-mammals” to emphasise their distance from “true or therian mammals”. According to Musser (2003), the comparatively ancient nature of some of the echidna’s features “has led most scientists to consider monotremes – in spite of their specialisations – to be primitive mammals far removed from marsupial and eutherian mammals” (p. 928). Abbie (1938, p. 150) described echidnas as “primitive mammals” and Lende’s (1964) study of echidna neurophysiology was titled “Representation in the cerebral cortex of a primitive mammal”. As recently as 2003 echidnas were still being referred to as “primitive mammals” (Hassiotis, Paxinos and Ashwell 2003, p. 829).

However, authors such as Graves et al. (1990) refute the idea that monotremes are not “true beasts”. Like eutherians, they are fur-bearing and suckle their young with milk from mammary glands and as such are defined as mammals. The major difference between eutherians, marsupials and monotremes is their means of nurturing their young in the very early stages – extended interuterine life in eutherians, attached to a teat in a pouch in marsupials and in an egg in monotremes. Graves et al. (1990) argue that these differences in their modes of reproduction are not stages in an evolutionary process but rather are adaptations to an uncertain environment where it is advantageous to produce disposable young. As such, they contend, marsupials and monotremes must be regarded as “true beasts”.

The dismissal of echidnas as ‘primitive’ also cannot be justified on evolutionary grounds. The echidna’s ancestors may have emerged early in mammalian evolution, and in that sense can be regarded as ‘evolutionarily primitive’, however that does not mean they necessarily represent the “ancestor of all mammals” (Krubitzer 1998, p. 1127) or the ancestral form (Northcutt and Kaas 1995; Rowe and Bohringer 1992) as they are often viewed. They have evolved from ancient stock, but their evolution has not stood still for the past 200 million-or-so years. As Musser (2003) points out, there is an “exceptionally long history for the group, allowing a great deal of time in which to lose ancestral features and develop new characteristics” (p. 928), in much the same way that today’s eutherian mammals do not resemble their early progenitors. Echidnas have retained some plesiomorphies (see above), but mosaic evolution (see section 1.4) allows for archaic features to occur alongside highly specialised or advanced features (Musser 2003; Northcutt and Kaas 1995).

According to Rowe (1990), the echidna’s “retention of phylogenetically ancient mechanisms for reproduction need not mean that other body systems have been constrained in their evolutionary adaptability” (p. 265). In fact studies have shown that echidnas are a unique mix of primitive features and unique specialisations in both their physiology (see section 2.1.1) and neurophysiology (see section 2.2.1). Krubitzer and Campi (2009, p. 52) stated: “Fossil records indicate that extant monotremes ... are highly derived, particularly in the structure of their bill, and in this respect do not resemble the first mammals.”

O'Brien and Graves (1990) describe monotremes as an independent and successful evolutionary attempt which parallels rather than precedes that of the more 'advanced' mammals. It can be argued that the success of the echidna is demonstrated by the fact that they are still a numerous and widely distributed species while many other, more recently evolved species are endangered or have become extinct. As Augee et al. (2006) point out; echidnas "have been around for a lot longer than placentals and have remained masters of their environmental niches" (p. 1).

Indeed, it may be the retention of some 'primitive' attributes that has proved the key to the echidna's evolutionary success. For example, burrowing enables echidnas to avoid predators and temperature extremes; its food sources are protected underground; it can forage in the dark using other highly attuned senses; body temperature and metabolism can be lowered and controlled in response to extreme cold or food deprivation and they are extremely tolerant to low oxygen conditions. These types of adaptations mean today's echidnas are well equipped to deal with crises such as bushfires, floods and cold winters and may have meant they were better able to survive challenging environmental changes that led to the extinction of more 'advanced' mammals (Augee et al. 2006).

2.1.3 External features

Echidnas are easily identified by their covering of long, sharp spines with hair present between the spines. Adults measure about 30-45cm in length and weigh up to 8kg, with males weighing about 25% more than females. The echidna's body is dorso-ventrally compressed with a domed back and flat or slightly concave ventral surface and there is no outward sign of a neck. An ear hole is located on either side of the head but the external pinnae are usually not discernable. The small eyes are situated well forward on the head and appear to be directed forward, rather than sideways. The small mouth (which can only be opened far enough to allow the passage of the tongue and prey) and large nostrils are located on the tip of the snout. The snout is covered by soft skin sensitive to tactile stimuli and measures 7-8cm in length in the adult. Echidnas have a rudimentary tail and short, powerful limbs with large digging claws (Griffiths 1989).

There is only one opening for the passage of waste and reproductive products, hence the name of the Order Mono (one) tremata (opening). Male echidnas have no scrotum and

the testes are internal while the pouch in females only develops during pregnancy, so there is little external indication of sex. However, juveniles of both sexes bear a small, sharp spur that is usually shed by the female later in life but persists in the male (Augee and Gooden 1993; Griffiths 1989).

2.1.4 Senses

2.1.4.1 Vision

The echidna's visual system is an unusual mixture of mammalian and reptilian characteristics (Augee et al. 2006) and is generally considered relatively unsophisticated. In his study of the echidna's retinal topography, for example, Stone (1983) found that in some ways the retina seemed "undifferentiated, perhaps primitive" (p. 176). It is not uncommon for non-scientists to believe echidnas are blind (Rismiller 1999), while scientists have compared them to the "virtually blind" mole and bat (Allison, Van Twyver and Goff 1972, p. 173) based on limited evidence (Gates 1973). However, although echidnas appear to rely more on olfactory, auditory and tactile sensory information (Griffiths 1968; Gates 1979), as would be expected for an animal whose subterranean prey is often not visible (Augee et al. 2006), experiments have suggested "echidna vision does not appear to be as dismal as some of the anatomists would have one believe" (Gates 1978, p. 155).

Contrary to early reports, the echidna is capable of changing the dioptric characteristics of its eyes to focus on both distant and close objects, suggesting its "visual system is more sophisticated than the anatomy of its eye would indicate" (Gates 1973, p. 112). The echidna's eyes are directed forward to some degree and there seems to be a significant overlap of the visual fields and some degree of binocular vision (Augee et al. 2006). Despite its lack of a corpus callosum, the echidna's visual system also involves interocular transfer of visual information, demonstrating a "reasonable degree of complexity" (Gates 1973, p. 112). In addition, the echidna's visual cortex appears to be substantially larger than that found in the platypus (Krubitzer et al. 1995; Rowe 1990), supporting Campbell and Hayhow's (1972) contention that vision plays a more significant role in the echidna than in its monotreme relation.

It has been argued that the fibre content of the optic nerve is a useful indicator of visual acuity as well as the importance of vision in an animal relative to its other senses (Bruesch and Arey 1942; Gates 1973; Woollard 1927). Estimates of the number of optic nerve fibres in the echidna, while small compared to those for highly visual animals such as monkeys and ducks, has nonetheless been described as “substantial” (Gates 1973, p. 110) and is more than double that for another “non-visual” animal, the bat, which is capable of making a simple visual discrimination (Gates 1973; Griffiths 1978). Another indicator of visual ability is found in the ratio of myelinated (“coated”) to unmyelinated (“uncoated”) fibres, with myelinated fibres being more effective as the insulating effect of the myelin coating allows for more efficient conduction of information (in the form of action potentials) in the optic nerve (Bear, Connors and Paradiso 1996). The echidna has very few of the less-effective unmyelinated fibres, and in this respect more closely resembles other mammals than non-mammals such as the frog, which has a large number of unmyelinated fibres (Gates 1973).

In practical tests of the echidna’s visual acuity, Gates (1973, 1978) demonstrated that echidnas are able to discriminate stimuli on the basis of black/white; vertical/horizontal stripes (down to 1mm in width) and oblique stripes. His series of experiments showed echidnas can see at least as capably as a rat and could use sight to forage (Augee and Gooden 1993; Gates 1978).

There has been considerable debate about whether echidnas possess colour vision, which is indicated by the presence of cone-shaped photoreceptors in the retina. Both O’Day (1938) and Prince (1956) found a few cones in a predominantly rod retina, but in a 1952 article O’Day states that the retina has rods only. Duke-Elder (1958) and Walls (1942) both claim there are rods only. However, many of these early studies have been criticised for their lack of methodological rigour (Gates 1973). More recently Rismiller (1999) claimed that echidnas have no colour vision, as their eye is a pure rod retinal system, while there is an uncited reference in Augee and Gooden (1993) claiming echidnas do have cones for colour vision. Griffiths (1978) even speculated that some echidnas might have a few cones while others have a purely rod retina. In one of the more recent references, Augee et al. (2006) claimed that 10 to 15 per cent of the photoreceptors in the echidna’s eye are cones (a figure replicated by Young and Pettigrew 1991), compared to about 5 per cent for humans. However, unlike most other

mammals, there is little regional specialisation in the way the cones are distributed. While the physiological studies are suggestive, no studies have directly tested the echidna's capacity for colour vision.

2.1.4.2 Smell

Current knowledge suggests that the echidna locates its prey primarily through its sense of smell (Abensperg-Traun 1990; Griffiths 1968). This theory is supported by the echidna's very well developed olfactory organs (not seen in the platypus) and the "enormous" area covered by the olfactory epithelium (Griffiths 1978, p. 182), as well as the large size of the olfactory tubercles in the echidna's brain (Griffiths 1968). In terms of the external morphology of the echidna's brain, Krubitzer (1998) describes "a striking expansion of the olfactory system, including the pyriform cortex and olfactory bulb" (p. 1142). While there have been no specific tests of the echidna's olfactory ability, the importance of olfaction to the echidna is further supported by observations of the echidna's foraging habits (Griffiths 1968), including their ability to forage in the dark and the fact that a number of blind echidnas have been known to survive successfully in the wild (Abensperg-Traun 1994; Augee et al. 2006).

While it has yet to be definitively tested, it is also believed olfaction plays an important role in echidna courtship and reproduction. A number of the normally solitary males find and follow a female in a "train" for between 7 and 37 days, with the female at the head and the males lined up nose to tail behind her, suggesting the action of a sexual pheromone. In addition, smell may play a role in hatchlings finding their mother's milk patch, since their sight and hearing are not fully developed at that stage (Augee et al. 2006).

2.1.4.3 Touch

Behavioural evidence from echidnas suggests they rely heavily on the tactile sense, both from the snout and tongue (Griffiths 1978; Augee and Gooden 1993) and from the distal limbs during digging and burrowing (Rowe, Mahns, Bohringer, Ashwell and Sahai 2003). In fact Rowe et al. (2003) claim monotremes "perhaps more than any other mammalian species ... display an enormous reliance upon tactile mechanisms (p. 884).

This assessment is reinforced by anatomical and electrophysiological studies that have revealed the prominent role of tactile inputs in the sensory-motor cortex (Rowe et al. 2003).

2.1.4.4 Hearing

The echidna's ears are internally fairly similar in structure to eutherian mammals and tests have demonstrated that the echidna's hearing is also very similar in frequency range to that found in many eutherians. In terms of sensitivity the echidna's hearing falls at the lower end of the eutherian scale, being somewhat less sensitive than that of a cat, and more closely resembling that of the Mongolian gerbil (Griffiths 1978). However, as Griffiths (1978) points out, a somewhat limited range of frequencies does not denote defective hearing – it is more likely that the echidna's sensitivity range is most effective for detecting noises emitted by its prey or vibrations transmitted through bone. In fact, the stiffness of the middle ear system is more suited to the transmission of bone-conducted rather than airborne sounds (Augee et al. 2006) and Johnstone (cited in Griffiths 1968) found that a tap on the snout elicited a large microphonic potential. According to Johnstone, “the echidna ear appears to be every bit as efficient as that in the Eutheria” (p. 115).

2.1.4.5 Electroreception

Monotremes are unique among mammals in that they share with some fish and salamanders the capacity for electroreception – the ability to detect weak electrical fields through a mosaic of mechanoreceptors and electroreceptors in their skin (Nicol 2003). Studies indicate the echidna uses electroreception through its snout to aid in the detection of food (Augee and Gooden 1992; Gregory, Iggo, McIntyre and Proske 1989; Nicol 2003) in a similar manner to its close relative the platypus, which uses electrical receptors in its bill to forage (Proske and Gregory 2003). However, the difference in the number of electroreceptors in the snout of the echidna (a few hundred to 2000) compared with the 40,000 receptors in the platypus' bill suggests that electroreception is not used to the same extent in the echidna as it is in the platypus (Krubitzer and Campi 2009).

2.1.5 Longevity, mortality and predation

Echidnas appear to be very long-lived and the maximum recorded life span is 49 years for a captive echidna at Philadelphia Zoo (Augee et al. 2006; Griffiths 1978). Longevity in the wild is difficult to assess, as it is not possible to determine the age of echidnas. Studies by Griffiths (1989) led him to estimate *Tachyglossus* can live in a natural habitat for at least 20 years, while echidna researcher Peggy Rismiller has reported a free-living echidna being observed over a period of 45 years (Augee et al. 2006).

A study of the causes of death in free-living echidnas found the leading cause of death was injury by motor vehicles, with most of the others dying from disease or parasites (Griffiths 1989). While the echidna has no active defensive or offensive weapons, its passive defence mechanisms are extremely effective. Firstly, they are hard to find, being rarely active during broad daylight, and hard to see, being well camouflaged in undergrowth or forest litter. Even if they are found, their sharp spines seem to deter most predators and when threatened they can curl themselves into a spine-covered ball or dig straight down and bury themselves completely in the soil for long periods. As a last-ditch effort, they eject a stream of unpleasant-smelling urine (Augee et al. 2006; Nicol and Andersen 2003). Faecal examination of foxes and dingoes show that these carnivores ingest echidna flesh but it is considered unlikely they could kill and eat an adult echidna and more likely scavenge carcasses. However, burrow young are known to be taken by feral cats, dingoes and goannas (Abensperg-Traun 1990; Griffiths 1989).

2.1.6 Home ranges

Echidnas do not exhibit territoriality – they are solitary, but mutually tolerant and will even share nest sites when they are in short supply. However they do have a definite home range, one that may overlap with other echidnas of both sexes. (Augee et al. 2006; Griffiths 1989) There have been a number of studies in which the home ranges of echidnas have been determined and, although different methodologies were used, there is a remarkable similarity between the average home range sizes across a range of different habitats

Augee, Ealey and Price (1975) found animals on Kangaroo Island, South Australia, have a mean home range size of 65 ha. Griffiths, Kristo, Green, Fogerty and Newgrain (1988) determined the home ranges of three lactating echidnas on Kangaroo Island to be 14, 28 and 50 ha, a mean of 31 ha. Abensperg-Traun (1991) found the average home ranges of adult echidnas in wheatbelt reserves in Western Australia to be 65 ha. Augée, Beard, Grigg and Raison (1992) calculated a mean home-range size of 42 ha for echidnas in the Snowy Mountains. Wilkinson, Grigg and Beard (1998) studied echidnas in the highlands of southeast Queensland and determined a mean home range size of 50 ha, while Rismiller and McKelvey (1994) found a mean of 55 ha for echidnas on Kangaroo Island. According to Nicol, Vanpé, Sprent, Morrow and Andersen (2011), the short-beaked echidna has a smaller home range than comparably sized eutherian carnivores and omnivores, consistent with their low metabolic rate (see section 2.1.8).

It has been observed that males have larger home ranges than females in some species (Platt, Brannon, Briese and French 1996). None of the aforementioned studies found a significant difference between the home ranges of males and females. However, Griffiths et al. (1988) found the mean home range of lactating echidnas was 31 ha, lower than that recorded in the other studies, which presumably included a combination of males and females. However, the fact that the lactating echidnas were caring for young may well have reduced their normal foraging range so no conclusions about the relative home range size of male versus female echidnas can be drawn. More recently, however, Nicol et al. (2011) radiotracked echidnas in Tasmania over a 13-year period and calculated the mean annual home-range size of males was 107 ha, twice that of females (48 ha).

2.1.7 Prey and foraging

The echidna is an insectivore whose diet includes small beetles, beetle larvae, lepidopteran larvae and earthworms. However, its main food source consists of ants and termites that it gathers by probing its snout into the galleries of nests and mounds and other places occupied by these insects (Abensperg-Traun 1988; Grant 1983; Griffiths, Greenslade, Miller and Kerle 1990; Griffiths and Simpson 1966).

Ants and termites are a reliable food source because their population levels are kept constant by the buffering effect of the mound or nest against environmental fluctuations. Both ants and termites are social insects with a highly aggregated distribution, being found in nests excavated either in the soil or decaying wood or in mounds built mainly of clay or earthy material (Gay 1970). However, both ants and termites have developed mechanical and chemical defences, such as increased size, chemical secretions, swarming, biting and stinging (Abensperg-Traun 1988, 1993, 1994; Abensperg-Traun, Dickman and De Boer 1991; Griffiths et al. 1990; Griffiths and Simpson 1966).

It is believed the echidna uses a variety of sensory mechanisms to locate prey. Smell is considered to be important; however the echidna's snout also contains a variety of sensory endings for touch, vibration and weak electric fields that may all play a part in prey detection. The echidna may also hear its prey moving in logs or underground transmitted via bone conduction from the snout to the inner ear. Vision may also play a role, but, as discussed above, is not necessary for echidna prey detection (Augee et al. 2006).

When prey is located, it is rapidly exposed by the digging claws on the forelimbs and taken in by the long, flexible tongue (Abensperg-Traun 1990). The name *Tachyglossus* means "fast tongue" and the echidna's tongue can be extruded up to 180mm at the rate of 100 times per minute. The tongue is covered with a sticky secretion so any ants or termites that come into contact with the tongue stick to it and are drawn back into the mouth. Echidnas have no teeth; instead insects are broken up by keratinised spines on the top of the tongue grinding against sets of spines on the roof of the mouth (Dawson 1983).

2.1.8 Thermoregulation, metabolism and hibernation

Monotremes were long assumed to have inferior thermoregulatory capabilities compared to other mammals due to the fact they have the lowest body temperature of any mammal. Even when active, an echidna's body temperature rarely goes above 34°C and its mean body temperature has been estimated at around 28-30°C (Grigg, Augee and Beard 1992) and 32°C (Nicol 2003; Nicol and Andersen 2003). They also have a lower metabolic rate than other mammals and use about one-third as much oxygen as a

dog, cow or human (Augee et al. 2006). These factors, along with a tendency to enter torpor, led Martin (1902) to write: “Echidna is the lowest in the scale of warm-blooded creatures” (cited in Nicol 2003, p. 796) and Robinson, in 1954, to describe echidnas as “the most primitive of the mammals with respect to their thermoregulation” (cited in Brice 2009, p. 256).

However, these supposedly ‘primitive’ attributes can also be seen as adaptively advantageous. It takes about two-thirds less energy and subsequently less food to maintain an echidna compared to a similar-sized placental, with even greater savings made during hibernation (Augee and Gooden 1993). Lactating females are also able to regulate their metabolism and compensate for the energy costs of milk production so that their daily energy budget is the same as that of non-reproductive females (Schmid, Andersen, Speakman and Nicol 2003). In addition, the echidna’s relatively low oxygen requirements may also be helpful in tolerating the reduced oxygen conditions experienced during burrowing, as well as other physiological adaptations such as: efficient tissue use of oxygen; bradycardia (slowing of the heart); redistribution of blood flow favouring the brain, heart and nervous system and blood haemoglobin with a high affinity for oxygen (Dawson 1983).

It was once widely assumed that hibernation was ‘primitive’ in both an evolutionary and functional sense – a return to a poikilothermic state due to metabolic failure (Augee and Gooden 1992). Martin, the author of the first studies of monotreme temperature regulation, stated in 1902 that “... during the winter echidna abandons all attempts at homeothermism” and “... echidna shows defective homeothermism” (cited in Augee and Gooden 1992, p. 174). However, it has since been demonstrated that echidnas in the wild do show ‘true’ hibernation (Grigg et al. 2003) and that this is not a failure of thermoregulation but an energy-saving mechanism tied closely to the reproductive cycle (Beard, Grigg and Augee 1992; Nicol and Anderson 2002; Nicol 2003).

According to Augee and Gooden (1992), hibernation in echidnas is both complex and highly adaptive. Echidnas undergo both daily torpor and hibernation – the pattern and extent of which vary in different climates (Schmid et al. 2003). Echidnas hibernate for between 6 and 28 weeks of the year from early winter to early or late spring, at least in the colder parts of their range, and during that time their body temperature falls to below

5°C, heart rate drops to 4-7 beats per minute and respiration drops to 0.3 breaths per minute. Like placental hibernators, echidnas periodically rouse themselves during hibernation and warm themselves to their normal body temperatures for a short period of time (Augee and Gooden 1993; Augee et al. 2006; Grigg et al. 1992). These bursts of metabolic activity contradict C. J. Martin's early view that the echidna "abandoned all attempts at keeping warm in winter and sank into a reptilian state" (cited in Augee and Gooden 1993, p. 50).

Echidnas are also remarkably flexible in their hibernation habits, showing a range of patterns in response to differing environmental and behavioural conditions. As well as shortening or lengthening their winter hibernation in response to reproductive activities (Augee and Gooden 1993), they also occasionally show periods of shallow torpor during the active season, such as during bad weather when they remain in a retreat and their body temperature falls to 14-20°C (Grigg et al. 1992). Echidnas also seem to hibernate in response to a relative, rather than an absolute, energy shortage, with all echidnas hibernating every year in snowbound areas where food is scarce, while only a proportion of echidnas hibernate each year in warmer areas with greater, if patchy, food availability (references in Brice 2009). For example, the Kangaroo Island echidna shows only short periods of reduced activity and torpor during the colder months between April and August (Rismiller and McKelvey 1996), while eastern echidnas show extended periods of deep hibernation (Beard and Grigg 2000; Grigg, Beard and Augee 1989; Nicol and Andersen 2002). Even the echidna's daily cycle is flexible and they can be active either day or night depending on ambient temperatures (Augee and Gooden 1993; Griffiths 1968).

2.1.9 Reproduction

Information about the echidna's reproductive behaviour is limited due to their cryptic nature (Morrow et al. 2009; Rismiller and McKelvey 2003). It is known that males and females only come together to mate (between May and September depending on environmental conditions, Augee and Gooden 1993) and males take no part in raising young. After a gestation period of between 21 to 28 days, the female lays an egg which is carried and hatches in the pouch after about 10 days, where the young is suckled with

milk for about 55 days. The young (sometimes called a puggle) then lives in a nursery burrow until it is weaned (Augee and Gooden 1993; Rismiller and McKelvey 2003).

One notable feature of the studies that have been undertaken is the variation in reproductive behaviour found between different echidna populations. There are significant differences in the use of nursery burrows and maternal care, with the timing and duration of the period the young spends suckling in the pouch and then in the burrow, as well as maternal behaviour throughout the entire reproduction period, varying considerably between different regions of Australia (Morrow et al. 2009). For example, Kangaroo Island echidnas wean the young at 204-210 days, but in Tasmania weaning occurs at 139-152 days, even though the masses of the young are comparable at weaning (Morrow et al. 2009).

Mating behaviour also varies. For example, the occurrence of so-called “echidna trains” (Rismiller and Seymour 1991, see section 2.1.4.2), where a female echidna is followed by male echidnas in single file during mating season, have been reported in New South Wales, Victoria, the Northern Territory and Kangaroo Island off South Australia (Griffiths 1978; Rismiller 1992; Rismiller and McKelvey 1996, 2000). However, studies of echidna populations at higher altitudes at Mount Kosciusko and south-east Queensland never found more than one male with a female (Beard and Grigg 2000; Beard et al. 1992). Another difference is the timing of mating, occurring soon after hibernation in eastern Australia, while Tasmanian echidnas show significant overlap between hibernation and reproduction (Morrow et al. 2009). Taggart, Breed, Temple-Smith, Purvis and Shimmin (1998) suggested there were fundamental differences in echidna courtship behaviour depending on the climate. According to Morrow et al. (2009, p. 281) these differences in mating behaviour may be the result of “behavioural flexibility in response to different climatic conditions”.

2.2 COGNITION

2.2.1 Neurophysiology

As discussed in section 2.1, monotremes have historically been considered primitive and uninteresting due to their evolutionary history and plesiomorphic characteristics.

When the brain of the echidna was studied, it was often merely as an example of a 'primitive' brain used to further the understanding of the evolutionary development of the mammalian brain (Dawson 1983). The brain of the echidna does contain some seemingly phylogenetically ancient features, such as the retention of a pars intercalis encephali (Griffiths 1968), the lack of any discernible claustrum (Butler, Molnar and Manger 2002; Divac, Holst, Nelson and McKenzie 1987) and the presence of commissural fibres rather than a corpus callosum (Griffiths 1968).

However, the brain of the echidna, compared to that of reptiles and birds, also contains many anatomical structures that indicate it is essentially mammalian – such as the size and configuration of the cerebellum, the mesencephalon, the telencephalon and the neocortex (Griffiths 1968). In addition, the growing acceptance of the ideas of mosaic evolution (see section 1.4) means that comparative neurologists are increasingly open to the idea that phylogenetically 'primitive' brain components can co-exist with more highly evolved mechanisms. Almost universally, studies have indicated that the echidna's brain is, in many respects, much more 'advanced' than its evolutionary history or physiology might suggest (Divac 1995).

2.2.1.1 Brain size

A number of scientists have suggested ways to predict the relationship between cognitive capacity and measures of cerebral development (for a review of early theories see Riddell and Corl 1977). One of the simplest proposals for determining the degree of brain 'advancement' is calculating relative brain size. According to authors such as Rensch (1956), the greater the brain size relative to body weight, the greater the learning capacity of that species.

Hassiotis et al. (2003) compared the echidna to other living and extinct metatherian and eutherian mammals on a brain and body weight graph. The region occupied by the echidna was similar to that of representatives of primates (squirrel monkey) and carnivores (cat). It was also found that the echidna brain weights lay substantially above the regression line showing the relationship between brain and body weight for mammals as a whole and were also considerably higher than both living and extinct metatherians of similar body weight. It is notable that mid-Triassic cynodonts, the

purported evolutionary forebears of both monotremes and therians (Dawson 1983; Griffiths 1978), have much smaller brains than any modern mammal of similar body weight. Considering monotremes and therian mammals are thought to have followed a separate evolutionary path for at least 200 million years (see section 2.1.2), brain expansion must have occurred independently in monotremes and therians (Hassiotis et al. 2003).

Another way of comparing brain size is to utilise encephalisation data. Brain size increases with body size at a characteristic exponential rate (Finlay, Darlington and Nicastro 2001). Jerison (1973) used regression equations to determine the expected brain size for any given species, then used known data about actual brain size to determine the “encephalisation quotient” (EQ), which indicated by what extent the brain of that species had developed over and above body size requirements. According to Jerison (1985): “Grades of encephalisation presumably correspond to grades of complexity of information processing” (p. 30).

The EQ of the echidna, 0.5 to 0.75, is in the range of ‘progressive’ species of marsupials such as kangaroos rather than the ‘primitive’ marsupials like opossums or basal insectivores such as tenrecs. It is much larger than any reptile or insectivore and is within the range for rodents (Divac 1995; Jerison 1973). In a similar fashion, Hassiotis et al. (2003) used the method outlined by Hofman (1982) to calculate the mean encephalisation index for the echidna and then compared that to other species. The echidna’s encephalisation index was 0.066, which places it in a similar range to carnivores (0.069) and prosimians (0.088) and is more than twice that of basal insectivores (0.030) (used as representatives of ‘primitive’ placentals).

The ratio of brain mass to spinal cord mass is also considered a useful indicator of neural organisation and ‘intelligence’. This theory is based on ratios, which vary from those for fish, in which brain mass is less than that of the spinal cord, to those for mammals. The ratio for cats is 4:1, for primates 8:1 and for man 10:1. The corresponding ratio for echidnas is a respectable 6:1 (Dawson, 1983).

However, the idea that brain size correlates to intelligence is not universally accepted. Macphail (1982) claims to have found “no convincing behavioural evidence ... that

brain-size measures do predict intellectual capacity” (p. 335), Bingham (1990) reports that there is no evidence to support the “brain size/intelligence story” (p. 347) and Holloway (1990) claims there is “no solid empirical evidence ... that any significant relationship exists between brain size and adaptive behavioural repertoires” (p. 360). Marler (1996) argues that a relatively small brain size has been no impediment to the “impressive” cognitive achievements of birds, an argument echoed by Chittka and Niven (2009) regarding insects. In an interesting twist, Gibson (2002) examined a number of studies and concluded that while absolute brain size predicts the known differences in cognitive ability between monkeys and apes, encephalisation measures do not, a result echoed for primates in general by Deaner, Isler, Burkart and van Schaik (2007).

Manger (2006) received extensive international publicity for claiming there was “no neural basis for the often-asserted high intellectual abilities of cetaceans” (p. 293), despite their volumetrically large brains – or, as *The Daily Telegraph* glibly put it: “Dolphins are flippin’ idiots” (*The Daily Telegraph* 2006). Manger (2006) based his assertion on a review of cetacean brain structure related to behaviour and evolution. According to Manger (2006), the dolphin’s sizeable brain is not based on neuron quantity but is instead due to a large number of glial cells that serve as insulation to protect the mammal against cold ocean temperatures. However, many cetacean experts have been highly critical of Manger’s conclusions – citing the numerous studies showing complex dolphin neuroanatomy and behaviour (e.g. Bonoguoire 2006; Marino et al. 2007; Sherriff 2006) – as well as of the paper itself. Lori Marino, for example, said it was “very unfortunate that such a methodologically and theoretically flawed paper as Manger’s has received any attention at all” (Whale and Dolphin Conservation Society 2006) and that the generally accepted view was that “the large brain of cetaceans evolved to support complex cognitive abilities” (Marino et al. 2007, p. 0966).

Despite some dissenting voices, many authors continue to equate brain size with intelligence. Byrne (1993) says there is “strong support to the belief that larger brains allow more intelligent behaviour” (p. 697) while Pearce (1997) claims that: “If two species possess the same body size but one has a considerably larger brain, then it is likely that this extra brain will enable its owner to be the more intelligent” (p. 9). Falk (1990) believes that “‘intelligence’ may have been related to the increase in brain size

for various groups of mammals across the Cenozoic ... [and] when controlling for allometry and comparing species ... bigger brains were and are better brains” (p. 344) and Krantz (1990) holds that it is clear that “intelligence is related to brain size” (p. 362), while Smith (1990) claims it “seems nearly absurd to argue, as some do, that evolutionary increase in brain size does not signify increased ‘intelligence’” (p. 366). This view has also affected species selection for cognitive testing. Herman (2002), for example, states: “An exceptionally large brain ... make[s] the bottlenosed dolphin (*Tursiops truncatus*) an ideal species for studying intellectual processes and potential” (p. 275). (For more references see Falk 1990).

Empirical testing of the relationship between brain size and learning ability has been limited. Rensch (1956) presented data from a variety of species that, he argued, showed a positive correlation between absolute brain size and learning ability. However, the data was all from different studies, making it hard to determine if the results instead reflected differences in task difficulty and/or training procedures (Johnston 1982). Riddell and Corl (1977) found that reliable relationships do exist between cerebral development (calculated using a number of different cerebral indices) and learning ability in a sample of 23 species. However, the criteria for learning ability was restricted to a small number of relatively simple tasks such as learning sets, successive discrimination reversals, delayed alternation, conditioned response reversals and extradimensional shifts. Similarly, Gossette (1968) found learning performance in birds and mammals correlates positively with relative brain size using successive discrimination reversal learning. More convincingly, Rumbaugh and Pate (1984) used an encephalisation index to accurately predict species differences between seven non-human primate species on a complex learning task.

Jerison (1985) suggests that learning ability, at least in its most basic form, does not require large amounts of brain tissue, citing the learning abilities of pigeons and other unencephalised species. Rather, he argues that there is empirical evidence for a correlation between “the grade of encephalisation and what an animal appears to know when it copes with a task” (p. 30) – that is, that brain enlargement is involved with the use of sensorimotor information and the subsequent “construction of representations of reality from neural data ... which may be another way to describe intelligence” (p. 30).

While it is important not to confuse correlation with causality (Healy and Rowe 2007), much of the support for equating bigger brains with increased ‘intelligence’ is based on the idea that additional brain size above that expected for body size (Jerison’s 1973 “EQ”) may be selected for specialised or elaborate behaviours or demanding niches. Indeed, those animals with high EQs do show a wider range of behavioural complexity – carnivores have a higher EQ than their prey; frugivores surpass folivores among prosimians and primates; and careful parents outrank careless ones (Finlay et al. 2001). A number of studies have also linked increased encephalisation to greater behavioural flexibility and adaptability to novel environments (Gossette 1968; Lefebvre, Reader and Sol 2004; Marino 2005; Ratcliffe, Brock-Fenton and Shettleworth 2006; Schuck-Paim, Alonso and Ottoni 2008; Sol 2009; Sol, Bacher, Reader and Lefebvre 2008; Sol, Duncan, Blackburn, Cassey and Lefebvre 2005). According to Finlay et al. (2001, p. 265), in general the “bottom feeders of each vertebrate radiation stake out the lowest edge of the EQ range” (Eisenberg 1981; Gittleman 1994, 1995; Jerison 1973; Stephan, Baron and Frahm 1988). These findings suggest the echidna, with its higher than expected encephalisation ratings, may display a higher degree of behavioural complexity than previously thought and is not a “bottom feeder”.

Another way in which many scientists justify the “bigger equals better” theory of relative brain size is by contending that there must be some adaptive advantage for animals to evolve large, complex brains. Schusterman, Reichmuth and Kastak (2000) theorise: “One can imagine large brains evolving in animals because of the adaptive value of some aspects of reasoning” (p. 1), while Northcutt and Kaas (1995) claim: “Mammals with large brains and expanded isocortex have not simply enlarged the isocortex but ... have acquired more complex cortical processing networks” (p. 375). According to Aboitiz (2001), neural processing power is primarily increased through neural network reorganisation, which benefits from increases in brain mass that allow more space for connectional rearrangements and increased synapse specificity.

As Deacon (1990) points out, the energetic cost of neural tissue means there would need to be strong selection pressure to evolve a larger brain. If brain tissue is not used to increase fitness (presumably through the development of more complex mental abilities), it tends to diminish through natural selection (Beilharz, Luxford and Wilkinson 1993). As Smith (1990) points out in relation to humans, in light of the

“enormous” costs of a large brain: “For natural selection to bring about enlarged brains, the benefit must exceed the cost” (p. 366).

Hassiotis et al. (2003) speculate that the low body temperature and metabolic rate of the adult echidna (see section 2.1.8) may mean its relatively large brain is less metabolically demanding and, by inference, may not require as great an adaptive ‘trade-off’. Addressing the first factor, low body temperature, it is true that the central nervous tissue is one of the most heat susceptible tissues in mammals (Brinnet 1990) and is considered by a number of authors to be a significant constraint on increased brain size (e.g. see review in Falk 1990). That the echidna’s thermoregulatory abilities and low body temperature might make it less costly to keep a larger brain cool seems a reasonable proposition. According to Caputa (1990), a low body temperature should be advantageous because in mild hyperthermia “brain temperature is likely to remain constant with little effort from the system for selective brain cooling” (p. 352). This idea also receives some support from Falk’s (1990) “radiator” theory that the increase in brain size in human evolution is due to the development of a cooling network of cranial veins that removed thermal constraints on brain enlargement.

However, as to the second factor, whether the echidna’s low overall metabolic rate translates to a brain with lower metabolic requirements is unknown. According to Barton (1990), as a rule the brain is a “metabolically expensive organ to run” (p. 345) while Krantz (1990) describes it as “an unparalleled metabolic drain” (p. 363). In humans, for example, the brain represents approximately 2% of body weight, but consumes about 20% of metabolic resources (Holloway 1990), compared with a 2% metabolic cost to an average, relatively small-brained marsupial (Smith 1990). This suggests that the development of large brains would have to be supported either by higher overall metabolic rates or the reallocation of a higher proportion of metabolic output to the brain – a situation that would seem to necessitate some kind of adaptive benefit. In addition, even if there were reduced metabolic pressure on adult echidnas, the growth of a large brain would still represent a considerable anabolic burden during a young echidna’s development (Hassiotis et al. 2003). Also, since metabolic rate increases by a negative allometric coefficient of 0.75 with body weight, it is more difficult for smaller animals like the echidna to maintain each gram of tissue (Smith 1990).

Finally, even if the echidna's low body temperature and metabolic rate were contributing factors in enabling echidna brain encephalisation, it would seem that these factors, much like Falk's (1990) "radiator" in humans, would be permissive conditions for the development of larger brain size rather than providing selective pressure for its evolution (Finlay 1990; Foley 1990). Larger brain size would still require some adaptive rationale, such as an ecological requirement for greater 'intelligence'. According to Jerison (1973, p. 7): "To the extent that intelligence is correlated with the mass of tissue in the brain, the monotremes are best considered to be at almost the same level as living progressive placental mammals; they presumably have reached that level by parallel evolution."

2.2.1.2 Cortical size and gyrification

A high proportion of cerebral cortex to total brain volume is also often related to a high degree of cognitive development (Hassiotis et al. 2003). Studies have shown that the echidna has a large proportion of total brain volume occupied by the cerebral cortex (43%), higher than that for basal insectivores (13%) and the American opossum (22%) and comparable to that found in eutherian mammals (prosimians 54%) (Pirlot and Nelson 1978).

Hassiotis et al. (2003) compared the echidna's relative brain cortical surface area to a wide group of therian mammals and found it to be similar to that of placental carnivores and well above that of a basal insectivore placental mammal like the hedgehog. The echidna's cortical surface area is also well above the relationship between basal cortical surface area and body weight (Hofman 1982). Results above the regression line are considered to indicate "there is an amount of 'extra' cortical tissue present, which may be associated with improved information processing capacity" (Hassiotis et al. 2003, p. 844). Analysis of cortical thickness also indicated that the echidna isocortex has a similar thickness to homologous areas in placental mammals of similar body weight (e.g. cat) (Hassiotis et al. 2003).

Another possible indicator of the echidna's brain development is the fact that its neocortex is markedly gyrencephalic (folded), in contrast to the neocortex of the platypus and many marsupials, which are smooth, or lissencephalic (Griffiths 1989;

Rowe and Bohringer 1992). The degree of cortical folding in the echidna is 36% of isocortex buried in fissures, comparable to that in many placental mammals such as the cat (40%) and squirrel monkey (39%) (Hassiotis et al. 2003).

The relatively large, gyrencephalic cerebral cortex of the echidna has been a source of amazement to neuroanatomists for many years. Elliot Smith wrote in 1902:

The most obtrusive feature of this brain is the relatively enormous development of the cerebral hemispheres which are much larger, both actually and relatively, than those of the platypus. In addition the extent of the cortex is very considerably increased by numerous deep sulci. The meaning of this large neopallium is quite incomprehensible. The factors which the study of other mammalian brains has shown to be the determinants of the extent of the cortex fail completely to explain how it is that a small animal of the lowliest status in the mammalian series comes to possess this large cortical apparatus.

Elliot Smith (cited in Griffiths 1968, p. 101)

Animals with gyrencephalic brains are often considered to be more ‘intelligent’, as well as perceptually and behaviourally more complex (Welker 1990). According to this theory, increasing the surface area of the cerebral cortex through folding allows for a greater number of cortical modules, and hence a greater number and diversity of brain functions, to be accommodated without increasing the size of the cerebrum (and head) beyond biologically feasible limits (Augee and Gooden, 1993; Dawson 1983; Jerison 1973). According to Hassiotis et al. (2003): “... a highly gyrified cortex is considered the hallmark of more neurologically advanced mammals such as carnivores, primates and cetaceans” (p. 827).

Some authors have sounded a note of caution about using gyrencephaly as an indicator of ‘higher’ brain development. They point out that many primates, particularly small primates (e.g. marmosets), are lissencephalic yet still exhibit cognitively complex behaviours (Rowe 1990; Russell 1979). Fuster (1997) further suggests that gyrification may be in part attributable to mechanical factors, not simply functional differentiation, and is largely a function of brain size. However, the fact that there are a number of animals whose brains are both relatively large and lissencephalic suggests this cannot be the whole story (Welker 1990). Even if it were the case, it does not explain why the echidna has such a relatively large brain to begin with.

Other scientists have suggested that cortical fissuration is to some degree attributable to increased innervation of specialised sensory surfaces (review in Welker 1990). This phenomenon is found in the echidna, which has a relatively large proportion of the somatosensory cortex allocated to the snout and tongue, reflecting the behavioural importance of these areas to the insectivore echidna (Johnson 1990; Lende 1964, 1969). However, these specialised sensory surfaces do not seem to be responsible for the echidna's highly gyrified cortex. Unlike the cortex of the platypus, which is nearly all sensory and motor regions, the total area taken up by the equivalent regions in the echidna are comparatively small and located in the caudolateral corner of the hemisphere (Johnson 1990; Krubitzer et al. 1995).

In 1902, Elliot Smith pointed out that other small terrestrial insect-eaters such as pangolins and anteaters and fossorial animals such as bandicoots, hedgehogs and armadillos have highly macrosomatic brains with large areas devoted to olfactory processes coupled with a small neocortex. By contrast the echidna, which has a seemingly similar lifestyle, has both macrosomatic features and a large complicated neocortex (Augee et al. 2006).

Interestingly, it has been argued that animals displaying the pattern of a large sensorimotor representation and small neocortex, such as the platypus and anteaters, constitute a more primitive group of mammals that reflect a less highly evolved stage of cerebral cortical development. Animals with smaller proportions of sensorimotor representation, such as the higher primates and cats (and also the echidna), are often considered to display a more advanced stage of cortical development, although this theory is not universally accepted (Dawson 1983; Lende 1969; Rowe 1990).

2.2.1.3 Forebrain size

Another puzzling aspect of the echidna's brain is the frontal cortex. In humans, the front 29% of the cerebral hemispheres has no specific motor or sensory representation and is therefore referred to as the "silent area" or the prefrontal cortex (Fuster 1997). In the echidna this area takes up a remarkable 50% of the cerebral cortex, proportionately more than any other animal including man (Augee and Gooden 1993; Lende 1969; Rowe 1990), prompting Divac, Holst et al. (1987) to describe the echidna's prefrontal

area as “outstandingly large” (p. 303). As mentioned in section 2.2.1.2, the sensorimotor area of the echidna’s brain is relatively small on examination of external morphology. However, when the sensorimotor regions of the echidna are opened completely, they are still quite extensive (Krubitzer et al. 1995) – it is the elaboration of the frontal cortex that has led to their caudal displacement (Lende 1969).

In 1969 Lende claimed the significance of the large expanse of frontal cortex in the echidna was obscure, saying there were “no broad hints of its function from either neuroanatomy or behavioural observations” (p. 272). The mystery continues, with Johnson, in 1990, saying: “The functional significance of the additional ‘silent’ cortex of the echidna remains to be determined” (p. 343).

While the function of the “silent area” in animals is still largely unknown, in humans it is believed to be involved in complex cerebral processes such as future planning, construction of alternative interpretations of events, novelty detection, behavioural monitoring, choosing between options, personality traits and memory (Augee and Gooden 1993; Augee et al. 2006). Imaging studies have shown that the prefrontal cortex is activated when human subjects plan (Dagher, Owen, Boecker and Brooks 1999) or solve problems requiring general intelligence (Duncan et al. 2000), and tests have shown a significant correlation between the volume of frontal grey matter and the results of intelligence tests (Thompson et al. 2001). Fuster (1997) describes it as “the substrate for neural activity of the highest order” (p. 6) and the “substrate of abstract intelligence” (p. 67). Oakley and Plotkin (1979, p. xiv) claim the evolution of the vertebrate forebrain, especially in birds and mammals, appears to relate to areas such as “learning, memory, intelligence, complex-problem solving, cross-modal integration, reasoning, consciousness, freewill, sleep and dreaming”. While the hippocampus is considered likely to be critical to long-term information storage (Hauser, Gardner, Goldberg and Treves 1993); Ashby, Isen and Turken (1999), Fuster (1997), Goldman-Rakic (1988, 1995) and others have suggested that the prefrontal cortex is the primary centre for working memory.

So, although there is still debate around the organisation of functions and processes in the frontal cortex, it is generally accepted that its functions in humans are relatively sophisticated. To perform this type of role, the area requires the association of incoming

sensory information, which is generally projected via the thalamus to the prefrontal cortex in eutherian mammals. Generally speaking, the thalamocortical relationships in the echidna are similar to those found in placental mammals, providing some support for the area having similar functions in both echidnas and placentals (Augee et al. 2006; see section 2.2.1.4). Indeed, the extensive frontal cortex of the echidna presented a problem for comparative neurologists who believed, firstly, that monotremes represented an archetypal mammalian form and, secondly, that the frontal cortex was an area whose relative size was assumed to increase in ascending the phylogenetic scale (Rowe 1990).

Some authors deal with this problem by claiming that humans possess the largest prefrontal cortex and simply ignoring the echidna altogether. Fuster (1997), for example, claims that “the frontal cortex becomes not only larger but more complex, more fissurated and convoluted, as mammalian species evolve. In primates the process reaches its culmination with the human brain” (p. 7). Other authors have questioned whether this region in the echidna can be considered homologous with that found in humans. Krubitzer (1998), for example, speculates it might be part of an olfactory specialisation. It has also been suggested that the area is used to process information from electroreceptors (Augee et al. 2006).

If the echidna’s frontal cortex is comparable to that of humans, the question arises: “Why should an animal like the echidna, with its apparently simple existence, have a frontal cortex comparable with that of man?” (Dawson 1983, p. 30). Jerison (1976) argues that forebrain structures became more complex because increasing demands were being made on the nervous systems of vertebrates as they moved into increasingly diverse and demanding ecological niches. If that is the case, the echidna’s adaptation to a wide range of ecosystems, from desert to alpine, could help explain its remarkable frontal cortex development (see section 6.3 for further discussion of possible triggers for neurophysiological development in the echidna).

2.2.1.4 Comparable microcircuitry

Despite the suggestive nature of the echidna’s brain structure, allometric data such as relative brain, neo-cortical and frontal cortical volumes should be interpreted cautiously.

Relative size is important to the functional properties of brains only if the microcircuitry is comparable and the cortical structures perform a similar function (Divac 1995) – facts which are by no means certain between species, particularly those that are evolutionarily distant. As Holloway (1993) points out, the brain of every species is somewhat different – each has a unique history of natural selection, drift, migration and neural ontogenesis, as well as the development of species-specific behaviours. Despite these caveats, some comparative data is available to support the argument that at least some of the echidna's brain structures may correspond with those found in eutherian mammals, a few examples of which are described below.

2.2.1.4.1 Frontal cortex

Two groups of scientists have attempted to determine whether the frontal area of the echidna corresponds to the prefrontal cortex in placental mammals by comparing the sources and destinations of efferent and afferent connections in the frontal cortex (Divac, Holst et al. 1987; Divac, Pettigrew, Holst and McKenzie 1987; Welker and Lende 1980). The prefrontal cortex has been defined as “the part of the cerebral cortex that receives projection fibres from the mediodorsal nucleus of the thalamus” (Fuster 1997, p. 41), a criteria that is widely supported (e.g. Akert 1964; Rose and Woolsey 1948; Uylings and Van Eden 1990). Both groups found the echidna's prefrontal cortex has connections with a region of the thalamus seemingly homologous to the mediodorsal nucleus. Non-thalamic efferent and afferent connections with the frontal cortex were also from similar sources to those found in placentals. These findings led the authors to conclude that the echidna's frontal area does correspond to the prefrontal cortex found in placental mammals (Rowe 1990).

2.2.1.4.2 Cerebral cortex

The echidna brain shares many other structural features with placental mammals. These include a six-layered isocortical structure (Hassiotis et al. 2003) and similar neuronal distribution. Hassiotis et al. (2003) found that values for neuronal density in the echidna cerebral cortex were comparable to those for placental mammals of similar body weight (e.g. macaque and cat) and that the number of glia per neuron in the echidna isocortex was actually substantially higher than in similar areas in therian cortex. They also found

that the echidna's cerebral cortex contains the same major groups of neurons found in the placental cortex, although with a higher proportion of unusual pyramidal cell morphologies than that found in placentals.

2.2.1.4.3 Sensorimotor region

Another possible indicator that the echidna's 'advanced' brain features are operating in a similar manner to eutherian mammals is if there is a comparable level of sensory input being processed. The use of microelectrodes has provided evidence that, in many species, there are several cortical maps of the receptive surface of each modality (e.g. retina, the organ of Corti and skin). It is believed that each map processes one aspect of the modality in question so a greater number of maps would allow an animal to extract more detailed information about an environment. Considerable variation in the number of sensory maps in the cortex of different species was found (Divac 1995).

Krubitzer et al. (1995) studied the organisation of the sensory cortex in monotremes and found they had four somatosensory maps, even though "the presence of complex, multiple representations observed in these species is generally not associated with primitive brains" (p. 284). The number discovered in monotremes is greater than that found in hedgehogs and American opossums (Johnson 1990). In addition, the authors found areas onto which different modalities converge in the back of the echidna's brain (an association cortex) as well as a number of cortical specialisations.

The idea implicit in a number of theories of cortical evolution that monotremes are 'primitive' and 'lower' also suggests that they will have less differentiated brains with fewer cortical subdivisions than 'advanced' or 'higher' mammals (Krubitzer et al. 1995; see Deacon 1990 for review and refutation). However, the studies by Krubitzer et al. (1995) on the organisation of the somatosensory cortex in monotremes led them to claim that: "The presence of multiple sensory areas, association cortex and anatomical and functional specialisations within a cortical field indicate that monotreme brains are not 'generalised and undifferentiated'" (p. 299). Divac (1995, p. 3) agreed, saying: "These observations suggest that the brain in monotremes is, in some respects, advanced."

Other features of the echidna's neural sensory apparatus have also proved comparable to those found in placental mammals. The internal structure of the auditory and visual cortices in the echidna exhibit a similar columnar array of cortico-cortical connections (Dann and Buhl 1995; Hassiotis et al. 2003) and the cortical columns in echidnas and monkeys are of the same width (Divac, Pettigrew et al. 1987). It has been observed that dendritic spine density of echidna pyramidal neurons in the somatosensory cortex and apical dendrites of motor cortex pyramidal neurons is lower than that found in eutheria, a factor which might limit functional capacity (Hassiotis et al. 2003). However, studies have also shown that morphology, density and distribution of synapses in the echidna somatosensory cortex is similar to that in eutheria (Hassiotis et al. 2003). Allison and Goff (1972) found the configuration of both early and late components of the evoked potentials recorded over the sensorimotor areas was very similar to those of placentals, implying similar underlying intracortical mechanisms. These results suggest that the echidna's brain is processing sensory information in equivalent detail to placental mammals (Rowe 1990).

2.2.1.4.4 Spinal cord

The echidna's spinal cord is relatively shorter than that of a human (possibly to facilitate its curled defensive posture), however corticospinal fibres extend down the greater length of the spinal cord. According to Augée et al. (2006), this is a feature of "advanced neurological organisation" (p. 54) found in primates and carnivores but not in marsupials and some placentals such as armadillos, hedgehogs and tree shrews (Augée et al. 2006; Rowe 1990). The arrangement of nerve cells is also similar to those found in eutherian mammals (Augée et al. 2006). Despite these suggestive findings, the cortical origins of the corticospinal fibres in echidnas have not yet been fully examined so the contribution of the sensory cortex to the corticospinal tract in the echidna has yet to be established (Johnson 1990).

2.2.1.4.5 Conclusion

The results of numerous comparative microcircuitry studies, such as those described above, led Hassiotis et al. (2003) to declare that, in most structural parameters, the

echidna's cerebral cortex is "comparable to those placental mammals usually considered neurologically advanced and behaviourally complex" (p. 848).

2.2.2 Cognitive studies

Why should an animal with a seemingly prosaic existence have a relatively complex brain structure? To examine this question requires methods for measuring relevant cognitive behaviour that can be examined in both natural and laboratory settings.

2.2.2.1 Foraging strategies

One of the most important tasks of any animal is to find food and one of the most effective methods of testing an animal's learning ability is to study its foraging behaviour. Feeding behaviour has long provided the central data for psychological theories of learning and motivation as it has a number of cognitive aspects such as goal orientation, self-initiation, adaptation, cost/benefit analysis and complex means activities such as search, detection, capture, handling and storage (Collier and Rovee-Collier 1981; Menzel and Wyers 1981).

Ants and termites are a potentially rewarding food item for predators because colonies represent a concentrated source of energy (Abensperg-Traun and Steven 1997) – a "food patch". Optimal foraging theory predicts that animals should respond to patchily distributed food resources and allocate their foraging efforts to maximise the rate of energy intake. Such efficient foraging leaves more time for other activities such as mating, increasing fitness in terms of lifetime reproductive success (Abensperg-Traun et al. 1991). Studies have found that echidnas do forage efficiently, allocating more foraging time to patches where food is most abundant (Abensperg-Traun and De Boer 1992; Abensperg-Traun et al. 1991).

However, one of the assumptions of optimal foraging theory is that foraging can be constrained by a number of factors. For example, animals may not maximise their rate of energy intake if they forage in suboptimal patches to avoid predation or competition or if there is a need for vigilance while feeding (Abensperg-Traun et al. 1991). Echidnas have few predators (Griffiths 1989), however they have been shown to be constrained in

their foraging by temperature extremes (Abensperg-Traun and De Boer 1992), shelter availability (Abensperg-Traun 1991; Smith, Wellham and Green 1989) and, in particular, the defence mechanisms utilised by their prey (Abensperg-Traun et al. 1991).

One way in which echidnas deal with ant and termite defences is through short-duration feeding, where foraging is limited to the point where exposure to the defence becomes intolerable (Abensperg-Traun 1990). Abensperg-Traun et al. (1991) found echidnas forage for short periods (<30 seconds) at food patches containing the large and well defended *Drepanotermes* termites and move before soldier-worker ratios increase to intolerable levels.

However, the relationship between echidna foraging and prey defence is not a simple one. Echidnas sometimes ignore prey defences if the energetic reward is particularly high. For example, the mounds of *Nasutitermes exitiosus* and *Drepanotermes tamminensis* termites are sometimes attacked during spring and autumn when the nests may contain energy-rich alates. For the rest of the year, these nests are rarely attacked by echidnas because of the ferocious defence of the inhabitants (Abensperg-Traun 1990; Abensperg-Traun and Steven 1997).

Griffiths and Simpson (1966) found echidnas attacked the highly aggressive mound-building ant *Iridomyrmex detectus* despite being affected by their defences. At the end of feeding one of the echidnas was observed to give “a display of great animation, rolling over, scratching furiously at his chest and abdomen with the grooming-toes to rid himself of tormenting ants” (p. 140). However, the attacks on the mounds occurred only in springtime, coinciding with the presence of virgin queen ants that contain 47.2% fat and provide a valuable energy-rich meal. When the virgin queens left the mounds, the attacks ceased. The employment of short feeding bouts (except for instances of high energetic reward) in response to prey defence is one indication of foraging efficiency and adaptability.

Another way to determine the echidna's foraging efficiency is to study its patch-selection strategy. Ant and termite mounds represent energy-rich food patches that, in practical terms, are very unlikely to be depleted during a feeding bout. In terms of optimal foraging theory, the most efficient foraging strategy for echidnas would seem to

be to “win-stay” and return to a previously rewarding food patch rather than to “win-shift” and avoid a previously rewarding location.

However, the effectiveness of their prey’s defences indicate echidnas should be more likely to employ a “win-shift” strategy and, at least in the short term, go to another food patch where prey defences have not been triggered. If echidnas are naturally predisposed to follow a win-shift strategy, they should be expected to learn the win-shift task faster and more effectively than the win-stay task at short retention intervals. This was the finding of a study by Burke, Cieplucha, Cass, Russell and Fry (2002) using a retention interval of five minutes. These results are supported by studies of wild echidnas, in which the echidnas were observed undertaking short-duration feeding bouts with a mean 1.63 minutes then moving on to another patch (Abensperg-Traun 1988; Abensperg-Traun 1990; Abensperg-Traun et al. 1991) – a win-shift strategy.

If the echidna’s win-shift strategy is dictated by its prey’s defences, it would be expected that they would switch to a win-stay strategy over longer retention intervals after their prey’s defences had dissipated. However, when the retention interval was increased to 90 minutes the subjects were unable to learn either of these strategies, suggesting they were unable to remember the locations they had visited (or not visited) (Burke et al. 2002).

2.2.2.2 Memory

Foraging behaviour has also provided the basis for studying the memory capacity of the echidna. It seems clear that to effectively forage in a stable, patchily distributed environment would require an effective spatial memory. Quince (1998) used a simulated foraging task to determine whether echidnas possess an accurate spatial memory. The experiment revealed the echidnas were able to learn the location of a food source (in this case a baited food dish) and encode it in their spatial memory in order to revisit the site after a retention interval of up to 10 minutes (Burke, personal communication). However, while the study did demonstrate that echidnas are able to use spatial memory for foraging, the tests were conducted over short time intervals and further studies would be required to determine whether similar results would eventuate from longer intervals. The study of win-stay/win-shift foraging strategies mentioned in

section 2.2.2.1 indicates that they are unable to remember previously visited locations after intervals of 90 minutes (Burke et al. 2002).

In contrast, Buchmann and Rhodes' (1978) study of instrumental learning in echidnas (see section 2.2.2.4) suggests echidnas are able to utilise long-term memory under a different testing condition. The 1978 experiments tested discriminations based on spatial and visual/tactile information. When three of the echidnas were re-tested one month after the conclusion of the experiments they rapidly achieved levels of performance comparable to those previously attained in late testing.

While all of the above studies seem to indicate echidnas possess an accurate short-term memory, the contrasting results of long-term memory performance between the Buchmann and Rhodes (1978) and the Burke et al. (2002) studies suggest there may be different memory mechanisms at work in different tasks. The first study largely involved the use of visual stimuli to perform a task, while the second was conducted using spatial information. It is possible echidnas, while possessing an effective long-term visual memory, have only evolved a short-term spatial memory strategy (a phenomenon that has also been observed in hummingbirds and rats) or that win-shift behaviour at short retention intervals is not a foraging adaptation at all (Gaffan and Davies 1981). Another possibility is that the mismatch between the test situation in the foraging study and the echidna's natural environment (such as the relatively large spatial scale over which echidnas actually forage, see section 2.1.6) may account for the subject's failure to remember locations at greater time intervals under these experimental conditions (Burke et al. 2002).

2.2.2.3 Social behaviour

Echidnas are largely solitary animals and generally only come together during the breeding season (Griffiths 1978). Two early studies aimed at documenting and evaluating the echidna's social behaviour were not promising. Brattstrom (1973) documented the social and maintenance behaviour of *Tachyglossus aculeatus aculeatus* in laboratory and outdoor cages and in a semi-wild state in Victoria. Brattstrom documented some 65 behavioural postures and found evidence of a loose hierarchy in laboratory situations, with subordinate individuals attempting to avoid contact with

dominant (larger) individuals. However, he concluded that the behavioural patterns and postures of the echidna were less complex than most mammals and even those of many lizards.

Augee, Bergin and Morris (1978) studied echidna behaviour in captive animals in an enclosure at Taronga Zoo, Sydney. The enclosure was exposed to natural weather and light conditions and presented a spacious and complex environment with opportunity for spatial segregation. In this study, the animals grouped together in preferred sites and were mutually tolerant. In contrast to Brattstrom's (1973) study, no evidence of territorial behaviour or of a hierarchy based on size was observed. There was a dominance hierarchy among animals of the same sex, but its basis could not be determined.

Even in naturalistic settings observations of the behaviour of captive animals can be misleading due to the artificial nature of the environment. In order to investigate echidna intelligence and learning ability, a small number of cognitive-based laboratory studies have been conducted.

2.2.2.4 Learning studies

Studying the echidna's behaviour in the wild has shown that it is capable of coping in a wide variety of environments, is very efficient at finding its prey and is able to determine the boundaries of its territory and keep to those limits even in a complex environment. It also displays behavioural flexibility in response to differing environments – for example, in the Snowy Mountains, presumably in response to the cold conditions, echidnas do not appear to form courtship “trains” as they do in other environments and females leave their young in their burrow rather than carry them in their pouch (see section 2.1.9). However, little is known about the echidna's ability to learn (Augee and Gooden 1993; Augee et al. 2006).

One of the first documented examples of learning in *Tachyglossus aculeatus* was found by Saunders, Teague, Slonim and Pridmore (1971). Using four echidnas they showed short-beaked echidnas were capable of easily forming a position habit in a simple T-maze when they were trained to select either left or right for a food reward, with

subsequent rapid extinction. The acquisition rate of choice behaviours was almost identical to that reported for a similar level of T-maze training in the rat. The improvement in running speed exhibited similar characteristics as that often reported for the rat in a runway situation.

Saunders, Chen and Pridmore (1971) used the T-maze to show that echidnas were capable of successive habit-reversal learning. This type of study has been widely used to make comparative estimates of intellectual capacity in a variety of vertebrates (e.g. fish, turtles, birds, rats, kangaroos and even mentally retarded children). These experiments involve teaching the subject to form a position habit in a simple two-choice alternative, such as the T-maze. Once criterion is reached, the situation is reversed so the alternate choice becomes the correct response. The important information is whether the animal shows any improvement across reversals.

Saunders, Chen and Pridmore (1971) used three echidnas as subjects and reversals were made every three sessions (each session consisted of ten trials). All three echidnas showed rapid improvement across a series of successive reversals, a similar performance to that found in eutherian mammals on similar tasks. They were also able to make 'one-trial' reversals, which have often been demonstrated in rats but never with nonmammalian (avian) species.

Gates (1973, 1978), in a study designed to examine the echidna's visual capabilities, showed echidnas were able to easily learn simple two-choice visual discriminations, including black/white, vertical/horizontal and circle/triangle. Gates pointed out that the echidnas obtained learning of an easy discrimination in about the same number of trials required for rats (Sutherland and Mackintosh 1971).

Buchmann and Rhodes (1978) investigated instrumental learning in *Tachyglossus aculeatus setosus* using repeated reversals of paired instrumental discrimination tasks. The echidnas had to press one of two pedals with the forefoot to receive a food reward. Two discriminations were used, positional (right/left) and visual/tactile (black/rough and smooth/white), with changes being made to the surface of the pedals.

The echidnas showed evidence of instrumental reversal learning in both the positional and visual/tactile conditions with results that compared favourably with those obtainable for eutherian mammals in comparable tests, including cats, rats and mentally retarded human subjects. Echidnas also appeared to be capable of achieving criterion performance “in a smaller number of reversals than other mammals tested on instrumental tasks” (Buchmann and Rhodes 1978, p. 142).

Buchmann and Rhodes (1978) also suggested the echidnas’ selective improvement (superior performance in reversal-shift conditions) was generally considered evidence of some form of stimulus organisation or stimulus coding (the animal storing, classifying and integrating the information it receives). Mackintosh (1974) considered this might be a property of highly organised neural systems that, if valid, may indicate echidnas possess a complex level of cerebral organisation.

In addition, Augée et al. (2006) suggest that the results show echidnas are able to store, classify and integrate visual and tactile information, “indicating a degree of attention characteristic of a highly organised nervous system” (p. 51). Interestingly, the authors also point out that this process is believed to be carried out in the frontal cortex – an area of the brain that is greatly enlarged in echidnas (see section 2.2.1).

2.2.3 Conclusion

The findings of the above studies of neurophysiology, foraging efficiency and cognitive ability suggest the echidna may possess a greater cognitive capacity than previously thought. However there is a paucity of experimental data and more studies are required to explore the abilities of this unusual animal. It is even possible echidnas possess abilities not tested by current procedures, particularly if they utilise unusual senses. For example, studies have demonstrated the presence of electroreceptors in the echidna’s snout and the ability to detect an electric field both in water and buried underground (Augée and Gooden 1992; section 2.1.4.5).

Buchmann and Rhodes (1978, p. 144) summarised the current state of knowledge of echidna intelligence when they wrote: “Further studies of learning will undoubtedly disclose important facts about the intelligence of these remarkable animals and modify

the quaint, explicitly and tacitly-held views that echidnas are little more than animated pin-cushions or, at best, glorified reptiles.”

2.3 RATIONALE

As discussed at the beginning of this chapter, the echidna is a suitable subject for this study because it fulfils the criteria of being both phylogenetically ‘primitive’ and ecologically diverse. In addition, there are a number of other factors that make the echidna an appealing subject for cognitive experiments. The echidna is of particular interest because it is a member of the unique phylogenetic class, monotremes. The general biology of echidnas has been well documented, particularly by Griffiths (1968, 1978); however there has been comparatively little study of their learning abilities. Monotremes are often considered more primitive than eutherians and are generally expected to be less successful at performing comparable tasks. However, the echidna’s successful adaptation to a wide variety of ecological niches, the surprisingly ‘advanced’ physiology of their brains and the results of the few cognitive studies that have been conducted show they are worthy candidates for further study of learning ability.

In addition to its intrinsic value, the echidna is also worth studying to provide a comparative study of mammalian evolution. Monotremes are thought to have followed a separate evolutionary course from placental mammals for at least 200 million years (see section 2.1.2). O’Brien and Graves (1990) describe monotremes as an example of parallel evolution, in which the echidna and platypus have successfully evolved to suit their evolutionary niches using different physiological and behavioural means than that of the more ‘advanced’ mammals. Such a distinct evolutionary history means the behaviour of the echidna provides a valuable comparison to the behaviour of eutherian mammals and may provide an appropriate control group for testing hypotheses about the evolution of behaviour in different mammalian families (Kimble and Whishaw 1994). Also, as argued by Bonney and Wynne (2003) in relation to marsupials, studying monotreme psychology could help address the issue of the relative influence of evolutionary history versus niche in determining learning ability.

Finally, there has been repeated criticism of the tendency in psychologically based animal learning studies to concentrate on only a few species (Beach 1950; Bitterman

1960; Kamil 1994). As Bonney and Wynne (2003, p. 188) pointed out: “Comparative studies of learning have traditionally used only a very limited range of species ... the range of species studied by comparative psychologists has remained quite small.” While the authors were lamenting the paucity of studies using marsupials, the point is even more salient when applied to monotremes (see section 2.2.2.4). This study attempts to address the imbalance by undertaking cognitive testing in a rarely studied species.

CHAPTER 3

THE TASK

As stated in the introduction, this study attempts to examine echidna cognition in the theoretical framework of both the hierarchical and modular viewpoints. To satisfy the hierarchical side of the equation – to test a ‘primitive’ animal on an ‘advanced’ cognitive task – it was necessary to provide the subject with a relatively complex cognitive problem. To incorporate the modular view, it was also important to select a task that, while providing the subject with a complex novel learning situation, would still draw on abilities the subject would likely have evolved in its natural ecology.

The selection of the echidna as a subject, for the reasons outlined in chapter 2, ruled out certain ‘advanced’ abilities completely foreign to the echidna’s experience, such as those with a basis in group dynamics or requiring specific physical abilities (e.g. imitation, language, tool use etc.). Previous studies with echidnas had already demonstrated their ability to perform basic visual discriminations (see section 2.2.2.4). It was therefore decided to build on those results by starting these experiments with some simple visual discriminations and then moving on to more complex category discriminations.

3.1 Discrimination

While not the main focus of this paper, it is important to provide a brief overview of basic discrimination for a number of reasons. Firstly, the basic visual discrimination experiments at the beginning of this study – conducted to confirm the results of earlier studies and to provide discrimination training – need to be put into context. Secondly, both the methodology and theories behind basic discrimination provide the foundation for an examination of categorisation, which will be discussed in greater detail in sections 3.3 to 3.8.

3.1.1 Definition and discrimination in nature

In order to survive and reproduce, animals must be able to discriminate. All animals need to find nutritious food and avoid poisonous substances as well as distinguish predators from harmless creatures. Social animals must be able to identify the group to which they belong, pair-bonded animals need to differentiate their mates, and parents and dependent offspring must be able to recognise each other (Pearce 1997).

For discrimination to have any adaptive value it must involve not only the ability to perceive differences between stimuli, but also to associate behaviours with particular stimuli. Classical ethologists have observed that a broad range of animals are able to use a variety of sensory modalities to make discriminations and respond selectively to objects in their environment. One of the most commonly cited examples of this phenomenon is the male stickleback. A male stickleback which is ready to breed performs a courtship display when he sees a female stickleback in breeding condition (identified by a swollen belly) enter his territory, but shows a head-down threat posture when another male (identified by a red belly) appears (Tinbergen 1951).

However, discrimination is not limited to visual stimuli. For example, ewes recognise and are attracted to the scent of their offspring (Kendrick, Levy and Keverne 1992) and birds are able to discriminate the vocalisations of their own species from those of other species and display more aggressive behaviour towards the latter (Nelson and Marler 1990).

Discrimination learning, then, occurs when different stimuli signal the occurrence of corresponding events to an animal and it behaves accordingly in their presence (Pearce 1994a). The literature on habituation and conditioning shows that animals can readily learn about biologically relevant stimuli through simple exposure to naturally occurring stimuli (Lea 1984a; Shettleworth 1998). However, it is difficult to isolate the factors controlling discrimination in naturally occurring stimuli so most discrimination learning studies involve training animals to discriminate artificial stimuli.

3.1.2 Discrimination training

While discriminative behaviour can be acquired through general experience, it can also be taught. Discrimination training involves differentially reinforcing animals for performing different, arbitrary responses to each of two or more stimuli (Shettleworth 1998).

3.1.2.1 Methods

Discrimination training involves the presentation of different stimuli to subjects and then arranging different schedules of reinforcement for responses to each stimulus (Mackintosh 1974). The stimuli could be presented either simultaneously on a single trial or successively on consecutive trials. Much of the traditional literature on discrimination training used T-mazes (in which the subject had to enter one of two arms) or jumping stands (in which the subject had to jump from a starting platform to one of two ledges).

To test a simultaneous visual discrimination, for example a black/white discrimination, one of the T-maze arms or doors (or the pictures in front of the jumping platform ledges) is randomly made black and the other white and only choices to one colour are reinforced, irrespective of the side on which it appears. In a successive black/white discrimination, the stimuli are presented consecutively and only one colour is reinforced. This “go/no go” discrimination can be assessed by comparing running speeds or latencies (Mackintosh 1974, Shettleworth 1998).

More recently operant methods have become more widely used because they provide for automated testing for numerous animals on numerous trials. Operant procedures have discrete trials, as in the T-maze, but also use free operant procedures where one or the other of the stimuli to be discriminated is always available and response rates are compared in different stimulus-reward conditions. A successive free-operant procedure is referred to as a multiple schedule, while simultaneous free-operant discriminations are called concurrent schedules. The ‘incorrect’ stimulus does not have to be completely unrewarded. Intermittent reinforcement can be provided in the presence of both stimuli and the response rates compared (Shettleworth 1998).

3.1.2.2 Stimuli

A broad range of visual stimuli has been used to demonstrate discrimination learning in an artificial setting. These range from very basic stimuli such as black versus white (Gates 1978) and geometric shapes (Baldwin 1981) to complex stimuli such as photographs (Davenport and Rogers 1971). Discrimination has also been examined

using other sensory modalities such as sound (Dewson and Burlingame 1975), smell (Michelsen 1959), taste (Stapleton, Luellig, Roper and Delay 2002) and touch (Buchmann and Rhodes 1978).

3.1.3 Discrimination experiments

As basic discrimination itself is not the focus of this study, a complete review of the extensive experimental literature on this topic would be superfluous. However, it is worth stressing the ubiquity of discriminative ability. The majority of discrimination experiments have been conducted with rats and pigeons due to their expediency as experimental subjects, but many other species have also been tested.

In an overview of discrimination learning among animal taxa Rensch (1967) cited numerous studies demonstrating discrimination learning in fish (e.g. perch, trout), reptiles (eg. lizards, iguanas), birds (e.g. pigeons) and mammals (e.g. mice, rats, zebras, donkeys, horses and elephants). Discrimination learning has also been demonstrated in many other taxa such as insects (Dyer, Neumeyer and Chittka 2005), amphibians (Gillette 2002), marsupials (Bonney and Wynne 2002a, 2002b) and monotremes (Gates 1978). Hennessey, Rucker and McDiarmid (1979) found that even a single complex cell, the protozoa *Paramecium*, could be trained to discriminate between two auditory stimuli. Considering the importance of discrimination to an animal's ability to survive and reproduce, it seems likely that virtually all animals are able to discriminate.

For a more extensive review of experimental discrimination learning, Mackintosh 1974 provides an overview of traditional work that is brought up to date in Mackintosh 1983 and Mackintosh 2000.

3.1.4 Discrimination learning theory

While general learning theory can be used to examine a wide variety of learning, including discrimination learning, many theorists have tried to explain more specifically how animals learn to discriminate stimuli. The discovery of three important discrimination processes – stimulus generalisation, transposition and peak shift – have

greatly facilitated the formation of such theories. These processes are described before discussing the major theories of discrimination.

3.1.4.1 Discrimination processes

3.1.4.1.1 *Stimulus generalisation*

Stimulus generalisation describes the phenomenon whereby reinforcement of a behaviour in the presence of one stimulus causes this behaviour to occur in the presence of similar, previously unseen, stimuli. The strength of the response to the novel stimuli tends to decrease as the degree of similarity to the training stimulus decreases. A well-known example of this type of generalisation gradient is found in an experiment conducted by Guttman and Kalish (1956). After training pigeons to peck at a yellow 580-nm key light, 10 other wavelengths were tested and a fairly symmetrical generalisation gradient was obtained with the most responding to the yellow training stimulus and gradually less responding as the wavelength became progressively shorter and longer either side of 580-nm (Mazur 2002).

3.1.4.1.2 *Transposition*

Köhler (1918) first demonstrated the process of transposition by training chickens to perform simultaneous discriminations between two grey cards of different degrees of brightness and select the lighter of the two (S+). The birds were then given a test using the original S+ card and a lighter card. The author found that the birds chose the lighter card, even though it meant rejecting the card they had been trained to select (cited in Pearce 1997).

3.1.4.1.3 *Peak shift*

In 1959, Hanson conducted an experiment examining wavelength discrimination in pigeons using successive, rather than simultaneous, presentation. During the testing phase, Hanson found the pigeons demonstrated peak shift – that is, the highest rate of responding occurred in the presence of light with a wavelength slightly less than S+, rather than S+ itself (Pearce 1997).

3.1.4.2 Discrimination theories

Using the phenomena described above as well as the results of other studies, a number of authors have sought to formulate formal theories of discrimination. These theories can be broadly divided into absolute and relational models.

3.1.4.2.1 *Absolute theories*

Absolute discrimination learning theories are based on the premise that animals solve discriminations using the absolute properties of the stimuli with which they are trained, not on the basis of any relationship between the stimuli. Absolute discrimination learning theories can be divided into two main categories: (i) the elemental approach which assumes that when two or more stimuli are presented for discrimination, each stimulus acquires excitatory or inhibitory strength independently; and (ii) the non-elemental (or configural) approach which assumes that entire stimulus configurations acquire excitatory or inhibitory strength.

3.1.4.2.1.i The elemental approach

Spence

Spence (1936, 1937) put forward the first formal theory of discrimination learning. He proposed that if an animal was rewarded for approaching a set of stimuli (S+) it would result in an increase in the tendency to repeat the response to each of the stimuli in the future. If the animal was not rewarded for approaching a set of stimuli (S-), the tendency to repeat the response to any of the stimuli would be reduced (Pearce 1997). According to Spence, animals learn about the absolute properties of stimuli. For example, in choosing between a black and a white stimulus an animal would not use relational information but would select the stimulus that had the highest approach strength. Spence's theory accounts for both transposition and peak shift, at least in successive discrimination experiments, by proposing that an excitatory generalisation gradient is created around the S+ and an inhibitory gradient around the S-. The approach strength of any stimulus is then determined by the difference between these two gradients.

Evidence for Spence's theory has been found in studies demonstrating that an inhibitory generalisation gradient does in fact develop around the S- (e.g. Honig, Boneau, Burstein and Pennypacker 1963). However, the theory fails to explain the results of other experiments, such as the so-called intermediate-size problem (Gonzalez, Gentry and Bitterman 1954, see section 3.1.4.2.2) and feature-positive discriminations, where the subject learns not to respond to a stimulus that has been intermittently paired with an S+ stimulus but never rewarded alone (Wagner 1969). According to Spence, any stimulus that has been rewarded, even intermittently, should gain a measure of excitatory strength and this has been shown not to occur in feature-positive discriminations (Pearce 1997; Mazur 2002).

Rescorla-Wagner

The Rescorla-Wagner model (1972) bears some similarity to Spence's theories. They both assume that conditioning can gradually change an animal's responding in either an excitatory or inhibitory manner and that animals learn about the absolute properties of stimuli. However, unlike Spence, Rescorla and Wagner believed that an animal's response to a stimulus could be affected by the properties of other stimuli that were present. Because of this, the Rescorla-Wagner model is able to explain feature-positive discrimination as the result of the associative strength of the S+ stimulus eventually blocking and reducing the associative strength of the intermittently reinforced stimulus (Pearce 1997).

The theory has also been able to explain other forms of discrimination more effectively than Spence's model, particularly with some modifications. One of these modifications (Blough 1975; Rescorla 1976) has been to assume that stimuli are composed of elements which gain and lose associative strength in the same manner as stimuli viewed as a single element. If the elements belonging to one stimulus are shared by other stimuli, the model is then able to explain stimulus generalisation and peak shift (Pearce 1997).

Another modification was suggested to account for negative patterning, in which animals are rewarded in the presence of stimulus A and stimulus B, but never in the presence of both (AB). The Rescorla-Wagner theory suggests that responding to AB

should be greater than either A or B as the response to the compound is created by the sum of the excitatory strength of A + B. However, the results of such experiments show the opposite to be true – A and B eventually gain more excitatory strength when presented separately. To overcome this problem Rescorla and Wagner (1972) suggested that when stimuli are presented together they create a hypothetical configural cue that acts as another stimulus. The configural cue is then assumed to acquire inhibitory properties that counter the excitatory influence of the individual stimuli (Pearce 1997).

Despite its success, the Rescorla-Wagner model cannot satisfactorily account for all discrimination experiments, particularly those concerning the influence of similarity on discrimination learning. In one experiment by Redhead and Pearce (1995), the authors used the Rescorla-Wagner model (including the configural cue modification) to show that the model makes incorrect predictions in the case of a three-stimulus discrimination (A+, BC+, ABC-) which seem to counterintuitively suggest that a discrimination between two sets of stimuli would be easier when they were similar (BC and ABC) than when they were different (A and ABC) (see Pearce 1994b, 1997).

3.1.4.2.1.ii The non-elemental approach

Configural theory

While the foregoing theories are elemental in the sense that they assume animals learn about each stimulus separately, configural theory (Pearce 1987, 1994a) holds that when a compound stimulus is presented for discrimination a configural representation is formed of the entire pattern that will have a single association with the outcome of the trial. (This is in contrast to the configural cue modification to the Rescorla-Wagner model mentioned above in which the configural cue operates as an additional stimulus feature). Generalisation to novel stimuli occurs not along separate feature dimensions but between patterns of stimuli. This theory appears to provide a more accurate explanation of the relationship between similarity and discrimination learning seen in the experiment by Redhead and Pearce (1995), described above (section 3.1.4.2.1.i.), as well as a simpler explanation for negative patterning.

Many absolute theorists continue to support the elemental approach (e.g. McLaren, Kaye and Mackintosh 1989), while others have argued that both elemental and

configural associations may form during discrimination learning (e.g. Kehoe 1988). However, none of these theories can account for instances where animals appear to be using relational information to solve discriminations (Pearce 1997).

3.1.4.2.2 Relational theories

While the absolute position on discrimination learning assumes that animals either respond to each stimulus without reference to any others or form a configural representation of the whole pattern, relational theory assumes that animals solve discriminations based on the relationship between the stimuli. By definition, there is no elemental approach to relational theories; instead they can be classed as a non-elemental or configural approach.

Köhler

One of the major proponents of the relational position was Wolfgang Köhler (1918), who explained the results of his transposition experiments (see section 3.1.4.1.2) by suggesting that the birds were solving the discriminations on the basis of the relationship between the cards (lighter/darker) rather than the absolute properties of the stimuli (cited in Pearce 1997).

While absolute theorists such as Spence (1936, 1937) and Rescorla and Wagner (1972) preferred to explain Köhler's simple transposition experiment using elemental theories, they are less able to explain other transposition experiments. For example, Gonzalez et al. (1954) demonstrated the intermediate-size problem when they trained chimpanzees to select the intermediate-sized stimulus from a set of three. Spence's theory predicts that when three novel stimuli are presented, the one closest to S⁺ should be selected. Instead, the subjects continued to select the intermediate stimulus, suggesting relational information had been used (Pearce 1997).

Further support for the relational position was provided by Thomas who used college students as subjects to demonstrate that the peak of a generalisation gradient tended to shift toward the middle of the range and that this peak shift could be controlled by the choice of stimulus. For example, if S⁺ was a bright light and S⁻ a low light, a peak shift

towards brighter lights occurred when the stimuli included some very bright lights (Thomas, Mood, Morrison and Wiertelak 1991) (Mazur 2002).

Abstract concept learning

While absolute theories of discrimination learning found wide acceptance for many years, particularly due to the influence of the Rescorla-Wagner (1972) model, the recent publication of increasingly more complex discriminations such as perceptual categorisation and so-called abstract concept learning has led to a renewed interest in relational theories. While absolute theories have been offered for demonstrations of complex perceptual categorisations, they have not been able to easily explain the ability of some animals to discriminate between stimuli representing abstract concepts such as same/different, larger/smaller, shorter/longer etc. that are readily explained as examples of relational learning. Both perceptual categorisation and abstract concept learning, and the theories that have arisen to explain them, are discussed sections 3.3 to 3.8.

3.2 Conditional discrimination

3.2.1 Definition

In a simple discrimination, one of the discriminative stimuli is always correct. However, in a conditional discrimination there is a second layer of stimuli, variously called a cue, sign or sample that informs the subject which stimulus to select on any given trial. Except sometimes during training, the subject is not required to respond directly to the sample; rather it comes to exert a kind of stimulus control over the subject's selection of discriminative stimuli (Carter and Werner 1978). Sidman (1986) suggested that conditional stimuli control responding indirectly via the significance they impart on other stimuli, while Cumming and Berryman (1965) proposed that a conditional cue functions as a "selector of discriminations", and provides "instructional control".

Zentall, Hogan and Edwards (1984) defined a conditional discrimination as follows: "In the presence of one or two (or more) conditional (or sample) stimuli an organism is given a choice between two (or more) choice or comparison stimuli. In the presence of one sample, one of the comparison stimuli is correct (i.e., reinforced); in the presence of

the other sample, the other comparison stimulus is correct” (p. 390). Thus, conditional discrimination embodies “if-then” conditional reasoning – if this happens then do that. For example, the subject should choose the discriminative stimulus B1 when presented with the conditional stimulus A1; and choose B2 when presented with A2 (Hanggi and Schusterman 1995).

However, while many authors continue to define a conditional relationship in terms of a hierarchical ordering of stimuli involving a superordinate (conditional) cue modulating the significance of a subordinate (discriminative) cue (e.g. Sidman 1986; Cumming and Berryman 1965), others believe there is no way to unequivocally assign uniquely conditional or discriminative status to stimuli in conditional discrimination tasks, especially when the stimuli are simultaneously presented (e.g. Thomas, Cook and Terrones 1990; Thomas and Schmidt 1989). Whether or not a hierarchical relationship exists, both sides agree that it is combinations of stimuli, rather than single stimulus elements, which signal reinforcement contingencies in conditional discrimination experiments, with the value of one cue modulating responding to a cue with which it is paired (Thomas et al. 1990).

The results of numerous studies suggest that a conditional discrimination is more difficult than a basic discrimination. In a large majority of studies using standard T-mazes, discrimination boxes or jumping stands where the discriminative stimuli are located on the goal boxes, goal arms or doors, it was found that a simultaneous discrimination is typically learned much faster than a successive conditional discrimination using the same stimuli (Mackintosh 1974). Although, as Deacon, Bannerman and Rawlins (2001) point out, this may be at least partly explained by the fact that not all the information needed to solve the conditional discrimination is simultaneously present in one trial. (See also the debate about simultaneous versus successive presentation of stimuli in section 3.7.2.1.5).

3.2.2 Conditional discrimination training

3.2.2.1 Methods

Like basic discrimination, conditional discrimination is generally trained using standard operant procedures using apparatus such as T-mazes, discrimination boxes or jumping stands where the discriminative stimuli are located on the goal boxes, goal arms or doors. Conditional discrimination can also be tested using either simultaneous or successive presentation of stimuli. (While outside the scope of this study, it is worth noting that conditional discrimination need not be studied using instrumental conditioning methods – e.g. Asratyan 1961; Looney, Cohen, Brady and Cohen 1977; Saavedra 1975) (Carter and Werner 1978). The conditional discrimination procedure can also be used to test other cognitive abilities such as transitive inference (if A is bigger than B and B is bigger than C, is A bigger than C?) (e.g. Higa and Staddon 1993; Treichler and Van Tilburg 1996).

3.2.2.1.1 Compound stimulus

In this form of conditional discrimination, one particular combination of stimuli is reinforced while all other combinations (including any that include only one of the stimuli present in the reinforced compound) are not reinforced.

3.2.2.1.2 Symbolic matching

One common variant of the conditional discrimination procedure involves symbolic matching, in which the subjects are taught to match stimuli that have been arbitrarily paired. A sample stimulus is shown, followed by the presentation of (or shown simultaneously with) two or more response alternatives. The subject must choose the response that goes with the sample – that is, the stimulus that has previously been paired with the sample through reinforcement.

3.2.2.1.3 Matching/non-matching-to-sample

In the matching-to-sample experimental paradigm, the subject must select from among a number of discriminative stimuli one that matches a sample stimulus. Alternatively, in the non-matching-to-sample paradigm, the discriminative stimulus that does not match the sample must be selected. These methods of conditional discrimination testing can be conducted using simultaneous or successive presentation of stimuli (delayed matching-to-sample) (see section 3.7.2.1 for fuller discussion). Matching and non-matching are viewed as conditional discriminations because the reinforcement contingencies change from trial to trial (Grant and Kelly 2001) and they can be solved using “if ... then” reasoning (i.e. if the sample stimulus is red, choose the red discriminative stimulus). However, there is ongoing debate as to whether matching/non-matching can also be used to demonstrate relational learning in terms of responding to stimuli on the basis of whether they are the *same* or *different* (see discussion in section 3.7.6.1).

3.2.2.1.4 Combined stimulus

In this method of testing conditional discrimination, which can be described as a combined stimulus method, the conditional and discriminative cues are combined in the same stimulus. There are a number of ways in which this method may be used.

One method, which has been called the ‘two-choice visual’ conditional discrimination (Schrier and Thompson 1980), uses visual stimulus panels that contain both background and foreground cues which operate independently as the conditional and discriminative stimuli.

Another way in which stimuli can be combined in conditional discrimination experiments involves using two different modalities (e.g. visual and spatial; visual and auditory). For example, in a ‘two-choice spatial’ conditional discrimination conducted in a T-maze, choosing the left maze arm is reinforced on presentation of one colour and choosing the right maze arm is reinforced on presentation of another colour (Schrier and Thompson 1980).

3.2.2.2 Stimuli

Conditional discrimination can be tested using fairly basic stimuli. For example, using the ‘two-choice spatial’ example cited above, a simple black/white T-maze conditional discrimination could involve successive trials where the T-maze arms or doors are either both black or both white on successive trials. When both sides are black a response to one side is reinforced, when both are white a response to the other side is reinforced (Mackintosh 1974). However, a conditional discrimination provision can also be added to a more complex experiment. For example, Burdyn and Thomas (1984) trained squirrel monkeys to select a pair of objects that manifested *sameness* when presented with a triangle and to select a pair of objects that manifested *difference* when presented with a heptagon (see section 3.7.4).

Like most discrimination experiments, the stimuli are usually visual; however stimuli from other modalities such as auditory (Zuckerman and Blough 1974), tactile (Thomas, Stengel, Sherman and Woodford 1987) and spatial location (Renouf and Gaborko 1988) have also been used. Different modalities have also been combined in conditional discrimination experiments (e.g. visual and spatial, Schrier and Thompson 1980, and auditory, visual and tactile, Honey and Ward-Robinson 2001).

3.2.3 Conditional discrimination experiments

There is an anecdotal report of conditional discrimination experiments dating back as far as 1799 and American and Russian investigators utilised the paradigm to study ‘conceptual’ behaviour in non-human primates during the 1920s and 30s (Carter and Werner 1978). However, one of the first published scientific papers to define both the importance of identifying the physical properties of the controlling stimuli and the extent to which that control could be transferred to novel stimuli was conducted by Lashley (1938b). In this classic series of experiments Lashley established conditional reactions in rats using a ‘two-choice visual’ combined stimulus method. Each trial consisted of the presentation of two stimulus boards. The discriminative stimuli (an upright and inverted white equilateral triangle) appeared on every trial, while the background was changed to function as a conditional cue. When the background was black, jumping towards the upright triangle was reinforced, when the background

consisted of horizontal stripes, the inverted triangle was reinforced. Despite Lashley's (1938b) success, he was unable to demonstrate a "generalised reaction" in accordance with the single-rule model, in which a stimulus which is correct in the presence of sign A is incorrect in the presence of sign B (see section 3.2.4.5) (Carter and Werner 1978).

According to Carter and Werner (1978), Lashley's failure to establish a single-rule, generalised conditional discrimination reaction using a combined stimulus method was partly responsible for the rise in popularity of the matching/non-matching methods. Two of the early pioneers of matching are Cumming and Berryman, who, together with their students, designed some of the matching procedures now commonly used with pigeons and other animals. In one of their early experiments (Cumming and Berryman 1961), pigeons were trained on simultaneous matching-to-sample using basic visual stimuli consisting of three hues – red, green and blue (e.g. if red, pick red). The birds exhibited a strong initial position bias and performance was poor for the first three or four sessions. Within six to nine sessions, however, the subjects reached at least 90% accuracy, then slowly improved to near 100% performance (Carter and Werner 1978).

Further matching experiments have confirmed pigeons have little difficulty performing simple two-choice conditional discrimination tasks (Williams, Butler and Overmier 1990), although zero-delay matching-to-sample (in which the sample is removed when the comparison stimuli are presented) appears to be harder to learn than simultaneous matching (Carter and Werner 1978).

Experimenters have also demonstrated that many animals can also learn to perform symbolic matching in which the stimuli have been arbitrarily paired (see section 3.2.2.1.2). Pigeons can easily learn symbolic matching based on hue (e.g. if red, pick blue), although not as easily as matching-to-sample (Cumming and Berryman 1965). As with regular matching, symbolic matching seems to be more difficult to learn using a successive rather than a simultaneous procedure (Carter and Werner 1978). (For more examples of matching and oddity see section 3.7).

Despite the early popularity of the matching/oddity method of testing conditional discriminations, the combined stimulus method continued to be used. A series of experiments with rats conducted in the 1950s, for example, received considerable

attention using the ‘two-choice spatial’ combined stimulus method described in section 3.2.2.1.4 (see Schrier and Thompson 1980). More recently, the combined stimulus method has experienced renewed popularity (e.g. Boneau and Honig 1964; Richards 1979; Thomas, Curran and Russell 1988; Thomas and McKelvie 1982; Thomas, McKelvie and Mah 1985), particularly as an adjunct to testing relational categorisations such as relative volume (Thomas and Ingram 1979) and same/different (e.g. Burdyn and Thomas 1984; Flemming et al. 2007; this study; see section 3.7.4).

Combined stimulus conditional discrimination methods have also been used to test more complex conditional paradigms. Riopelle and Copelan (1954) successfully trained five rhesus monkeys to perform discriminations conditional on the colour of the tray on which two stimulus objects (which were changed after 12 or 14 trials) were presented. The monkeys were then able to generalise the conditional discrimination performance to other tray colour sequences, including conditional cues consisting of up to four colours. This ability to easily generalise the conditional discrimination performance to novel conditional cues demonstrates that the subject’s responses were not dependent on the specifics of the cue itself, but rather “response to a *change* in colour is critical” (Riopelle and Copelan 1954, p. 145). One of the most impressive conditional discrimination performances was demonstrated by a chimpanzee that was able to successfully master 16 inter-related, concurrently presented conditional discrimination problems – each demanding simultaneous responsiveness to five distinct cues (Nissen 1951).

Other animals that have demonstrated conditional discrimination learning include rhesus monkeys (Spaet and Harlow 1943; Warren 1964), squirrel monkeys (Barge and Thomas 1969; Burdyn and Thomas 1984; Thomas and Kerr 1976), capuchin monkeys (D’Amato, Salmon, Loukas and Tomie 1986), pigeons (D’Amato et al. 1986) and rats (Honey and Watt 1999). “Experiments using conditional discriminations have confirmed that animals such as some birds, primates, sea lions and dolphins are capable of making associations between sample and comparison stimuli” (Hanggi and Schusterman, 1995, p. 543).

Even goldfish have been shown to acquire a conditional discrimination using both the compound stimulus and matching/oddity methods. Zuckerman and Blough (1974)

demonstrated that goldfish responded more often to a reinforced compound stimulus made up of a particular combination of light and sound intensity than to combinations that were not reinforced, even when they included one of the stimuli present in the reinforced compound. Goldman and Shapiro (1979) found goldfish were also able to acquire a conditional discrimination in which the reinforced stimulus on each trial depended on the identity of a second stimulus that also differed from trial to trial (i.e. matching-to-sample and oddity-from-sample, see section 3.7). In addition, Zhang, Lehrer and Srinivasan (1999) used a successive choice task to demonstrate conditional discrimination in honeybees.

Despite the success of many species in conditional discrimination experiments, the task appears to be more difficult for some species to learn. Harbour seals, for example, have shown little ability to master either visual matching-to-sample (Constantine 1981; Renouf and Gaborko 1988) or visual symbolic matching tasks (Hanggi and Schusterman 1995). Similarly, while pigeons easily learn a simple two-choice conditional discrimination with a retention interval of a few seconds (e.g. Honig 1978), there is a profound deterioration of matching performance at longer retention intervals (e.g. Roberts and Grant 1976).

However, changes to experimental procedures can influence conditional discrimination performance. For example, pigeons appear to find some types of stimuli more discriminable than others, performing more accurately with hue samples (e.g. red and green hues) versus line samples (e.g. horizontal and vertical lines) (Carter and Eckerman 1975; Urcuioli and Zentall 1986; Zentall, Urcuioli, Jagielo and Jackson-Smith 1989). Carter and Eckerman (1975) concluded that the rate of matching to sample (or conditional discrimination) acquisition in pigeons was determined by the discriminability between samples and between comparisons, with sample discriminability having a more pronounced effect.

It has also been shown that animals learn conditional discriminations faster and more accurately when the reinforcers for each of the correct choices are either qualitatively or quantitatively different (Trapold 1970), a phenomenon known as the differential outcome effect (Peterson and Trapold 1980). In one such study, Brodigan and Peterson (1976) demonstrated that pigeons showed improved performance compared to a control

group when qualitatively different reinforcers (food or water) were correlated with each conditional cue – a result that became more pronounced as retention intervals were increased. Other authors such as DeLong and Wasserman (1981), Peterson, Wheeler and Trapold (1980), Santi (1989) and Santi and Roberts (1985a) have shown similar results with pigeons while the effect has also been demonstrated in other species such as horses (Miyashita, Nakajima and Imada 2000), rats (Trapold 1970) and human children (Maki, Overmier, Delos and Gutmann 1995).

Williams et al. (1990) further demonstrated that reliably correlating the spatial locations of reinforcers and response keys could also lead to enhanced performance in pigeons in a conditional discrimination task. Three groups of pigeons were taught to select the correct response key of two vertically arranged response keys when presented with one of two colours. The groups in which the location of the key was consistently correlated with the location of the feeding tray (either top-key to top-feeder/bottom-key to bottom-feeder or top-key to bottom-feeder/bottom-key to top-feeder) showed better performance than the group in which the locations of the response keys and feeding trays were randomly correlated, particularly over longer retention intervals. Other experiments have also demonstrated that utilising different response locations leads to improved performance in simultaneous, zero-delay and delayed matching tasks (Eckerman 1970; Zentall, Hogan, Howard and Moore 1978).

While stimulus discriminability, reinforcer type and the spatial location of reinforcers and response keys have been shown to improve conditional discrimination performance, it has been suggested that the effect is not caused by these factors themselves, but rather by the subject's behavioural responses to them. According to Urcuioli and Honig (1980): "When sample-specific responding is occasioned by sample stimuli in matching and oddity tasks with pigeons, such responding controls the choices between comparison stimuli" (p. 251). The authors have put forward several lines of evidence to support their hypothesis. Urcuioli and Honig (1980) introduced differential sample-response requirements into matching and oddity tasks using both easy to discriminate (hue) and difficult to discriminate (line) stimuli. The authors found the pigeons used sample-specific responding to control choice on the difficult to discriminate line stimuli but not the easy to discriminate hue stimuli and that the sample-specific behaviours effectively replaced the visual stimuli as the conditional cue. (Cohen, Looney, Brady

and Aucella, 1976, also found differential sample-response requirements led to greater facilitation of performance with line samples than with hue samples). Secondly, Urcuioli and Honig (1980) concluded that Brodigan and Peterson's (1976) differential reinforcer experiments described above probably demonstrate stimulus control by differential sample-response topographies due to the fact that the topography of a pigeon's key peck is affected by reinforcer type (food vs. water) (Jenkins and Moore 1973). Finally, Urcuioli and Honig (1980) point out that Eckerman (1970) has demonstrated that sample-response locations are sufficient to operate as conditional cues even when the samples that occasioned them are removed.

Another procedural factor that can affect conditional discrimination performance is whether the stimuli are presented simultaneously or successively. In a series of experiments using a blue or red keylight and a subsequently presented vertical or horizontal line, Thomas et al. (1990) directly compared simultaneous and successive presentation of stimuli. They found that pigeons were able to learn the successive conditional discrimination only after relatively intensive training. However, when the presentation of the colours overlapped the presentation of the lines (simultaneous presentation), they were able to learn the task fairly easily. According to the authors, the difference in the way animals appear to deal with simultaneous and successive conditional discriminations probably accounts for the differences in the difficulty of mastering the two tasks (see section 3.2.4.7). Even when conditional discrimination problems are presented simultaneously, factors such as the physical proximity of the stimuli can also affect performance (see the experiments of Thomas and colleagues in section 3.2.4.1).

In addition to overall performance, experimental design can also affect the strategies employed by subjects in conditional discrimination experiments. For example, numerous experiments (mainly with pigeons) have studied coding strategy in delayed successive conditional discriminations – essentially whether the subjects utilise retrospective coding (remembering the sample they saw at the beginning of the trial, e.g. Roberts and Grant 1976) or prospective coding (remembering which comparison stimulus to respond to after the retention interval, e.g. Santi and Roberts 1985b).

Studies have provided evidence supporting both coding theories. Blough (1996) examined a number of papers and claimed that: “Most of the evidence from these studies favours prospective coding ...” (p. 118). Honig and Wasserman (1981) also argued in favour of prospective coding based on their experiments showing that the rate of forgetting was greater for a conditional compared to a simple discrimination. (Retrospective coding based on the sample stage would be of equivalent difficulty for both types of discrimination, while prospective coding for the comparison stimulus stage involves a more complex response procedure for conditional discriminations, hence the greater rate of forgetting). However, Urcuioli and Zentall (1990) found the enhanced retention in the simple discrimination task obtained by Honig and Wasserman (1981) could be accounted for by mediation of retention by differential outcome expectancies (see above for discussion of the differential outcome effect). At the sample stage in the simple discrimination, one sample always meant food and the other always meant no food, whereas in the conditional discrimination that was not the case. When Urcuioli and Zentall (1990) and Grant and Kelly (2000) modified the simple discrimination procedure so all trials ended in reinforcement, they found no enhanced retention in the simple discrimination compared to the conditional discrimination, leading the authors to support the retrospective coding theory.

A third alternative to the coding dichotomy was suggested in experiments conducted by Zentall et al. (1989), which found that the discriminability of stimuli, as well as the number of stimuli in the sample and comparison sets, led the subjects to utilise both coding strategies – “birds may retrospectively code hue samples because they are particularly discriminable. With less discriminable line samples, they may prospectively code” (p. 176) (see also Jackson-Smith, Zentall and Steirn 1993). However, experiments using symmetrical reinforcement conducted by Grant and Kelly (2000) using both colour and line samples and multiple test stimuli found no difference between a simple and conditional discrimination task, leading the authors to conclude that, at least with visual stimuli, “pigeons encode and remember the initial stimulus (i.e. code retrospectively)” (p. 41).

While this section has discussed a number of procedural factors that can affect conditional discrimination performance in animals, the ability of an individual species to perform a particular task may also be related to ecological and behavioural factors.

For example, although harbour seals failed in visual conditional discriminations (see above), they were able to learn a spatial matching-to-sample task (Renouf and Gaborko 1988), suggesting spatially based cues may be more salient for this species (see Hanggi and Schusterman 1995 for fuller discussion). Similarly, visual cues have been shown to be more effective than auditory cues in conditional discrimination experiments with pigeons (Thomas et al. 1988; Thomas et al. 1985).

3.2.4 Conditional discrimination learning theory

3.2.4.1 The configuration model

This theory of conditional discrimination holds that rather than two levels of stimulus control operating independently, “all aspects of the stimulus situation or configuration that can be detected by the subject come to exert some control over the discriminative response” (Carter and Werner 1978, p. 566) – basically each problem is dealt with not as a combination of elements but rather as a unique configuration (Pearce 1987). For example, in a basic conditional discrimination, rather than there being two discriminative responses modulated by a second layer of two conditional cues, in fact four discriminations are learned based on the four combinations of discriminative and conditional cues (Carter and Werner 1978). This approach has found some support (e.g. Gullikson and Wolfle 1938). Thomas (1996) describes this phenomenon as rote learning, and has argued that most conditional discrimination studies are disqualified from having shown evidence of conditional reasoning because rote learning may have been used (see Burdyn and Thomas 1984).

According to Thomas and Kerr (1976), the large number of trials taken to master some complex conditional discriminations mentioned above (section 3.2.3) – 4320-6840 for Spaet and Harlow’s (1943) monkeys and 15,796 for Nissen’s (1951) chimpanzee – suggest that the primates learned the specific configurations rather than utilising a more generalised rule. Studies by Gollin and Liss (1962) and Barge and Thomas (1969) have also reported evidence suggesting specific configuration learning in conditional discrimination testing in children and squirrel monkeys respectively.

However, while the configuration model may account for some instances of conditional discrimination learning, it cannot be universally applied. If the configuration model holds, the results of matching and oddity experiments should show equal rates of acquisition for the same number of stimulus alternatives. However, experiments such as that conducted by Cumming and Berryman (1965) demonstrate this is not the case (Carter and Werner 1978).

In addition, evidence of transfer to novel stimuli would suggest that something other than configuration learning has been demonstrated. Lashley, for example, rejected the configuration model explanation for his conditional discrimination experiments with rats (Lashley 1938b, see section 3.2.3) after later finding instances of transfer to novel stimuli containing variations of the discriminative stimuli, of the conditional stimuli or both (Carter and Werner 1978). Similarly, the series of 'two-choice spatial' conditional discriminations conducted with rats in the 1950s (see section 3.2.3.) suggested the animals were using stimulus selection (e.g. if both black go left) rather than simply learning to approach two of the four stimulus compounds (e.g. black-left or white-right) based on the configuration of the entire set of discriminative stimuli (Schrier and Thompson 1980).

A universal configuration theory also seems inconsistent with the findings of Thomas and colleagues. Thomas, McKelvie, Ranney and Moye (1981) demonstrated pigeons could easily learn a conditional discrimination task based on wavelength discrimination modulated by the physical context in which the different wavelengths were learned (e.g. houselight on and tone present; houselight off and white noise present). However, Thomas et al. (1985) were unsuccessful in attempting to train pigeons in a conditional discrimination in which the stimuli of a vertical versus a horizontal line was conditional on the colour of the stimulus background (red or blue), despite using a similar procedure (see also Boneau and Honig 1964; Richards 1979 for examples of the difficulty pigeons have acquiring conditional discriminations when both the conditional and discriminative cues have been projected on the response key). Thomas and McKelvie (1982) did obtain conditional discrimination learning with line angle and background colour combinations, but had to use a more intensive training procedure.

While the stimuli in both the Thomas et al. (1981) and Thomas et al. (1985) experiments were simultaneously presented, Thomas and colleagues argue the configuration model predicts the physical proximity of the stimuli in the second experiment should more readily facilitate the formation of a perceptual unit or configuration and thus enhance performance (Thomas et al. 1990; Thomas et al. 1988). In fact the results suggest that, at least in some cases, stimulus configuring in the perceptual sense actually hinders learning a conditional discrimination. Furthermore, when the unsuccessful Thomas et al. (1985) experiment using line orientation and background colours was repeated using a simultaneous procedure designed to prevent configuring (the background colour preceded and then overlapped the presentation of the lines), the experiment was successful (Thomas et al. 1988).

3.2.4.2 The compound-cue model

Spence (1952) postulated that responding in a conditional discrimination experiment could be controlled by compounds or patterns of cues, such as the nominal discriminative cue and its spatial location. Also known as the unique-cue account, essentially the theory holds that there are configural elements that behave just like other elements, except that they are active not when a single element is present but when there is a particular conjunction of two or more stimuli (Wagner and Brandon 2001). So, each conjunction of stimuli (e.g. X and Y) activates representations unique to X and Y and also activates an additional cue unique to their conjunction (Honey and Ward-Robinson 2001). (See also Brandon, Vogel and Wagner 2000; Rescorla 1972; Saavedra 1975; Wagner and Rescorla 1972).

While the configuration model and the compound-cue model are sometimes confused, Schrier and Thompson (1980) argue that careful attention should be paid to the distinction between the two approaches as they “both have their applications in the area of conditional discrimination learning in addition to the multiple-rule and single-rule models” (p. 293).

3.2.4.3 The synthetic model

Honey and Ward-Robinson (2001) claim the results of their series of experiments with rats casts doubt on the adequacy of both the compound-cue model and the configuration model. For example, Honey and Watt (1999) trained rats in a conditional discrimination where in one pair of contexts (A and B), two relationships were in force ($X = \text{food}$, $Y = \text{no food}$) and in another pair of contexts (C and D) the opposite relationships were in force ($X = \text{no food}$, $Y = \text{food}$), where X and Y were auditory stimuli. After they had acquired this discrimination, the rats were given an aversive conditioning procedure in which presentations of Context A were paired with a shock and those of Context C were not. Subsequently, the rats showed a greater fear response in Context B than in Context D – a generalisation between the contexts that had been associated with the same food/no-food outcome. According to Honey and Ward-Robinson (2001), this result cannot be explained by either the configuration or compound-cue models, which are both activated by specific conjunctions of stimuli. In the Honey and Watt (1999) experiment, Contexts A and B were not combined with one another at any point during the study.

Honey and Watt (1998) developed a theory to explain this type of result, which they described as a synthetic account. According to this model, stimuli that have been presented on different trials (e.g. Contexts A and B) that have the same outcome (e.g. $X = \text{food}$) can come to be associated with one another via the same ‘hidden unit’ which is associated with a representation of the outcome of the trial. Experiments by the authors (e.g. Honey and Ward-Robinson 2001; Honey and Watt 1998, 1999; Ward-Robinson and Honey 2000) show support for the synthetic account by demonstrating that rats show transfer between one contextual conditional discrimination and another when the contexts are linked to the same associative relationships. The theory is also consistent with the pattern of results found with different species, stimuli and procedures (e.g. Delamater and Joseph 2000; Urcuioli, Zentall and DeMarse 1995; Zentall, Steirn, Sherburne and Urcuioli 1991). (See Honey 2000 for a full treatment of this account).

3.2.4.4 The multiple-rule model

The multiple rule model involves learning about stimulus-specific relations and assumes the subject has learned a set of 'if ... then' rules based on the stimuli with which it has been trained. In this case, the introduction of novel stimuli should disrupt an established conditional discrimination performance. There are two variations of the rule – one based on selecting the correct choice and one based on avoiding the incorrect choice – which may be distinguished by the extent to which novel choices, rather than novel cues, disrupt performance (Carter and Werner 1978).

In order to make predictions about how subjects would respond to novel stimuli, several investigators have added an assumption to the multiple-rule model known as the coding hypothesis. Many forms of the coding hypothesis have been proposed, however the most influential in conditional discrimination studies involves an intervening event between the stimulus itself and the subject's response. According to this version of the hypothesis, stimulus-response correlations are mediated by another response that is usually not observed. The subject then reports not directly to some aspect of the stimulus, but instead on the occurrence of the (often covert) response made directly to the stimulus. Thus the reporting response (R_2) is conditional on the occurrence of the coding response (R_1) (Carter and Werner 1978).

Since the coding response is usually unobserved, its existence must be inferred from behavioural data. Several lines of such evidence have been put forward to support the coding response theory. Firstly, experiments have shown the importance of requiring a response to sample as part of the experimental procedure (e.g. Eckerman, Lanson and Cumming 1968; Maki, Gillund, Hauge and Siders 1977; Zentall, Hogan and Holder 1974) as well as demonstrating that different observing responses are made in the presence of different sample stimuli (Berryman, Cumming and Nevin 1963; Blough 1959), particularly when the different samples are paired with different reinforcers (Brodigan and Peterson 1976). Secondly, studies concerned with transfer to novel stimuli have shown subjects transferring an already-learned coding response from a familiar stimulus onto a novel stimulus (Cumming, Berryman and Cohen 1965). Because of the difficulty of observing a coding response, some investigators have tried to exert experimental control over their subject's coding response by requiring

experimenter-directed sample-specific responses to stimuli. These experiments have shown that requiring sample-specific behaviour facilitates conditional discrimination learning (Cohen et al. 1976; Eckerman 1970; Lydersen and Perkins 1974; Perkins, Lydersen and Beaman 1973; Urcuioli and Honig 1980). However, in common with other coding response experiments, these studies “demonstrate the usefulness of coding responses, but they fail to demonstrate that conditional discriminations must be mediated by coding responses” (Carter and Werner 1978, p. 577) (Carter and Werner 1978).

3.2.4.5 The single-rule model

The single-rule model can be described as a ‘generalised reaction’ based on a single rule: “Any stimulus which is correct in the presence of conditional cue A is incorrect in the presence of conditional cue B”. The most important feature of this model is the condition that the subject will continue to respond correctly in a new situation as long as each new discrimination fits the rule. Provided the subject continues to choose the correct stimulus in accordance with previous training despite the use of novel stimuli, performances using either the matching/non-matching method or a combined stimulus method may be viewed as behaviour governed by a single rule (Carter and Werner 1978).

According to Schrier and Thompson (1980, p. 293), single-rule learning involves “the learning of an abstract rule or concept that enables an animal to solve a new conditional discrimination problem more quickly than it did the original problem”. In order to conclude single-rule learning has taken place, the authors required that the superior novel-trial performance must not be due to stimulus generalisation or be due to non-specific transfer based on additional testing (i.e. adaptation to testing); a phenomenon which has arisen in testing for ‘concept’ learning in monkeys (Schrier and Thompson 1980).

Nissen (1953) proposed two potential solutions to conditional discrimination problems: “As long as problem-solution involves a fixed and invariable number of stimuli, the possibility of response to specific stimulus-combinations or patterns remains. Only when this possibility has been ruled out will there be a compelling need for the concept

of the conditional stimulus as a predisposing set” (p. 281). According to Thomas and Kerr (1976), if the opportunity for the first solution was available, then a conceptual interpretation could not be conclusively suggested. Eliminating the potential for specific configuration learning would require successful performance on the first (or only) trial of a specific conditional discrimination.

When Thomas and Kerr (1976) tested squirrel monkeys on a conditional discrimination task using single-trial oddity problems, the monkeys were able to achieve criterion performance of 90%. Similarly, Riopelle and Copelan (1954) reported perfect performance on the first trial transfer tests in their tray-colour conditional discrimination described above. According to Thomas and Kerr (1976), both these studies justify a conceptual interpretation: “Since there is no opportunity to learn specific stimuli or stimulus patterns, successful performance may be interpreted as having a conceptual basis” (p. 333).

Whether demonstration of ‘single-rule’ learning is evidence a subject is utilising an ‘abstract rule’ or even a ‘concept’ (Carter and Werner 1978; Schrier and Thompson 1980) is discussed further in sections 3.6 to 3.8.

3.2.4.6 Conjunctive reasoning

Thomas (1996) proposes that some experiments purporting to show conditional discrimination may in fact be demonstrating conjunctive reasoning. Using the experiment cited in section 3.2.2.2 (Burdyn and Thomas 1984), of which Thomas was one of the authors, he describes how either conditional or conjunctive reasoning could have been used to accomplish the task. Using conditional reasoning the rules of the task would be “*if* a triangle is presented, *then* choose the sameness pair” and “*if* a heptagon is presented, *then* choose the difference pair”. Using conjunctive reasoning the rules would be “a triangle *and* a sameness pair go together so choose the sameness pair when you see a triangle” and “a heptagon *and* a difference pair go together so choose the difference pair when you see a heptagon”. While studies with humans have confirmed the use of conditional reasoning (Bourne 1970), Thomas admits it would be problematic to design an experiment which would isolate which form of reasoning was being used in non-human animals.

3.2.4.7 Multiple strategies

As Schrier and Thompson (1980, p. 293) point out (in relation to the difference between the configuration and the compound-cue model), it is “probably not a question of this or that model being correct, but of one model being appropriate under some circumstances and another under other circumstances”.

For example, as mentioned in section 3.2.1, a number of theorists contend that there is a fundamental difference in the way successive and simultaneously presented conditional discriminations are solved. Thomas et al. (1990) claim that simultaneously presented stimuli are not necessarily dealt with in a hierarchical manner, in which one stimulus serves as a conditional cue indicating the correct selection of a discriminative cue. Rather, that the subjects learn “what goes with what”. Thomas and Schmidt (1989) conducted a generalisation test with pigeons that showed that if either of the S+ elements in a simultaneous conditional discrimination was held constant while the other was varied along a dimension, the subjects would respond maximally to the appropriate value of the varied dimension. According to the authors, this indicated that the pigeons knew what values of the two cues went together, rather than utilising a unidirectional instructional relationship between the cues.

In the case of successively presented stimuli, however, Thomas et al. (1990) believe the task does involve sequential order, and thus a hierarchical structure. They base this theory on experiments showing that when primates and pigeons are tested on a previously learned matching-to-sample task in which the order of stimulus presentation has been reversed, they are largely unsuccessful (e.g. D’Amato, Salmon, Loukas and Tomie 1985; Sidman et al. 1982).

In a series of experiments Holland (1983; 1986a; 1986b; 1989) found the temporal arrangement of stimulus presentation affects the way rats solve feature positive conditional discriminations (in which a compound stimulus (XA) is reinforced, but one of its elements (A) is separately nonreinforced). When X and A are presented simultaneously, X acquires the ability to evoke a conditioned response based on its association with the unconditioned stimulus, while A has little or no effect on responding. However, when X is presented before A in a successive procedure, X

comes to modulate the association between A and the unconditional stimulus – effectively X “sets the occasion” for responding to A. According to Holland (1989), the subjects in his experiments clearly used different strategies in solving the successive and simultaneous conditional discriminations – an “occasion-setting” (i.e. hierarchical) strategy for successive discriminations and an “associative” (i.e. configural) strategy for simultaneous procedures.

3.3 CATEGORISATION

3.3.1 Definition

While a simple discrimination involves a single stimulus signalling a reward, categorisation is a more complex discrimination in which the reward is signalled by a variety of stimuli that share some common characteristic (Pearce 1994a). Categorisation can be defined as the ability to treat stimuli that are similar (but not identical) as equivalent – by sorting them into categories and reacting to them in the same manner (Harnad 1987; Huber 2001; Medin and Smith 1984).

Considering the vast amount of sensory information organisms receive, categorisation could be seen as an effective response to evolutionary pressures to minimise processing requirements (Cook, Wright and Kendrick 1990; Delius, Jitsumori and Siemann 2000; Huber 2001). Categorisation allows an animal to identify novel stimuli as members of a particular class and generalise information about that class to the new members. This enables an animal to respond appropriately to a wide variety of stimuli without having to be conditioned to each and every example. This has obvious adaptive advantages as it reduces the demands on an animal’s sensory and information-processing systems, freeing them to deal with other competing exigencies of survival (Herrnstein 1984; Wasserman 1993b).

According to Wasserman (1993b), categorisation means “an organism need not be bound to respond to only those stimuli with which it has had prior experience, correspondingly enhancing its ability to cope with a continually changing world” (p. 216). Similarly, Hanggi (1999) states that: “Grouping objects or events enables an organism to respond efficiently and appropriately to stimuli” (p. 244). The utility of

categorisation led Huber (1995, p. 135) to observe: “The critical adaptiveness of generic categorisation makes us not wonder about its wide dispersion among vertebrate species.”

3.3.2 *Types of categorisation*

For the purposes of this study discussions of categorisation experiments and theory have been organised into three sections based on Zentall, Galizio and Critchfield’s (2002) nomenclature of the main types of categorisation – perceptual categorisation, associative categorisation and relational categorisation.

Because of the large number of experiments that have been conducted in this field it is neither practical nor advisable to try and list them all. Instead this review attempts to provide an overview of categorisation experimentation while still conveying an understanding of the broad spectrum of both species and stimuli that have been used in testing.

Many of the experiments listed in this section are referred to by their authors as studies of ‘concepts’, ‘concept learning’, ‘conceptualisation’ etc. However, due to the continuing debate over what constitutes conceptualisation, it was decided to take a more conservative approach and label these studies as they would be fairly universally accepted – as examples of categorisation. Whether any or all of them are also examples of concept learning will be discussed in section 3.8.

3.4 PERCEPTUAL CATEGORISATION

The first type of categorisation in Zentall et al.’s (2002) list is perceptual categorisation. As the echidna had previously demonstrated basic discrimination (see section 2.2.2.4) but had never been tested on categorisation, perceptual categorisation seemed the next logical ability to test. However, as the intent of this study was to test its subject with a task generally perceived as ‘complex’ or ‘difficult’, it first needed to be established whether perceptual categorisation met that criteria. A brief summary of this review has been included, both to demonstrate why perceptual categorisation was considered unsuitable for this study and also because perceptual categorisation forms both the

historical and theoretical background to more complex forms of categorisation (for reviews see Harnad 1987; Herrnstein 1984; Huber 1995; Pearce 1994a; Thompson 1995; Watanabe, Lea and Dittrich 1993).

3.4.1 Definition and perceptual categorisation in nature

This type of categorisation, also referred to as open-ended categorisation, relies on some principle of “perceptual similarity” (Herrnstein 1990, p. 136) between items that belong to a given class. While this similarity principle may be acquired with a given set of exemplars, unlike categorisation by rote it should also generalise to novel examples of the same kind (Herrnstein 1990; Zayan and Vaclair 1998).

The stimuli in these experiments generally have two properties. Firstly, all the positive stimuli would be labelled by a human, and are labelled by the experimenter, with a single name (e.g. person, pigeon, oak leaf etc.). Secondly, while they are based on perceptual similarity, there is no obvious single perceptual property shared by all the positive and/or negative stimuli (Lea 1984b).

Numerous observational studies have confirmed that animals demonstrate categorisation in the course of their normal activities. One of the most well known examples of categorisation in the wild is that of predator-specific alarm calls. Vervet monkeys studied in their natural habitat in Kenya categorised different aerial and ground predators by giving different alarm calls and responding appropriately to them (running into the trees for leopard alarms, looking up for eagle alarms and looking down for snake alarms) (Seyfarth, Cheney and Marler 1980a, 1980b). The authors claim that by giving alarm calls to some species and not others, and giving distinct calls to different predators, the monkeys were creating broad categories of ‘predator’ and ‘non-predator’ and further categorising different types of predator. Predator-specific alarm calls have also been demonstrated in other species such as chimpanzees (Goodall 1986), ground squirrels (Owings and Leger 1980), prairie dogs (Ackers and Slobodchikoff 1999; Slobodchikoff, Kiriazis, Fischer and Creef 1991) and chickens (Evans, Evans and Marler 1993).

Observations of naturally occurring categorisation in animals are not limited to identifying predators. Animals also use categorisation in other important areas of their lives, such as social interaction and finding food. Guinea baboons, for example, have been found to use visual categorisation to identify conspecifics (Zayan and Vauclair 1998) and a number of bird species (black-capped chickadees, bluejays and pigeons) have demonstrated the ability to categorise leaves based on whether they have been damaged by caterpillars (Cerella 1979; Heinrich and Collins 1983; Real, Iannazzi, Kamil and Heinrich 1984) (Shettleworth 1998).

3.4.2 Perceptual categorisation training

3.4.2.1 Methods

As with discrimination learning, comparative psychologists have devised numerous laboratory experiments to better understand both the scope and mechanics of nonhuman categorisation. The subjects are trained using operant procedures similar to those used in simple discrimination experiments (see section 3.1.2) to respond differentially to the stimuli according to an experimenter-defined category (e.g. ‘person’, ‘non-person’).

3.4.2.1.1 Operant procedures

Successive presentation – go/no-go

One procedure used to test category learning is the go/no-go procedure (also used in discrimination studies) where stimuli are presented successively and the subject is rewarded for responding in some way (e.g. pressing a lever, pecking a key) in the presence of one category (S+) and not responding in the presence of the other (S-) (see review in Herrnstein 1984).

Simultaneous presentation

In simultaneous presentation, the stimuli are presented at the same time and the subject is rewarded for selecting the stimulus that is a member of one experimenter-defined

category (S+) and not the stimulus that is a member of another experimenter-defined category (S-).

Match-to-sample

A third commonly used testing procedure is match-to-sample. This can be conducted using either successively or simultaneously presented stimuli (see section 3.7.2.1 for fuller discussion). In the successive presentation (called delayed matching-to-sample), the S+ stimulus is first presented alone, then removed. After a designated delay period, two or more stimuli are presented – an S+ stimulus and one or more S- stimuli – and the subject is rewarded for selecting the S+ stimulus. In the simultaneous presentation, the subject is able to view the sample and comparison stimuli at the same time. If the sample and comparison S+ stimuli are identical, rather than just being members of the same category, the match-to-sample procedure can also be used to test the subject's ability to perform a same/different categorisation task (see section 3.7.2.1).

3.4.2.1.2 Evidence for successful performance

Transfer to novel stimuli

Once the subject of a perceptual categorisation experiment has been trained to select the correct (S+) stimuli and its performance has reached a pre-selected criterion level, proof is required that they have not merely memorized the training stimuli. In most cases, the behavioural evidence that the subjects perceive, or have successfully learned, the categorisation task being studied is their ability to transfer their performance spontaneously to novel exemplars of both the S+ and S- stimuli. According to Ohl, Scheich and Freeman (2001, p. 733): “Transfer to novel stimuli is considered to be the most decisive behavioural index for category learning.” (See also Lea 1984b).

Analyses of error patterns

In some studies, analyses of error patterns rather than correct responses to novel stimuli are used to determine the nature and boundaries of the subjects' categorisation performance (Thompson 1995). For example, an animal that responds to novel pictures

containing people, but not those containing monkeys or other mammals, could be considered to have successfully learned the category ‘people’. Another animal that responds to novel pictures containing people and monkeys, but not to those containing other mammals may have learned the category ‘primate’ rather than ‘person’ (Schrier and Brady 1987).

3.4.2.2 Stimuli

The stimuli used are usually visual, ranging in complexity from simple line drawings (Cerella 1980; Huber and Lenz 1993) to colour photographs (Herrnstein and Loveland 1964; Lumsden 1977) to three-dimensional objects (Cabe 1976; Delius 1992; Watanabe 1993) and even motion (Herbranson, Fremouw and Shimp 2002), however perceptual categorisation experiments have also been conducted using other modalities such as sound (Porter and Neuringer 1984; Sturdy, Phillmore, Price and Weisman 1999; Weisman, Njegovan and Ito 1994; Wetzel, Wagner, Ohl and Scheich 1998).

Perceptual categorisation experiments are often separated into two groups based on the type of stimuli used – natural categories such as people or trees and artificial categories such as letters or numbers. That delineation has been followed here with a caveat – just what makes a natural category ‘natural’ is by no means certain. Intuition or common sense is usually invoked to determine the naturalness of a category, for example, trees are natural, letters and numbers are artificial. While applying a more scientifically based definition has proved problematic (Herrnstein 1984), this study has used the generally accepted delineations. It is important to note, however, that assuming that stimuli depicting ‘natural’ objects or scenes are more ecologically valid than artificial stimuli on the basis that animals perceive them as representing real objects or places is considered ill-founded by a number of authors (Fetterman 1996; Shettleworth 1998) (see also section 3.8.3.1.3).

3.4.3 *Perceptual categorisation experiments*

Herrnstein and Loveland’s 1964 study is generally considered the pioneering work in this field as it was one of the first studies in which the stimulus properties were not easily specified by physical measurements (Malott and Siddall 1972; Huber 2001).

Most studies begin their review of this literature with Herrnstein and Loveland's study, and that convention will be followed here. However it is worth noting that perceptual categorisation in animals, using more easily defined stimulus properties such as size, shape or colour, was being tested prior to that study. The categories used in these experiments included size (Kluever 1933), colour (Weinstein 1945), triangularity (Andrew and Harlow 1948), numbers (Hicks 1956), novelty (Brown, Overall and Blodgett 1959; Brown, Overall and Gentry 1958), patterns (Kelleher 1958) and even guided missile targets (Skinner 1960) (see Malott and Siddall 1972).

Regardless of where one starts, however, a review of the literature soon demonstrates that perceptual categorisation is extremely common among a wide variety of species. Indeed, Herrnstein (1990, p. 138) asserts categorisation has "turned up at every level of the animal kingdom where it has been competently sought".

3.4.3.1 Pigeon studies

Pigeons have been the most common subject of categorisation experiments due to their convenience as laboratory animals, acute perceptual capacity and lack of language competencies (Huber 2001; Lea 1984b; Mackintosh 1995; Wasserman 1991), as well as the fact that their basic behaviour and nervous system has been studied in great detail (Zeigler and Bischof 1993). Because of the pigeon's ubiquity as a test subject, and the fact that the pioneering experiments in the field of non-human perceptual categorisation were conducted using pigeons, they have been dealt with separately.

Natural categories

The seminal work in this field was conducted by Herrnstein and Loveland (1964), in which they demonstrated that pigeons were able to discriminate slides containing people from those that did not. The pigeons were trained by being rewarded with food when they pecked in response to slides containing people. The subjects were able to quickly learn the task and were easily able to transfer the performance to novel slides.

The groundbreaking aspect of this experiment was that, unlike the earlier categorisation experiments mentioned in section 3.4.3, the positive and negative instances varied in a

large number of visual dimensions. As Huber (2001) points out, even the positive 'person-present' stimuli varied in number (from a single person to groups), appearance (clothed, semi-nude, nude; adults and children; men and women; sitting, standing, lying; different races), lighting and colouration etc. It was also determined that there was no difference in average brightness between the positive and negative slides that might provide an alternate explanation for the pigeons' performance (Lea 1984b). According to Herrnstein and Loveland (1964), the 'person-present' slides constituted "a class of visual stimuli so diverse that it precludes simple characterisation" (p. 549).

However, Herrnstein and Loveland's (1964) experiment drew criticism for a number of reasons. It did not show the course of the criterion acquisition, as the data was restricted to two selected sessions after discrimination performance had been stabilised. In addition, the experiment used rates of pecking at stimuli to determine response rather than discretely different behaviours. While Herrnstein (1990) has since claimed measures based on the rate of responding in the presence of a stimulus in go/no-go procedures have been shown to provide "sensitive and stable estimates of the subject's categorisation" (p. 140), other authors such as Siegel and Honig (1970) thought such procedures left the results open to interpretive error.

These issues were addressed, and the results of Herrnstein and Loveland's (1964) experiment confirmed, by Siegel and Honig (1970) who again demonstrated that pigeons could discriminate between person-present and person-absent in a complex visual display. They also found their subjects could generalise the discrimination to novel examples even when reinforcement was omitted and when displays were inverted 180°, and transfer the discrimination from a successive to a simultaneous presentation condition.

The 'people' experiment has been extended even further in one study using subclasses of humans – human faces, human torsos and groups of humans – as the correct response (Malott and Siddall 1972) and in another in which pigeons showed they could learn to categorise pictures of a particular person not just of people in general (Jitsumori and Yoshihara 1997; Troje, Huber, Loidolt, Aust and Fieder 1999).

Pigeons have also demonstrated the ability to categorise stimuli based on whether or not they contained pictures of pigeons. In a study by Poole and Lander (1971), pigeons were able to discriminate between photographs containing pigeons and those containing other birds or objects. Following training, tests revealed almost complete transfer to new displays of pigeons and significantly less to other species of birds. The results showed more rapid acquisition and higher level of discrimination than that for human beings and approximated those for simple colour and form discriminations. This is likely due to the salience of the stimuli and their relative simplicity. The significant responses to pigeons compared to other birds show the discrimination was more specific than just 'birds'. The fact that the subjects were also able to transfer to new displays containing unusual looking pigeons suggests the discrimination was not based solely on physical similarity (Poole and Lander 1971).

Experiments have also demonstrated that after training pigeons can categorise on the basis of numerous natural categories, including food (Watanabe 1991; 1993), man-made objects (Lubow 1974), trees (Herrnstein, Loveland and Cable 1976; Herrnstein 1979; Vaughan and Herrnstein 1987), bodies of water (Herrnstein et al. 1976), oak leaves (Cerella 1979), fish (Herrnstein and de Villiers 1980); pigeons (Herrnstein 1990; Watanabe and Ito 1991; Watanabe 1992); spherical/non-spherical objects (Delius 1992); people, cars, cats, flowers and chairs (Bhatt, Wasserman, Reynolds and Knauss 1988), birds and other animals (Roberts and Mazmanian 1988); geographic location (Honig and Stewart 1988; Wilkie, Willson and Kardal 1989) and even bad parts on an assembly-line inspection, such as defective pharmaceutical capsules or diodes (Cumming 1966; Verhave 1966).

Although most laboratory experiments use static stimuli, a number of studies have also demonstrated the ability of pigeons to categorise on the basis of motion. It has been postulated that, due to the role of motion discrimination in such vital tasks as knowing whether a predator is approaching or a prey escaping, that motion perception may have evolved before other visual processes such as colour perception or visual acuity (Husband and Shimizu 2001; Sekuler 1975; Walls 1942). In addition, it would be expected that the flight characteristics of birds would lead them to evolve complex motion perception and precise abilities to process dynamic visual stimuli (Herbranson et al. 2002; Zentall et al. 2002). A study by Herbranson et al. (2002) showed that pigeons

can accurately categorise the dynamic properties of a moving target in terms of its speed and direction and Dittrich and Lea (1993) and Dittrich, Lea, Barrett and Gurr (1998) demonstrated that pigeons are able to form abstract categories of naturalistic movement patterns such as walking or flying.

Artificial categories

While it seems reasonable to assume pigeons would gain a fitness advantage in being able to categorise on the basis of natural stimuli such as ‘trees’ and ‘pigeons’, they have also proved adept at categorising on the basis of fairly abstract artificial categories. These range from the perceptually simple category of ‘triangle’ (Watanabe 1991) to more complex categories such as cartoon characters (Cerella 1980), schematic faces (Huber and Lenz 1993, 1996), squiggles (Vaughan and Greene 1984), dot patterns (Watanabe 1988), letters of the alphabet (Lea and Ryan 1983, 1990; Morgan, Fitch, Holman and Lea 1976) and even the paintings of Monet and Picasso (Watanabe, Sakamoto and Wakita 1995).

While most categorisation studies are conducted using visual stimuli, pigeons have also displayed the ability to categorise on the basis of artificial auditory stimuli. In one such experiment, pigeons were able to correctly categorise excerpts of two pieces of music – Bach’s Toccatas and Fugues for organ and Stravinsky’s Rite of Spring. When other pieces of music were introduced during the testing phase, the pigeons tended to place modern music into the ‘Stravinsky’ category and baroque music into the ‘Bach’ category (Porter and Neuringer 1984).

3.4.3.2 Other animal studies

In addition to pigeons, a number of other avian species have also demonstrated perceptual categorisation. For example, categorisation has been shown using auditory stimuli, including budgerigars with contact calls (Trillmich 1976a; 1976b), chickens with flock members (Ryan 1982; Ryan and Lea 1990), swamp sparrows with birdsongs (Nelson and Marler 1989), zebra finches with song-note type (Sturdy et al. 1999), Japanese quails with human speech phenomes (Kluender, Diehl and Killeen 1987), Java sparrows with human language (English versus Chinese) (Watanabe, Yamamoto and

Uozumi 2006), European starlings with rising and falling tones (Hulse, Cynx and Humpal 1984) and black-capped chickadees with chickadee call-note types (Sturdy, Phillmore and Weisman 2000). Like pigeons (see section 3.4.3.1.1), Java sparrows can also categorise on the basis of musical styles – in this case classical versus modern. Not only could they discriminate Bach (classical) from Schoenberg (modern) and transfer the discrimination to novel pieces by the same composer, they also demonstrated transfer of the discrimination to composers in the same style (i.e. Vivaldi, classical, and Eliot Carter, modern) (Watanabe and Sato 1999).

Other avian species have also demonstrated the ability to form categories based on visual stimuli, such as blue jays with moths (Pietrewicz and Kamil 1977) and leaf damage caused by caterpillars (Real et al. 1984) and Bengalese finches with conspecifics (Watanabe, Yamasita and Wakita 1993).

A different approach to perceptual categorisation in birds has been demonstrated by an African Grey parrot called Alex. The parrot was able to respond to verbal questions about the stimulus properties of particular objects (e.g. “What colour?” or “What shape?”) with an appropriate vocalisation (e.g. “blue” or “four-corner”) and transfer those labels to novel stimuli (Pepperberg 1983).

One of the earliest reports of picture categorisation in animals was conducted with chimpanzees by Hayes and Hayes (1953). The subject successfully learned to choose between pictures of two different object categories (eg. dog, cat, house) for reinforcement. Each trial used new pictures of different members of the two classes and a different set of categories was used every day. The first trial served as the training trial. The subject later learned to match a real object with a picture of an object from that class, even though the picture did not show the same object (Bhatt et al. 1988).

Numerous studies have demonstrated visual categorisation in monkeys of both natural and artificial visual stimuli such as food and animals (Fabre-Thorpe, Richard and Thorpe 1998), humans, monkeys and the letter A (Schrier, Angarella and Povar 1984), monkey faces, human faces, flowers, fruit and trees (Sands, Lincoln and Wright 1982), humans (D’Amato and Van Sant 1988; Schrier and Brady 1987), conspecifics (Fujita 1987), other species (Swartz 1983; Yoshikubo 1985); individuals of their own species

(Bruce 1982; Rosenfeld and van Hoesen 1979); birds and other animals (Roberts and Mazmanian 1988) and fish and trees (Vogels 1999a, 1999b).

Perceptual categorisation has also been shown in other primates including chimpanzees with sign language vocabulary (Gardner and Gardner 1985) and humans (Fujita and Matsuzawa 1986), baboons with alphanumeric characters (Vauclair and Fagot 1996), gorillas with conspecifics, orangutans, humans, primates, animals and food (Vonk and MacDonald 2002) and orangutans with conspecifics, primates and animals (Vonk and Macdonald 2004).

Primates have also demonstrated perceptual categorisation using auditory stimuli, including Japanese macaques with their own and other animals' calls (May, Moody and Stebbins 1989) and vervet monkeys with alarm calls, both natural (Owren 1990a) and synthetic (Owren 1990b) and rhesus monkeys with human speech phonemes (Kuhl 1987; Waters and Wilson 1976).

Mammals other than primates have also shown the ability to perform perceptual categorisations. Hanggi (1999) found horses could categorise geometric shapes on the basis of whether they had an open or a filled centre, while Sappington and Goldman (1994) demonstrated horses' ability to categorise triangles of various shapes and sizes. Chinchillas have demonstrated auditory discrimination of the phonemes of human speech (Burdick and Miller 1975; Kuhl 1987; Kuhl and Miller 1975; Ohlemiller, Jones, Heidbreder, Clark and Miller 1999), house mice can categorise on the basis of ultrasound vocalisation (Ehret 1987) and Mongolian gerbils can categorise on the basis of ascending and descending tones and transfer the ascending/descending category to novel stimuli (Ohl et al. 2001; Wetzel et al. 1998).

As can be seen from the examples above, perceptual categorisation can be found in a wide variety of species. It has even been demonstrated in insects and fish. Bumblebees, for example, can categorise food items (flowers) to optimise foraging and are able to generalise to novel exemplars (Dukas and Waser 1994) while carp can categorise music on the basis of style (blues versus classical) (Chase 2001). However, it is likely that different species' characteristics and varying experimental methodologies give rise to

divergent methods of achieving a successful performance. The next section examines a number of theories about how animals accomplish perceptual categorisation.

3.4.4 Perceptual categorisation theories

Therefore, it is often difficult to specify, on the basis of the subjects' response patterns, the exact array of stimulus properties exploited, let alone the underlying perceptual or cognitive mechanisms (von Fersen and Lea 1990).

(Troje et al. 1999, p. 354)

As demonstrated in the previous section (3.4.3), perceptual categorisation appears to be fairly widespread in the animal kingdom. This suggests it might be unsuitable as a task for this experiment as it indicates it is not a particularly 'difficult' or 'complex' task (one of the criteria for this experiment – see section 1.6). The issue of the task's ubiquity is compounded by the fact that there is a lack of consensus over how it is accomplished – whether using basic perceptual mechanisms or more complex cognitive processes. Categorisation has been described as “a secret” (Herrnstein 1985, p. 129), “utterly mysterious” (Marler 1982, p. 87) and “shrouded in mystery” (Premack 1983a, p. 357) (Huber 2001). While the studies listed in the previous section show many species can readily solve perceptual categorisation problems and generalise to other instances of the categories, they provide little insight into the perceptual and cognitive mechanisms underlying that performance. The polymorphous nature of many of the categories studied make it very difficult to identify these categorisation mechanisms – the categories cannot be defined in terms of any single stimulus dimension and no single perceptual feature is likely to be a “necessary or sufficient” condition for category membership (Herrnstein 1985). (See Roitblat and von Fersen 1992).

In broad terms, members of a category can be described as sharing a “family resemblance” (Rosch 1975). To successfully categorise those members the animal must adopt a response strategy based on its perception of similarity (Medin 1989). Further, it must be able to separate the relevant cues from the irrelevant ones and be flexible in the representations of the attributes of category members so it can treat some distortions and transformations as irrelevant (Cerella 1982; Greene 1983). However, even assuming perceptual categorisation is a largely a matter of assessing similarity, there is little agreement about the level of abstraction used to sort open-ended categories (Huber

2001) and numerous theories have been proposed to explain animals' ability to learn these types of perceptual categorisation tasks.

3.4.4.1 The genetic hypothesis

This theory suggests that a subject comes into a concept learning experiment with pre-existing concepts. The idea was raised in Herrnstein and Loveland's (1964) experiment, where the authors suggested that the speed with which the subjects learned the task indicated they had merely been taught the experimental procedure and had entered the experiment with the concept 'person' already formed.

The genetic hypothesis was also invoked in Herrnstein et al.'s (1976) study showing pigeons could learn to categorise pictures of trees. The authors suggested pigeons form categories on the basis of both visual stimulus generalisation and the formation of object categories. They proposed the formation of the object categories might be genetically based, with objects with evolutionary significance, such as trees and water, being grouped together on the basis of having similar psychological consequences.

Whether or not this idea has merit, it does not account for the numerous categorisation studies conducted using stimuli that the subjects would not have encountered before, such as fish (Herrnstein and de Villiers 1980) and chairs (Bhatt et al. 1988).

3.4.4.2 Rote learning

One possible explanation for successful performance of a perceptual categorisation is that the animal simply memorises each stimulus and its appropriate response. Considering the number of possible examples of a perceptual concept such as 'person' is prohibitively large this explanation initially seems unlikely, however the number of examples actually used in any particular experiment is comparatively small and they are often repeated over sessions (Lea 1984b).

3.4.4.2.1 Evidence for rote learning

This type of categorisation is dependent on an animal's memory storage abilities and a number of studies have demonstrated the plausibility of this explanation. A study by Vaughan and Greene (1984) showed pigeons successfully sorted up to 160 exemplars of squiggles and 320 photographs into arbitrary categories and exhibited evidence of memory retention when tested with the final 80 slides more than two years later. Similarly, Von Fersen and Delius' (1989) study showed pigeons could discriminate 100 different positive stimuli from a further 625 similar negative stimuli. Cook, Levison, Gillett and Blaisdell (2005) conducted an experiment in which pigeons were able to access, on average, approximately 830 memorised picture–response associations and retain them for months at a time.

A prodigious capacity to classify arbitrary exemplars is not unique to pigeons. Research from naturalistic settings has shown that a variety of birds can find a large number of sites in which they have cached seeds, an ability thought to be an evolved adaptation for food storing. While the recovery of these caches by marsh tits usually occurs within 24 hours after caching (Cowie, Krebs and Sherry 1981; Sherry 1982, 1984; Sherry, Krebs and Cowie 1981; Shettleworth and Krebs 1982), Clark's nutcrackers can still find thousands of cached food sites after several months (Kamil and Balda 1985; Vander Wall 1982). Similarly, Hawaiian honeycreepers are able to visually keep track of which flowers (among more than 1000) they have already visited (Kamil 1978). Monkeys have also been shown to have an excellent long-term memory for relatively large numbers of pictorial stimuli (Ringo and Doty 1985) and humans have also demonstrated an impressive capacity for rote categorisation (Nickerson 1965; Shepard 1967).

3.4.4.2.2 Evidence against rote learning

If memorisation was in fact the basis of these types of experiments then similarity among stimuli and the identity of the category would be irrelevant and perceptual categorisation, as it has been defined here, would not have been demonstrated. However, while it is likely that some aspects of categorisation might be based on memory (Cheney and Seyfarth 1990), numerous experiments have indicated that memorisation is not the sole basis of this type of performance.

Even with the pigeon's memory capabilities, rote learning seems an unlikely explanation for Herrnstein et al.'s (1976) experiment showing categorisation of pictures of trees, bodies of water and a particular person. During training, the authors changed the slides each day using a pool of 1840, 1760 and 1600 slides respectively for each of the three experiments. An even less likely candidate for rote learning was demonstrated in one of the experiments in Bhatt et al. (1988). Pigeons were able to learn a four-category discrimination (people, cars, flowers and chairs) using 2000 non-repeating slides, demonstrating that repetitive training with a limited number of stimuli is not necessary for successful perceptual categorisation performance. Indeed, in a natural setting, even a prodigious memory would likely prove insufficient where the number of exemplars of a given class (e.g. acorns for a foraging squirrel) would be open ended (Cheney and Seyfarth 1990).

More significantly, most studies require the successful categorisation of transfer trials using novel stimuli that the subject could not have stored in its memory (e.g. Bhatt et al. 1988). According to Herrnstein (1990): "The test of a categorisation beyond rote is generalisation" (p. 145) and, as Zayan and Vauclair (1998) point out: "There is an abundant literature showing the abilities of animals from different species to successfully categorise to novel instances at their first presentations" (p. 90). Even authors who argue that the ability of animals to categorise familiar objects is based on them remembering each instance and the category to which it belongs (e.g. Astley and Wasserman 1992; Pearce 1988, 1989, 1991) acknowledge that some other mechanism must be employed to account for successful categorisation of novel stimuli.

It is true that some authors have questioned whether successful transfer to novel stimuli is sufficient to demonstrate categorisation (e.g. Wasserman, Kiedinger and Bhatt 1988; Zayan and Vauclair 1998). One possibility is that the categorisation of novel stimuli is due to the stimuli in the training set being indistinguishable from those in the testing set so that, rather than exhibiting categorisation, the subjects are simply not able to tell them apart. According to Sturdy et al. (1999): "Transfer to untrained exemplars is arguably the single most important feature of categorisation, but transfer alone is insufficient to show that any given discrimination is based on open-ended categorisation. One must also show discrimination among exemplars" (p. 210). One possible example of the inability to discriminate within a category is found in Cerella

(1979) where the pigeons were able to distinguish oak leaves from non-oak leaves but were unable to distinguish between a specific oak leaf and oak leaves in general. A similar inability to discriminate between within-category stimuli was found using alphanumeric characters with baboons (Vauclair and Fagot 1996). However, while this may account for successful transfer in cases where the stimuli are perceptually similar, it does not explain the numerous instances of non-similarity based categorisation (see section 3.4.4.3.4.ii); suggesting that rote learning alone is insufficient to explain perceptual categorisation.

3.4.4.3 Exemplar theory

One theory that attempts to explain transfer to novel stimuli is exemplar theory (Astley and Wasserman 1992; Pearce 1988, 1991), which parallels the non-elemental configural theory of discrimination (see section 3.1.4.2.1.ii). Like rote learning, exemplar theory assumes that individual, intact stimuli are stored in memory. However exemplar theory also makes an important additional assumption that animals show primary stimulus generalisation from one picture to another. Stimulus generalisation means the tendency to respond to previously seen stimuli will generalise to a similar, novel stimulus. According to this theory, the only information used to make perceptual categorisation decisions is the memorised training stimuli and the degree of similarity between known and new exemplars. The exemplar model, then, assumes a fairly elementary level of categorisation – relying on common psychologically significant consequences rather than a rule, common feature or abstract representation (Huber 2001; Roberts 1998).

3.4.4.3.1 *Evidence for exemplar theory*

Support for the exemplar view of perceptual categorisation has been found in a number of experiments. Bhatt et al. (1988) and Schrier et al. (1984) showed that performance is often better in the presence of photographs that have been used during the training period than with novel photographs belonging to the same category. This suggests that animals can learn about individual training stimuli and that this information could be at least partly responsible for successful categorisation. A similar phenomenon is also found in humans, where it is referred to as the “exemplar effect” (Homa, Dunbar and Nohre 1991) (Pearce 1997).

Furthermore, in a study examining symmetry recognition using chessboard patterns, Huber et al. (1999) found pigeons used similarity to training stimuli, rather than a symmetry concept, to generalise to novel stimuli. The authors found the pigeons generalised only very conservatively from the training stimuli in a similar manner to the template-matching system described by Cerella (1990).

However, the most common method for determining whether simple stimulus generalisation is responsible for transfer to novel stimuli is to use artificially constructed stimulus sets called “pseudocategories” or “pseudoconcepts” (Lea 1984b). Lea and Ryan (1990) have divided such experiments into two categories – the “perverse pseudoconcept task”, which involves the arbitrary assignment of category and non-category exemplars to positive and negative classes, and the “random pseudoconcept task” in which no ‘concept’ exists within the stimulus set.

A number of categorisation experiments utilising pseudoconcept tests have supported the exemplar theory by concluding that the animals achieved discrimination by learning only about the specific stimuli in the training phase (Cook et al. 1990; Schrier et al. 1984; Vaughan and Greene 1983). Cook et al. (1990) found uniform rates of discrimination acquisition between birds trained using a true category condition and those trained using a pseudoconcept and that transfer was determined by the specific nature of the training exemplars. Their results influenced Huber (2001, Chapter 2, online) to conclude that exemplar-based categorisation theories are “a plausible alternative to more relational and analytic processing mechanisms”; while Roberts (1998) claimed exemplar theory accounts for most picture classification experiments.

3.4.4.3.2 Evidence against exemplar theory

However, other authors using a similar pseudoconcept procedure have shown that pigeons learn about category-specific information instead of, or in addition to, item-specific information. Unlike the previous experiments, these showed that there was a difference in responding between the ‘concept’ and ‘pseudoconcept’ groups, with better performance in the concept groupings (e.g. Edwards and Honig 1987; Herrnstein and de Villiers 1980; Wasserman et al. 1988). A similar result was found in zebra finches by Sturdy et al. (1999), who demonstrated that the birds learned pseudocategory

discriminations more slowly than true song-note category discriminations of the same notes.

Results from studies in which subjects showed higher responding to negative stimuli drawn from the same category as the positive exemplars have supported these results by suggesting animals detect the perceptual coherence within natural categories and do not rely solely on arbitrary relationships established during training (e.g. Astley and Wasserman 1992). Similarly, Fujita and Matsuzawa (1986) and Fujita (1987) used a procedure that allowed categories to emerge without reinforcement to demonstrate that at least some primates appear to respond spontaneously to categories such as ‘human’ and ‘conspecific’.

However, not all authors view the results of these types of pseudocategory experiments as evidence against exemplar learning. Shettleworth (1998), for example, argues that slides belonging to a perceptual category like ‘people’ or ‘fish’ will have more in common than members of a random group of slides, such as certain colours or contours. If that is the case, stimulus generalisation will tend to improve performance among category members and impede performance of pseudocategory members. Huber (2001) argues that even if exemplar-based categorisation strategies are a plausible alternative to more sophisticated mechanisms, the relevance for pigeons and other animals in the wild has not been determined.

3.4.4.3.3 Why both types of results?

Several authors have attempted to determine why pseudoconcept studies have shown such contradictory results. Wasserman and Astley (1994) distinguish between item-specific and category-specific aspects of stimuli – the first used to discriminate between instances of the same class and the second to discriminate between instances of different classes. The use of category-specific information significantly facilitates classification in terms of acquisition and transfer to novel stimuli. However, if category-specific information is either unavailable or unable to be distinguished, then category learning would be restricted to learning about each stimulus individually (Huber 2001).

Similarly, Cook et al. (1990) suggests that categorisation may consist of two phases – a “stimulus learning” phase in which only item-specific information that distinguishes an exemplar from all other stimuli is learned; and a “concept” phase in which category-specific information is extracted. Huber (2001) argues that in cases where the second phase does not follow the first, such as in his symmetry experiment mentioned above as an example of exemplar learning (Huber et al. 1999), then true open-ended categorisation has not been achieved. Another possibility is that the differing outcomes are the result of experimental variables, such as the number of exemplars used, leading to different strategies being employed by experimental subjects (see section 3.4.4.6).

3.4.4.3.4 Problems with exemplar theory

Huber (2001) points out there are a number of potential problems with exemplar theory: i) How many exemplars can be stored and retrieved for comparison, and ii) how similarity can be determined to ensure the subject responds only to instances of the same category.

i) Number of exemplars

The first problem is the number of exemplars. Because exemplar theory relies on comparison of a new stimulus with a known exemplar of the category, the individual stimuli have to maintain their “memorial integrity” no matter how many stimuli are presented (Huber 2001). However, there is no consensus on the number of exemplars that can be remembered. As discussed in section 3.4.4.2, while the rote learning capacity of species such as the pigeon is impressive, some tasks have been successfully performed using stimulus numbers so large it seems unlikely they could all be memorised (e.g. Herrnstein et al. 1976). There is also no way to account for studies using large numbers of non-repeating stimuli (e.g. Bhatt et al. 1988).

Some authors have attempted to address this problem by creating variants of exemplar theory which assume that categorisation is based on a small subset of the total number of stimuli, or that specific retrieval rules determine which patterns are most likely to be accessed (Huber 2001).

ii) Assessment of similarity

The other problem with exemplar theory is that it is limited to stimuli that are similar to the training stimuli. While exemplar-based mechanisms may be effective for categories with highly similar members, it does not account for generalisation to dissimilar new instances. It is also difficult to determine what defines similarity between two stimuli that happen to be members of the same experimenter-defined category.

Lea (1984b) suggests that the simplest possibility is that two stimuli are similar if they have features in common. Novel examples of human natural-language categories such as 'person' or 'fish' will inevitably be somewhat similar to the training stimuli and simple stimulus generalisation could account for correct discrimination in these cases (see Shettleworth 1998; section 3.4.4.3.2).

However, this does not account for instances of categorisation where simple physical similarity does not appear to have been the only controlling factor. For example, in Herrnstein et al.'s (1976) experiments showing pigeons' ability to categorise 'tree' versus 'non-tree', the positive stimuli did not need to have the typical features of trees to be correctly classified – they did not need to be green or have leaves, trunks or branches. Also, some of the non-trees exhibited tree-like features such as leaves or branches, albeit in different configurations to that found on trees. For example, a picture of celery, which was visually similar to a tree, was correctly identified as a non-tree. It could be argued that this performance was aided by prior familiarity with trees on the part of the pigeons (Herrnstein 1982). However, a similar result was found using slides of fish of varying degrees of physical similarity (Herrnstein and de Villiers 1980), a subject the test pigeons would not have previously experienced (Herrnstein 1982).

The study by Cook et al. (1990), cited in section 3.4.4.3.1 as providing evidence for exemplar theory, also revealed an apparent theoretical inconsistency in the way in which the stimuli were stored in the pigeons' memory. The authors found that the stimuli were not stored in their entirety; rather that the pigeons had selectively attended to specific aspects of the stimulus array. Classification behaviour was controlled only by animal figures in the pictures, irrespective of the background, rotation or reflection about a vertical axis. This type of analytical process is more in line with feature theory.

3.4.4.4 Feature theory

An alternative explanation for non-human perceptual categorisation that accounts for generalisation to dissimilar novel stimuli is based on common features of the positive and/or negative stimuli. According to feature theory, objects are characterised by the set of perceptual features of which they are composed. A 'feature' can refer to any elementary property of a stimulus that is psychologically processed. In a similar manner to the elemental theories of discrimination learning (see section 3.1.4.2.1.i), features gain a positive association when they are associated with trials with a positive (rewarded) outcome and a negative association when associated with a negative outcome. Membership of a category is then determined by whether or not a stimulus contains one or more necessary defining features (Huber 2001).

There are two main schools of thought regarding feature theory:

Single features: This theory holds that a single common feature, such as some property of the spatial frequency spectrum of the stimuli, is responsible for perceptual categorisation. As discussed earlier, one of the tenets of perceptual categorisation is that there is no single perceptual feature common to all members of a category, so this theory would relegate animal categorisation to simple discrimination. However this theory is largely dismissed as being lacking in empirical evidence (Lea 1984b).

Multiple features: This version of feature theory acknowledges that natural categories are polymorphic in nature (Ryle 1949) and suggests that no single feature can account for categorisation. Instead the subject uses some conjunctive, disjunctive or additive combination of features. Discriminations designed to be solved using this method are easily handled by pigeons (e.g. Lea and Harrison 1978; Von Fersen and Lea 1990). Multiple feature theory also provides a plausible explanation of how novel stimuli are correctly discriminated. As long as the new stimuli contain the right combination of features they should elicit the same response as the training stimuli (Lea 1984b).

3.4.4.4.1 Evidence for feature theory

A number of authors have acknowledged that attempts to prove a feature theory of perceptual categorisation have been hindered by the difficulty in determining what, if any, features are controlling the subject's behaviour when richly detailed natural stimuli are used (Cook et al. 1990; Fetterman 1996; Herrnstein 1984; Lea 1984b; Thompson 1995). Some evidence for feature-based control of categorisation performance has been elicited by analysing slides that have been grossly misidentified. Monkeys trained to categorise slides on the basis of whether or not they contained people were found to be selecting slides partly based on the presence or absence of patches of red colouration: slides showing a piece of watermelon or a hyena carrying a dead flamingo were treated like slides of people (D'Amato and Van Sant 1988). Similarly, experiments by both Greene (1983) and Honig and Stewart (1988) with pigeons showed stimulus choice being controlled by features of the background of photographs instead of the relevant subjects (Huber 2001).

A more effective way of testing feature theory is to use artificial stimuli that, without the complexity of natural scenes, can be modified to try and isolate the particular features controlling the animal's performance. For example, Morgan et al. (1976) and Schrier et al. (1984) found their subjects (pigeons and macaques respectively) were using multiple features to categorise alphanumeric characters. A number of these types of artificial-stimulus experiments have been conducted to more closely analyse feature-based categorisation, and these generally fall into two categories.

Post-hoc analysis

The first type of experiment involves post-hoc analysis. Researchers attempt to interpret their results by trying to identify the features that controlled the animal's classification performance. This is done either by correlating the features the experimenter was attending to with the subject's actual responses or by conducting sophisticated statistical procedures such as cluster analysis and multidimensional scaling (see Blough 2001; Huber 2001).

One often-cited series of experiments was conducted using the Peanuts cartoon characters (Cerella 1980, 1982, 1986). In these experiments pigeons were initially taught to discriminate Charlie Brown from other cartoon characters. They were then tested with slides of Charlie Brown that were deformed in some way (e.g. scrambled, truncated, upside-down). The pigeons treated the unusual slides as equivalent to the intact training stimuli, as “collections of local features rather than as representations of three-dimensional objects” (Cerella 1980, p. 1). This result can be explained by feature theory because the unusual slides contained all the features of the training stimuli, albeit presented in a novel way (Pearce 1997).

Conversely, similar experiments conducted using budgerigars showed greater latencies when the birds were viewing scrambled budgerigar faces compared to normal budgerigar faces, suggesting the configuration of features is also important (Brown and Dooling 1993). However, the influence of some sort of special face recognition (such as that found in sheep, Kendrick et al. 1995, and monkeys, Phelps and Roberts 1994) as well as the budgerigars’ extensive prior testing with normal faces raises some doubts about these results (Shettleworth 1998).

The synthetic approach

This type of experiment involves an a priori method that enables the experimenter to more rigorously test the subjects’ ability to extract the relevant features. This is a synthetic approach in which artificial concepts are constructed that can be defined by a small number of independent features, each with a predetermined probability of occurrence (Huber 2001).

Huber and Lenz (1993) employed simple line drawings of human faces to test a linear feature model. The faces contained four features that could be assigned one of three values (-1, 0, +1) according to their position in the face and these values were then arbitrarily assigned to categories. The combination of the values of the four features determined whether it belonged to the negative or positive category (patterns with a feature sum of zero were eliminated). In order to successfully categorise the stimuli the pigeons had to be able to attend to all four features equally and combine that information in an additive manner.

The authors found the pigeons were able to perfectly divide all the stimuli into the experimenter-defined categories after only three weeks. Analysis of pecking rates confirmed that all four features had exerted equal control over the birds' responding and that the values were combined in an additive manner, leading Huber and Lenz (1993) to interpret their results in terms of feature theory.

3.4.4.4.2 Evidence against feature theory

While feature theory has drawn support from a number of authors (e.g. Cerella 1986; Herrnstein et al. 1976; Lea 1984b; Morgan et al. 1976) it is not universally supported either theoretically or empirically. Critics argue that tests of linear feature models are usually conducted using artificial instead of natural stimuli and often lead to conflicting results (Lea and Ryan 1990; Huber and Lenz 1993) (see Thompson 1995).

In addition, while it seems likely that animals make some use of features in solving perceptual categorisation experiments, it is by no means certain that it is the only method used. While authors such as Cerella (1980, 1986) have argued that pigeons merely process "particulates" (local features) of visual information irrespective of their global relationships to one another, other experimenters have demonstrated that pigeons use information about both the properties and the spatial relationships of stimulus features (Kirkpatrick-Steger and Wasserman 1996; Kirkpatrick-Steger, Wasserman and Biederman 1996, 1998; Steele 1990; Wasserman, Kirkpatrick-Steger, Van Hamme and Biederman 1993; Watanabe and Ito 1991).

3.4.4.4.3 Why both types of results?

In an overview of stimulus processing by pigeons, Cook (2001) suggests a number of factors that might lead to the conflicting results of studies both supporting and refuting a strict feature-based account of perceptual categorisation. Based on his own and others' studies, Cook (2001) has concluded that pigeons use both feature and global information to solve these types of categorisations depending on the experimental design, a view that was demonstrated empirically by Matsukawa, Inoue and Jitsumori (2004). Some of these design factors could include stimulus complexity, viewing distance, stimulus location, attention reinforcement, and the relative salience of featural

and configural information (Cook 2001), as well as the method used to scramble stimulus objects (Kirkpatrick-Steger et al. 1998). For example, Cerella (1986) may have found feature-based stimulus control because cartoon characters such as Charlie Brown are designed to contain very strong and simple features. Conversely, the use of stimulus objects made up of geons (simple, geometrical volumes modelled into objects, e.g. can, handle, spout and nozzle = watering can) may have led to the global-based stimulus control observed by Wasserman et al. (1993). Alternatively, Watanabe (2001) theorised that pigeons were more sensitive to the global arrangement of what they saw as ‘real’ objects. The author found that scrambling photographs of people and pigeons severely suppressed responding in pigeons, scrambling cartoons of pigeons suppressed responding to a lesser extent, while scrambling cartoons of people had only a small negative impact. (See also section 3.4.4.6).

3.4.4.5 Prototype theory

Another theory widely used in discussions of human concept learning (e.g. Shanks 1994) is that in viewing a number of exemplars, animals form a category prototype – an ‘ideal’ exemplar that represents the central tendency of the all exemplars viewed (Shettleworth 1998). Once formed, it is assumed that the prototype is activated whenever an exemplar is presented and that activation will elicit the appropriate response for the category. The likelihood of the prototype being activated, and hence the appropriate response being given, is related to the degree of similarity between the exemplar and the prototype (Pearce 1997).

3.4.4.5.1 *Evidence for prototype theory*

Evidence for this theory was found in human studies that showed categorisations were made more easily when there was a close resemblance between the exemplar and the prototype (Posner and Keele 1968). Initial attempts to replicate this effect in animals were unsuccessful (e.g. Lea and Harrison 1978; Pearce 1987), however recent experiments have proved more fruitful (Aydin and Pearce 1994; Von Fersen and Lea 1990). Jitsumori (1996) trained pigeons to discriminate artificial polymorphous stimuli differing along three six-valued features. Exemplars of the two categories were created by manipulating the features of two different prototypes. When the pigeons were tested

for transfer to novel stimuli (which included the two prototypes), the most pronounced discrimination occurred between the prototypes rather than between the extreme positive and negative stimuli. After ruling out a feature-based explanation using distorted stimuli, the authors concluded that a prototype model best explained their findings.

3.4.4.5.2 Evidence against prototype theory

Despite some success, experimental support for prototype theory remains relatively weak. A number of studies have demonstrated that the prototypical effect in humans can be explained by either feature (McClelland and Rumelhart 1985) or exemplar (Hintzman 1986; Shin and Nosofsky 1992) categorisation theories and the same seems to hold true for animals (Pearce 1997).

While pigeons in the studies by Aydin and Pearce (1994) and Von Fersen and Lea (1990) did show better categorical performance with prototypical stimuli, the evidence was tempered by the fact that prototypical forms had actually been presented to the subjects before testing (Zayan and Vauclair 1998). Dépy, Fagot and Vauclair (1997) showed baboons classified prototypes more accurately than other exemplars; however analysis showed the monkeys had actually used feature and exemplar-based associations. Further, a number of other studies have reported no difference between prototypical and non-prototypical stimuli in birds (e.g. Huber and Lenz 1993; Jitsumori 1993; Lea, Lohmann and Ryan 1993; Watanabe 1988) and primates (Jitsumori 1994).

In addition, a number of researchers have found that even when animals seem to be sensitive to the same natural categories as humans, their idea of the ‘ideal’ exemplar is not always the same. Experiments conducted by Herrnstein (1979), Herrnstein and de Villiers (1980) and Roberts and Mazmanian (1988), for example, showed animal pictures rated by humans as ideal, or typical, exemplars did not match pictures that were highly discriminable by animal subjects. Similarly, Cook et al. (1990) used line drawings rated by humans on the basis of their prototypicality to train two groups of pigeons on ‘good’ and ‘poor’ exemplars respectively. The authors found that transfer was not influenced by the typicality of the test stimulus. Whatever features determined the ‘good’ exemplars for humans were not salient for the pigeons, whose choices were

determined by the range of training exemplars rather than the particular features of a prototype (Thompson 1995). In all these cases, however, the influence of people's prior experience compared to that of pigeons must be taken into account. Herrnstein and de Villiers' (1980) study used photos of fish, presumably much more familiar to people than pigeons. Unlike the pigeons, prior experience enabled human subjects to correctly select photos of partially obstructed fish; however, it also led them to incorrectly select whales.

3.4.4.6 Multiple strategy

A complement to the theories put forward to explain animal perceptual categorisation is the idea of multiple strategy – that is, that animals don't use just one of these mechanisms but a combination. Which methods an animal uses to perform a categorisation task may depend on how the experiment is conducted. Studies have shown that pigeons, for example, will utilise simpler methods if they are able. "The methodological problem is ... that pigeons can categorise at levels of abstraction that defy both explanation and simulation, but they do not have to" (Troje et al. 1999, p. 354). Kendrick, Wright and Cook (1990) found their perceptual categorisation study with pigeons was controlled by rote memorisation when only a few stimulus items were used, exemplar processing when more items were involved and by prototype learning when even more items were used. Similarly, Wright and Katz (2006) claimed too few training stimuli led to item-specific rather than relational learning in same/different categorisation in pigeons (see section 3.7.3.1). A comparable effect is seen in humans, where having fewer training stimuli appears to promote learning of individual stimuli while the use of many training exemplars enhances category learning (Cook et al. 1990).

Pearce (1997) suggests that animals may employ different strategies depending on the complexity of the stimuli being used. In addition, the nature of some tasks may encourage animals to focus on components of stimuli, in line with feature theory, while other tasks may lead to a more global perspective, such as that described in exemplar theory (see Huber and Lenz 1993). In a series of experiments Cook and colleagues found pigeons were quite elastic in how they processed visual information. Texture stimuli consisting of large arrays of smaller elements with strong edges and surface-like

characteristics led the pigeons to attend to global differences, while the use of hierarchical figural stimuli led to a stronger influence of local, feature-based information. Dynamic, object-like stimuli, on the other hand, suggested control by an integration of object and motion properties over time (Cook 2001).

Greene (1983), in replicating Herrnstein and Loveland's (1964) person/non-person experiment, found that the pigeons' performance had been controlled not only by the category-relevant features of the people but also by irrelevant features in the background. According to Greene, the pigeons seemed to use memorisation initially and then use higher-order techniques when necessary. Similarly, in D'Amato and Van Sant's (1988) 'person' category experiment described in section 3.4.4.4.1, the presence of a red patch was not the only method used by the monkeys to identify person-present slides. Many slides without red colouration were correctly classified as showing people. Huber et al. (1999) also provided evidence of pigeons' tendency to switch between learning about a symmetry category rule to relying on perceptual cues.

This phenomenon of multiple strategies being utilised within experiments may be at work in the line-drawing discrimination study by Cook et al. (1990). Cited in section 3.4.4.3.1 as an example of exemplar learning, the authors also found aspects of feature learning in the pigeons' performance (see section 3.4.4.3.4). By using test variants of the pictures, the authors found some features of the stimuli, such as 90-degree rotation or reflection about the vertical axis, were not controlling the pigeons' classification performance. The birds also seemed to have selectively attended to specific aspects of the stimuli and decomposed the pictures into at least the basic features of figure and ground (Huber 2001).

Roitblat and von Fersen (1992) suggested the complexity of categorisation behaviours required the creation of a more comprehensive theory that incorporated feature and exemplar-based theories (e.g. relaxation theories). Finally, one important factor to take into consideration when evaluating perceptual categorisation theories is the fact that the vast majority of experimental studies are conducted with pigeons. The avian visual system contains specialised structures and functions (Cook 2001), casting some doubt on the universality of findings from pigeon-based studies.

3.4.4.7 Concept learning

Despite the numerous perceptual mechanisms described above, many authors have claimed that animals are able to successfully perform perceptual categorisations because they possess a concept. What the term concept might mean when applied to non-humans and whether perceptual categorisation, or indeed any form of animal categorisation, can reasonably be called conceptual will be discussed in section 3.8.

3.5 Associative categorisation

The next type of categorisation in Zentall et al.'s (2002) list (see section 3.3.2) is associative categorisation. It was decided not to test the echidna on this level due to the paucity of experimental literature and, like perceptual categorisation, the lack of support for the relative complexity of the task. However, it is worth providing a brief overview as associative categorisation provides a theoretical backdrop to the next level of categorisation.

3.5.1 Definition and associative categorisation in nature

While perceptual categorisation is based on some form of physical similarity, in associative (or secondary) categorisation the stimuli within classes “bear no obvious physical similarity to one another, but rather cohere because of shared functional properties” (Zentall et al. 2002, p. 241). This shared function can include a common response engendered by the stimuli or a common consequence with which they are correlated.

Studies of the social relationships between animals have suggested categorisation based on mediating associations other than perceptual similarity. Dasser (1988a, 1988b), for example, used discrimination and match-to-sample tasks to demonstrate that two adult female Java monkeys were able to discriminate mother-offspring and sibling pairs from within their social group. There was no evidence that the discrimination was based on physical similarity or extraneous cues. Rather the author concluded that, during the years they had spent in the group, the subjects had been exposed to common functional associations such as physical proximity and distinctive interactions leading to the

formation of social categories. Rhesus macaques have also shown they can categorise on the basis of dominance relations among conspecifics (Bovet and Washburn 2003).

Similarly, studies of vocal categories have also suggested that animals can perform associative categorisation based on functionally equivalent categories. Vervet monkeys give two acoustically different calls (labelled 'wrrs' and 'chutters') at the approach of a neighbouring group – that is, both calls belong to the same functional category. Cheney and Seyfarth (1988) first measured a group of vervet monkeys' reaction to one individual's 'chutter' call (based on gazes towards the caller). The group was then repeatedly played that individual's 'wrr' call until they had habituated to it (as measured by a reduction in gazes towards the caller), then replayed the initial 'chutter' call. The monkeys showed less interest in the 'chutter' call after being habituated to the 'wrr' call, suggesting that perhaps the monkeys categorise both calls on the basis of their common referent (Thompson 1995).

Cheney and Seyfarth (1988) then conducted a similar experiment using two alarm calls ('leopard' and 'eagle') that differed acoustically but, unlike the wrr and chutter calls, had different referents. This time there was no reduction in response to the repeat of the first 'eagle' call following habituation of the 'leopard' call, presumably because they were associated with different referents and as such were in different categories (Thompson 1995).

It is also possible that some experiments described as examples of perceptual categorisation may have been solved using associative mechanisms. In the studies of vervet monkey alarm calls (see section 3.4.1), in which the monkeys give different alarm calls in response to different predators, it could be argued that the monkeys formed categories based on both perceptually based stimuli (leopard, eagle, snake) and associatively based stimuli (predator, non-predator) (Seyfarth et al. 1980a, 1980b). Similarly, stimuli that have been successfully categorised by pigeons in the perceptual categories 'food' (Watanabe 1991, 1993) and 'pigeon' (Poole and Lander 1971) may have been classified according to functional labels such as 'edible' and 'conspecific' (Watanabe 1991).

3.5.2 Associative categorisation experiments

There has not been an extensive history of testing for this type of categorisation performance and most of what has been done has been conducted with language-trained animals. Premack (1976, 1986) showed language-trained chimpanzees were easily able to categorise different parts of fruit, such as seeds, as fruit even when symbols, rather than real objects, were being used. Similarly, Savage-Rumbaugh, Rumbaugh, Smith and Lawson (1980) showed language-trained chimpanzees were able to group both items and the symbols for those items into superordinate functional classes such as ‘food’ and ‘tools’ (see also Gardner and Gardner 1984, 1985).

In 1990 Cheney and Seyfarth claimed that up until that time only language-trained chimpanzees had demonstrated associative categorisation in an experimental setting. However, Tanaka has demonstrated non-language trained chimpanzees are able to classify items according to complementary relationships. Tanaka (1995) found five chimpanzees could use complementary relationships between objects (e.g. a bottle and cap) to sort objects in an object-sorting task. Tanaka (1996) also found a non-language trained female chimpanzee was able to match physical items (and their photographs) on the basis of learned functional relationships in a matching-to-sample task. For example, she could match one part of a two-part object to its other part (such as a box and its lid), a container to its tool and a tool to its container, even when non-matches looked more like the sample.

Bovet and Vauclair (1998) demonstrated that non-language trained baboons could categorise novel pairs of objects based on their functional relationships (food versus non-food). The authors also showed that the baboons could master the task even when pictures, rather than the actual objects, were used as stimuli. Watanabe (1993, 1997) proved pigeons could also correctly sort objects into food and non-food categories. As with the Bovet and Vauclair (1998) study, the pigeons were able to generalise the performance to novel stimuli regardless of the type of stimulus used (picture or object).

It has also been argued that non-language trained animals have demonstrated the ability to perform associative categorisation in experiments using artificially created associative categories. Instead of being solved based on ‘real life’ functional

associations, these categories are made up of initially unrelated stimuli grouped together by means of a common reinforcement history, forming equivalence classes (Lea 1984b). (See section 3.7.6.1.1 for a discussion on the evidence for and against the formation of equivalence classes in animals). One of the most popular ways in which the ability to form these categories has been tested is through the use of a many-to-one matching procedure in which two or more samples are associated with the same comparison stimulus. Following training, a number of studies have found relationships emerging between samples associated with the same comparison – a result also known as common coding (Zentall 2000a) – and associatively based pseudocategories being formed (see section 3.4.4.3.1 for more examples of pseudocategory experiments).

The most direct evidence for common coding is found when the introduction of new stimuli transfer to the entire pseudocategory. This occurs when, following the creation of the pseudocategories, one member of each of the pseudocategories is associated through common reinforcement with novel stimuli. This association between the novel stimulus and a single category member is then found to generalise to the remaining members of the pseudocategory (e.g. Urcuioli et al. 1995; Urcuioli, Zentall, Jackson-Smith and Steirn 1989).

Additional evidence for pseudocategory formation following many-to-one matching is seen in experiments where it has proved difficult to reverse sample-comparison associations which involve one member of the pseudocategory and not the other (Nakagawa 1986; Zentall et al. 1991). Further, it has also been found that pigeons are less able to discriminate between samples that have been associated with the same comparison than those associated with different comparisons (Kaiser, Sherburne, Steirn and Zentall 1997). Finally, support for pseudocategory formation is found in tests of retention function in delayed matching-to-sample. Samples containing line orientation are not remembered as well as those containing hues. However, there is comparable retention of line orientation samples when they are associated with the same comparison as a hue sample (Urcuioli et al. 1989; Zentall 2000a; Zentall et al. 1989).

Secondary categorical relationships can also form between perceptually similar items using serial reversal training. Vaughan (1988), for example, reinforced pigeons for responding to one set of tree slides but not another. After the initial discrimination had

been mastered, the author then conducted discrimination reversals in which the S+ and S- categories were alternated. After dozens of reversals the pigeons were able to reverse the categories after the first few trials, suggesting they had formed two separate categories from a pool of perceptually similar stimuli. However, it has been suggested that the fact so many trials were required to achieve successful category reversal may mean that perceptual similarity could impair the formation of secondary categorical associations using standard training procedures (Thompson 1995). Kastak, Schusterman and Kastak (2001) also used a discrimination reversal procedure to demonstrate that California sea lions were able to classify stimuli into functional classes. The sea lions were then able to transfer the emergent relations to a matching-to-sample procedure.

Not all experiments have supported the idea that training pseudocategories in animals leads to the formation of true equivalence classes. Bhatt and Wasserman (1989) found pigeons originally trained to categorise a pseudocategory were unable to generalise new responses trained to a subset of the category to the other members of the category. However, Wasserman, DeVolder and Coppage (1992) found the opposite result when they used a variation of the procedure. The authors trained pigeons to make the same response to two groups of perceptually dissimilar stimuli – chairs and cars. A new response was then trained for just one of the groups (e.g. cars). When the pigeons were tested on the second group (e.g. chairs), they tended to give the new response rather than the old, despite having never been reinforced for doing so. The authors concluded that because the two groups had previously been associated with a common response, they had formed a new encompassing category consisting of physically different but functionally equivalent items – an equivalence class.

3.5.3 Associative categorisation theories

3.5.3.1 Language training

Pearce (1997) suggested it was conceivable that language training was responsible for the ability of animals such as the chimpanzees in Savage-Rumbaugh et al.'s (1980) experiment to sort objects into functional categories. The chimpanzees were trained with arbitrary lexigrams representing a class of objects – food and tools – which became symbolic substitutes (like words) for the objects they represented. However, the ability

of non-language trained animals to categorise non-similar stimuli into pseudocategories based on common reinforcement history (see section 3.5.2) suggests that something other than language-based ‘concepts’ are responsible for associative categorisation, a position supported by Pearce (1997).

3.5.3.2 Mediated generalisation

One way in which animals may solve associative categorisations that have not been expressly trained is by mediated generalisation (also called secondary stimulus generalisation). This relies on the fact that different classes of objects tend to elicit different responses. For example, in the Savage-Rumbaugh et al. (1980) experiment mentioned above, a chimpanzee might react in some consistent way to food items, such as by salivating. To solve the discrimination, the animal merely has to learn that objects that elicit this reaction should be treated in one way and items that do not elicit this reaction should be treated in another (Pearce 1997).

This method of solving associative categorisations could also account for the subjects’ ability to categorise other stimuli such as ‘predator’ (Seyfarth et al. 1980a, 1980b) and ‘conspecific’ (Poole and Lander 1971) as these groups might be expected to elicit a different response which could theoretically be used to solve the task.

Evidence for mediated generalisation can be seen in experiments like those described in section 3.5.2 in which reinforcement is used to create artificial associative categories (pseudocategories) of arbitrary stimuli that function as equivalence classes. In these instances the mediating factor is the reinforced response rather than a spontaneous response to some aspect of the stimulus.

3.5.3.3 Concept learning

Another possibility is that associative categorisations are solved using conceptual means, an issue which will be addressed in section 3.8.

3.6 Relational categorisation

As discussed earlier, because of the continuing debate over whether successful perceptual categorisation experiments with non-human animals are due to ‘high-level’ mental processes such as concept learning or the result of more prosaic mechanisms, testing the echidna on this type of task would not provide sufficient evidence of ‘advanced’ mental abilities. Similarly, the possibility that associative categorisation can be performed using mediated generalisation, in addition to the paucity of experimental precedent in this area, meant that it too was not an ideal candidate for this study. Relational categorisation, however, provides a more promising avenue for investigation.

3.6.1 Definition and relational categorisation in nature

Abstract concepts are rules about relationships (e.g., identity) among stimuli. Abstract concepts are distinct from so-called “natural” concepts (e.g., trees), which have some stimulus feature(s) in common. Abstract concepts transcend the individual features of stimuli and depend instead upon the relationship between the stimuli being judged.

(Katz and Wright 2006, p. 80)

While perceptual categorisation is based on the perceptual similarity between stimuli and associative categorisation is based on the functional commonality of stimuli, relational categorisations (often described as abstract or relational concept learning) are solved using the relationship between stimuli. Relational categories are described as abstract because they transcend the specific attributes of the stimuli used to train them (Wright 1997). According to Thomas (1996), the operational difference between what he defines as an absolute class concept (perceptual categorisation) and a relative class concept (relational categorisation) is that in perceptual tasks there is no need to compare stimuli, while in relational tasks “the subject must compare the stimulus objects to determine which one manifests the concept” (p. 160). Herrnstein (1990) described the categorisation of abstract relations as dealing “not with the exemplars themselves, but with relations between and among concepts” (p. 138).

Relational categorisation has been demonstrated using ecologically relevant stimuli. For example, MacDougall-Shackleton and Hulse (1996) found starlings could form an

abstract auditory concept based on rising versus falling tones at the same time as attending to the absolute pitch of the sequences. According to the authors, the birds were sensitive to both the absolute values of the stimuli and their relationships. However, other studies using ‘natural’ stimuli have proved more difficult to interpret.

One possible naturally occurring relational category is based on social relationships. In section 3.5.1, Dasser (1988a, 1988b) interpreted her finding that Java monkeys can correctly categorise slides of pairs of monkeys from its social group based on whether they are mother and offspring or siblings as an example of associative categorisation. Shettleworth (1998) suggested insufficient evidence exists to determine whether this ability is based on forming relational categories or if some role is played by perceptual or associative mechanisms. Cheney and Seyfarth (1990) argue that association rates alone are insufficient to explain this ability, as related pairs of individuals do not always interact in the same way or at the same rate as other pairs of the same relation. For example, some mother-offspring pairs are close and relate often, while others are more distant (e.g. Altmann 1980; Hinde 1974). Still, all are placed in the same social relationship category (Dasser 1988a).

Field studies have also suggested that some species of monkey can learn about social relationships. For example, when vervet monkeys are played screams of juveniles from their group they look at the mothers (Cheney and Seyfarth 1980; Seyfarth and Cheney 1994) indicating a possible relational category ‘mother-offspring pair’. Similarly, monkeys have been observed displaying redirected aggression, in which monkeys that have been attacked retaliate against the aggressor’s affiliates (Aureli, Cozzolino, Cordischi and Scucchi 1992; Cheney and Seyfarth 1986, 1989). Bovet and Washburn (2003) claim these types of field studies, and the results of their own experiments with rhesus macaques showing categorisation based on dominance relations, “seem to indicate that monkeys can use abstract social concepts” (p. 400).

Another contentious example of relational categorisation in nature is found in studies of vervet monkeys’ functionally equivalent ‘wrr’ and ‘chutter’ calls given at the approach of a neighbouring group (Cheney and Seyfarth 1988; Seyfarth and Cheney 1988). As discussed in section 3.5.1, Thompson (1995) interpreted these results as “evidence of categorisation via secondary generalisation mediated by a common response or

referent” (p. 207) – associative categorisation. However, the original authors claimed the monkeys compared the stimuli based on an abstract relationship. “Results provide clear evidence that vervet monkeys use meaning to make judgments about the relation between two vocalisations ... Such judgments require that an animal both recognise the relationship between a call and its referent and compare two referents” (Seyfarth and Cheney 1988, p. 74).

3.6.2 Relational categorisation experiments

While the above experiments do suggest that some animals perform categorisations based on relationships in their natural environments, the lack of consensus about whether they in fact understand relatedness or instead make use of perceptual or associative mechanisms has led to numerous experiments being conducted to test the idea using artificial stimuli.

Early evidence suggesting relational learning in non-humans was found in discrimination experiments such as that conducted by Gonzalez et al. (1954) (see section 3.1.4.2.2). More recently a number of other techniques have been developed to test relational learning in animals. These studies have suggested that at least some animals may be able to discriminate on the basis of a variety of abstract relational criteria, such as self-concept in chimpanzees (Gallup 1970), serial order in monkeys (D’Amato and Colombo 1988), insideness in pigeons (Herrnstein, Vaughan, Mumford and Kosslyn 1989), symmetry in bees (Giurfa, Eichmann and Menzel 1996), relative size in horses and parrots (Hanggi 2003; Pepperberg and Brezinsky 1991), relative volume in squirrel monkeys (Thomas and Ingram 1979); relative numerosity in pigeons and dolphins (Honig and Stewart 1989; Jaakkola et al. 2005), above and below in bees (Avargues-Weber, Dyer and Giurfa 2011), capuchin monkeys (Spinozzi, Lubrano and Truppa 2004) and baboons (Depy, Fagot and Vauclair 1999), and transitive inference in chimpanzees (Gillan 1981).

However, the majority of relational categorisation experiments are designed to test the subject’s ability to categorise on the basis of whether items are the same or different. For this reason, as well as those outlined in section 3.9, it was decided to focus on

same/different discriminations rather than one of the other examples of relational learning.

3.7 Same/different categorisation

3.7.1 Definition

When defining same/different categorisation (often called same/different concept learning), as it will be used in this study, it is important to clarify what it is not. The ability to recognise whether an object is novel or has been previously seen (with the concomitant changes in reactivity) is a seemingly ubiquitous attribute in the animal kingdom (see section 1.2.1.1). However, this kind of passive detection of like/unlike relations is generally considered insufficient evidence of true same/different learning. Instead a more active detection of sameness/difference is required – in broad terms, an ability to make specific relational comparisons regardless of individual stimulus qualities (Delius 1994).

In humans, the ability to classify events and objects into categories of *same* or *different* based on relational information is considered an essential cognitive skill upon which many other cognitive abilities are based. It is a skill that, at least since Aristotle's time, has been considered virtually universal among human adults (Delius 1994) and which has more recently been demonstrated in human infants as young as seven months old (Tyrrell, Zingaro and Minard 1993).

Noted psychologist C. Lloyd Morgan (1894) claimed non-human animals could not learn abstract concepts like *same* and *different*, a claim reiterated a century later by French (1995, p. xvi): "It is this subtle ability, perhaps more than any other, that sets human cognition apart from any other on our planet." However, because same/different categorisation is often seen as the basis for reasoning in humans, its existence in animals has been a popular avenue of study for scientists seeking to examine the phylogenetic origins of human cognition (Delius 1994).

Kohts (1923) conducted one of the earliest experiments attempting to demonstrate that same/different categorisation might not be the exclusive domain of humans by testing

chimpanzees. Although his results were inconclusive, he started a research tradition that has since demonstrated the ability not only in primates, but also in numerous other species (Delius 1994). There are a number of procedures for testing same/different categorisation, including spontaneous sorting (McClure and Culbertson 1977; Matsuzawa 1990) and analogical reasoning (Gillan, Premack and Woodruff 1981). Far more common, however, are matching/non-matching to sample, oddity and paired comparison same/different tasks, all of which will be examined in this review.

3.7.2 Same/different categorisation training

3.7.2.1 Methods

3.7.2.1.1 Experimental paradigms

Same/different categorisation is generally tested using four main experimental paradigms, which can be classified as:

- i) **matching to sample** – in which subjects are presented with a sample stimulus and then required to select one of a number of comparison stimuli that is the same as the sample stimulus (see also section 3.4.2.1.1);
- ii) **non-matching to sample, or oddity-from-sample** – is the same as matching except the subjects are required to select the comparison stimulus which is different from the sample stimulus;
- iii) **oddity** – in which a single odd stimulus must be selected from a group of identical stimuli, and;
- iv) **paired comparison** – in which a different response is required depending on whether the presented stimuli are the same as or different from one another or, alternatively, in which subjects are required to discriminate between two stimulus complexes, one containing identical elements and the other containing dissimilar elements.

(adapted from King 1973)

Same/different categorisation experiments, whether they are conducted using matching/non-matching or paired comparison procedures, can be conducted in a number

of ways that can be broadly grouped according to the way in which stimuli are presented – successively or simultaneously. In successive categorisation, a test stimulus is presented followed by one or more comparison stimuli which are either the same as or different from the test stimulus. In simultaneous categorisation, the test and comparison stimuli are presented at the same time. Like perceptual and associative categorisation, both methods of same/different categorisation training require the use of a testing phase, such as transfer to novel stimuli, to ensure the task has not been solved using rote learning (Premack 1983a; see section 3.4.2.1.2).

3.7.2.1.2 Successive presentation of stimuli

The successive method of same/different testing is usually conducted using a delayed matching-to-sample procedure. In a delayed match-to-sample task the sample stimulus is presented for a selected time period and then removed. After a delay interval, which may be virtually instantaneous (zero-delay matching) or of longer duration (delayed matching), two or more comparison stimuli are shown, one of which is the same as the sample. If the task is to select *same*, the comparison stimulus that matches the sample must be selected to gain a reward (e.g. Nissen, Blum and Blum 1948; Tavares and Tomaz 2002). Successive same/different categorisation can also be tested by reinforcing the subject for choosing the comparison stimulus that does *not* match the sample (i.e. *different*) (e.g. Irle and Markowitsch 1987). This is called delayed non-matching to sample, or oddity-from-sample. (See also Carter and Werner 1978; Roitblat 1984).

Although more commonly used for matching and non-matching, successive presentation of stimuli can also be utilised in paired comparison same/different tasks. In such cases, the sample stimulus is followed by the presentation of only one comparison stimulus and the subject reinforced for responding in one way if the comparison matches the sample and responding in another way (or not responding) if it doesn't (Katz, Sturz and Wright 2010b). Another variation of a successive procedure was used by Cook, Kelly and Katz (2003), in which two different or two identical pictures were alternated for 20 seconds (with inter-stimulus intervals) and the subject rewarded for responding to the *same* sequence. A variation of this has been used to test same/different using auditory stimuli, with subjects being required to respond

appropriately to sequences of sound that are either the same or different (e.g. Cook and Brooks 2009; Hoeschele, Cook, Guillette, Hahn and Sturdy 2012).

Discrimination testing using successive presentation of stimuli can also be used to test abilities other than same/different learning. For example, delayed matching-to-sample has proved a popular method to test memory in non-humans. By varying the time between the presentation of the initial test stimulus and the presentation of the comparison stimuli, the subject's short-term or working memory can be examined (e.g. D'Amato 1973; Grant 1976; Grant and Kelly 2000; Sands et al. 1982; Tavares and Tomaz 2002). This technique can be further modified to test serial list memory by presenting a single probe stimulus following a sequence of stimuli. The subject must then decide if the probe stimulus appeared in the initial sequence (e.g. Thompson and Herman 1977). Another experiment using successive presentation of stimuli is delayed alternation, which involves the subject being reinforced for responding to the stimulus to which it didn't just respond. (See also Shettleworth 1998; Thompson 1995).

3.7.2.1.3 Simultaneous presentation of stimuli

Simultaneous presentation of stimuli is the most commonly used procedure for the paired comparison same/different task. One variation of the procedure involves two (or more) stimuli being presented at the same time (either separated or contained within a single stimulus panel) and a different response (such as hitting one of two response keys or symbols) being required of the subject depending on whether they are the same or different (e.g. Edwards, Jagielo and Zentall 1983; Wasserman et al. 1995). This method is sometimes referred to simply as the same/different procedure (e.g. D'Amato and Colombo 1989; Wright et al. 2003), as distinct from a matching procedure.

Another technique involves a paired comparison task in which one stimulus containing all the same elements and one stimulus containing all different elements are presented at the same time and the subject is required to directly select the S+ (*same* or *different*) stimulus (Blaisdell and Cook 2005; Chausseil 1991). (This procedure was the one selected for use in these experiments.)

Matching to sample can also be conducted using simultaneous presentation. In this type of task, the subject is presented with a test stimulus and then, usually after an observation period, two or more alternatives are presented so both the test and comparison stimuli can be viewed simultaneously. The subject must then select the sample most like the test stimulus (e.g. Gabor and Gerken 2012). Similarly, non-matching-to-sample can be conducted simultaneously, with the subject having to select the sample most unlike the test stimulus. Oddity learning can be tested simultaneously without using the matching/non-matching procedure. In this scenario, a number of stimuli are presented and the subject must select the single odd stimulus from among the rest of the identical stimuli.

3.7.2.1.4 Combined successive/simultaneous presentation of stimuli

It is worth noting that some procedures could be described as hybrids combining elements of both successive and simultaneous methods. For example, a match-to-sample procedure in which the sample stimuli is presented first by itself followed by the presentation of the comparison stimuli is generally described as a successive procedure (see section 3.7.2.1.2). However, if the sample stimulus remains visible when the comparison stimuli are shown, it has been argued (by Carter and Werner, 1978, for example) that the procedure is simultaneous. Rather than being one or the other, elements of both procedures seem to come into play in this type of experimental design and it is possible that aspects of both procedures influence how such experiments are solved.

3.7.2.1.5 Successive versus simultaneous presentation of stimuli

While successive presentation of stimuli is a popular method of testing memory (see section 3.7.2.1.2), a number of authors contend that it is less effective than simultaneous methods for testing same/different relational learning because it can more readily be solved using other means. Being able to categorise two or more stimuli as being the same or different must by definition be based on the relationship between those stimuli. Mazur (2002) points out that relational theory has been found to better explain the results of simultaneous discriminations. According to Premack (1983a, 1983b), the same/different task is far easier for a subject to perform using successive rather than

simultaneous discrimination and less likely to be solved using relationships: “Unfortunately, the animal literature largely conflates the two cases, calling the animal’s response in both cases “same/different” ... the successive task may have little to do with same/different” (Premack 1983b, p. 127).

For example, it has been argued that in non-human animals successive discriminations aren’t solved using judgements about same/different, rather that the subject simply reacts to whether it has experienced the item before. When stimuli are presented successively, they do not need to be compared to determine whether they are members of the same category and the stimuli can be accepted or rejected as a category member on the basis of absolute discriminative features alone. Using the principles of associative conditioning (see section 1.2.1.2), if the *same* stimuli evoke the same concrete referent, the subject need only decide if it had previously occurred (Premack 1983a; Steirn and Thomas 1990; Thomas 1980; Thompson 1995). Instead of same/different, it has been alleged that these experiments may actually be a test of novelty in which stimuli are selected on the basis of relative familiarity rather than identity (Premack 1983b; Shettleworth 1998). In addition to relative novelty, it has also been argued that successive procedures like delayed matching-to-sample can be solved on the basis of other non-relational means such as conditional discrimination, the exclusion effect, configural theory and the oddity preference effect. (See section 3.7.6.1 for fuller discussion).

According to Castro, Kennedy and Wasserman (2010), simultaneous presentation improves same/different discrimination performance by promoting comparison of the same/different arrays. This encourages learning about the relative values of the stimuli rather than item-specific learning. In their view, sameness is difficult to understand without also referring to the twin relation of differentness.

While most criticism has been reserved for successive presentation of stimuli, Siegel and Honig (1970) claim several early studies (e.g. Cahill and Hovland 1960; Hovland and Weiss 1953) suggested that “concept attainment” (p. 385) was unduly facilitated by simultaneous presentation. In addition, Honig (1962) found that the simultaneous procedure produced fewer errors and more rapid extinction of the negative stimulus. He argued that true extinction to the negative instance was achieved only in the successive

case because with simultaneous training the pigeons could use the negative instance as a cue to switch to the positive instance. This view was partly based on the fact that the pigeons in his experiment could transfer from successive to simultaneous scenarios but not the reverse. When Siegel and Honig (1970) compared successive and simultaneous presentation in a people-present/people-absent categorisation using pigeons, they also found performance improved when transferring from successive to simultaneous presentation. However, in terms of overall performance, there was no appreciable difference between the two testing methods in the acquisition of the discrimination, providing little support for favouring successive over simultaneous presentation in testing relational learning.

In an uncommon take on the argument, Fetterman (1996) suggests that animals may perceive successive tasks as representing a single stimulus array, in which case there would not be any significant difference between successive and simultaneous procedures. “It is customary to distinguish between the apprehension of simultaneous and successive stimulus patterns in terms of perceiving versus remembering, but this dichotomy may be based on preconceptions about stimuli as discrete, momentary events” (p. 10). Some support for this view can be found in Nakagawa (2000), who examined transfer of learning between matching (or non-matching)-to-sample discriminations and same/different discriminations and concluded that the same mechanism governs the formation of associations between stimuli in both tasks.

3.7.2.2 Stimuli

Overwhelmingly, the stimuli used in same/different experiments tend to be visual, ranging from pictures of simple geometric shapes (e.g. Cook 2002b) to photographs (e.g. Cook, Katz and Kelly 2000) to three-dimensional objects (Keddy-Hector, Allen and Friend unpublished; Tavares and Tomaz 2002). (For a review of visual exemplars see Bovet and Vauclair 2000). However other stimulus modalities such as odour (Langworthy and Jennings 1972) and sound (D’Amato and Colombo 1985; Dooling, Brown, Park, Okanoya and Soli 1987; Herman and Gordon 1974; Wright, Shyan and Jitsumori 1990) and even unusual sensory modalities such as echolocation (Roitblat, Penner and Nachtigall 1990) have also been used. They can also vary across more than one dimension. For example, matching-to-sample can be conducted using a single

dimension (e.g. hue) or two dimensions (e.g. hue and geometric shape) (Carter and Werner 1978).

Much of the initial research on paired comparison same/different categorisation in animals used just two visual items to represent *same* or *different* (e.g. Edwards et al. 1983; Santiago and Wright 1984; Wright, Santiago, Urcuioli and Sands 1983). Recently, however, a number of researchers have shown that same/different judgments could be made using multi-element displays (e.g. Astley and Wasserman 1998, 1999; Cook, Cavoto and Cavoto 1995, 1996; Cook, Katz and Cavoto 1997; Cook and Wixted 1997; Wasserman et al. 1995; Young and Wasserman 1997; Young, Wasserman and Garner 1997). In the majority of experiments using multi-element displays, the displays are presented one at a time, with a different response required for *same* and *different* arrays. While not literally a ‘paired’ comparison, multi-element stimuli have been grouped together with paired comparison same/different categorisation as they also make use of a single simultaneous comparison rather than a successive procedure.

3.7.3 Same/different categorisation experiments

Due to the debate about whether matching/non-matching experiments constitute same/different categorisation (see section 3.7.6.1), this experimental review has been separated into sections reflecting the most common methods used to test same/different learning.

In most academic literature reviews, delayed and zero-delay matching-to-sample (see section 3.7.2.1) are generally grouped together under the label matching-to-sample without the procedural method being individually specified and that convention is followed here unless it is relevant to the discussion. The majority of experiments appear to utilise the delayed procedure.

3.7.3.1 Matching-to-sample

Matching experiments, in which subjects are required to respond to a stimulus that is the same as a sample stimulus, have been a popular method for testing a number of different cognitive abilities since early studies by Kohts (1923) and Weinstein (1941)

(see section 3.7.2.1.2). However, the focus here is on the use of the matching procedure to test same/different categorisation. Whether matching provides sufficient evidence of true relationally based same/different categorisation is discussed in section 3.7.6.1.

Matching-to-sample has been comprehensively established in primate species such as chimpanzees (Nissen et al. 1948; Oden, Thompson and Premack 1988; Smith, King, Witt and Rickel 1975); monkeys (D'Amato and Colombo 1985; D'Amato and Cox 1976; D'Amato, Salmon and Colombo 1985; D'Amato et al. 1986; Mishkin and Delacour 1975; Mishkin, Prockop and Rosvold 1962; Tavares and Tomaz 2002; Washburn, Rumbaugh and Richardson 1992), gorillas and orangutans (Vonk 2003).

However, it is certainly not limited to primates. Matching has been demonstrated in a wide variety of species including rats (Roitblat and Harley 1988), pigeons (Maki and Leith 1973; Roberts and Grant 1976; Zentall and Hogan 1974, 1975, 1976, 1978), dolphins (Herman and Gordon 1974; Herman, Hovancik, Gory and Bradshaw 1989; Roitblat et al. 1990), sea lions (Kastak and Schusterman 1994; Pack, Herman and Roitblat 1991), corvids (Wilson et al. 1985b), horses (Gabor and Gerken 2012), budgerigars (Manabe, Kawashima and Staddon 1995), goldfish (Goldman and Shapiro 1979; Zerbolio and Royalty 1983) and honeybees (Giurfa, Zhang, Jenett, Menzel and Srinivasan 2001). Matching-to-sample has even been demonstrated using less common sensory modalities, such as Roitblat et al.'s (1990) study in which a dolphin was trained to perform a three-alternative delayed matching-to-sample task using only echolocation.

While matching-to-sample seems to be a relatively ubiquitous ability, a number of studies have indicated some species find it easier to learn the task than others. For example, the majority of the goldfish in Goldman and Shapiro's (1979) matching (and oddity) studies reached 75% performance level by the end of 70 training days, whereas pigeons tested using a similar experimental paradigm reached accuracies of 90% or better after 20 training days (Cumming and Berryman 1965). Differences in performance between species also become apparent when transfer tests with novel stimuli are introduced. Monkeys and chimpanzees have demonstrated the ability to match novel stimuli after learning just one matching problem (although the monkeys did not show complete transfer) (D'Amato, Salmon and Colombo 1985; Oden et al. 1988). However, when pigeons and corvids (relatively closely related species) were

tested using a similar experimental paradigm, the corvids were able to perform generalised matching when the pigeons could not (Mackintosh 1988; Wilson et al. 1985b). Other experiments have also demonstrated pigeons failure to transfer a matching performance to novel stimuli (e.g. Berryman, Cumming, Cohen and Johnson 1965; Cumming and Berryman 1961).

Matching in pigeons

Due to the prevalence of pigeons as an experimental subject, an examination of some of the issues surrounding matching-to-sample in this species provides a good overview of some of the general factors affecting non-human matching performance. The difficulty experienced by species such as pigeons in transferring a previously learnt matching performance to novel stimuli may be due to the utilisation of conditional rather than ‘conceptual’ rules (Cumming et al. 1965). It has been suggested that pigeons trained using only a small number of stimuli do not seem to match novel samples but apparently memorise conditional rules, i.e. “if the sample was red, choose red” (Shettleworth 1998) – a multiple-rule model conditional discrimination (see section 3.7.6.1.1). Indeed, there has been an ongoing debate about whether pigeons could learn the general principles of identity and oddity required to fully master this task (Lombardi, Fachinelli and Delius 1984; Vonk 2003).

D’Amato et al. (1986) compared the performance of capuchin monkeys and pigeons trained on both a matching (‘identity’ – S+ stimulus is the same as the sample) and a conditional matching (‘symbolic’ – S+ stimulus not the same as the sample) task. The authors argued that if a subject possessed a matching ‘concept’, identity and conditional relations should be processed in different ways resulting in a larger difference in response latency when conditional tasks were interspersed among identity trials than when the reverse situation was tested. This pattern was found in the monkeys but not in the pigeons, leading the authors to conclude that the monkeys were utilising a “matching concept” on the identity tasks while the pigeons were processing identity tasks in the same manner as the symbolic conditional relations.

Other studies have also indicated that pigeons perform equally well whether the ‘matching’ pair of sample and comparison stimuli is the same or not. For example,

Wilson, Mackintosh and Boakes (1985a) found no systematic difference between matching and conditional discriminations. Similarly, in a series of experiments comparing matching and symbolic matching, Carter and Eckerman (1975) found identity between a sample and one of the comparison stimuli appeared to play no role for pigeons – “matching-to-sample is just as symbolic as is the symbolic matching problem” (p. 664). In both paradigms, according to the authors, the pigeons learned a set of specific “if ... then” conditional discrimination rules in which the sample stimulus served an “instructional” function indicating the correct comparison stimulus. Even a number of early pigeon matching experiments that purported to show a matching “concept” (e.g. Honig 1965; Malott and Malott 1970) were later criticised by Premack (1978) and Carter and Werner (1978) respectively as being solved by more prosaic means (Schrier and Thompson 1980).

While Zentall and Hogan (1974, 1975, 1976, 1978) claimed their series of matching experiments demonstrated that pigeons could learn a relational “concept”, their conclusion was not based on above chance transfer to novel stimuli, but rather on a savings effect on acquisition – that is, better performance on novel (different coloured) stimuli by those pigeons kept in the same (e.g. matching to matching) condition than those shifted to the reversed (e.g. matching to oddity) condition. However, authors such as Carter and Eckerman (1976), Carter and Werner (1978) and Premack (1978) concluded that the differing results were due to interference with learning the new task for the shifted birds rather than evidence of positive transfer in the non-shifted group.

After reviewing numerous conditional discrimination experiments with pigeons, Carter and Werner (1978) claimed that there was no evidence pigeons were capable of single-rule “concept” learning using traditional matching procedures: “... at least with the conditional discrimination procedures in common use, pigeons learn a set of sample-specific ‘if ..., then ...’ rules” (p. 594). However, despite their pessimistic appraisal, Carter and Werner (1978) were “unwilling to assume that pigeons cannot learn such concepts” (p. 596). Similarly, Wilson et al. (1985a) found pigeons in their experiments did not utilise relational information to solve matching (or oddity) problems. However, they concluded: “The present results do not, and could not, prove that pigeons are incapable of such learning. It remains quite possible that under other conditions ... evidence for relational learning could be found” (p. 309). Similarly, Premack (1983a)

suggested: “The pigeon’s poor record on generalized match-to-sample may be due more to experimental artefacts than to limitations in intelligence” (p. 355).

In fact, studies have suggested that at least some differences in performance between species may be the result of the suitability of the training procedures. According to Wright (1997), in the basic matching-to-sample format, pigeons’ preferred strategy seems to be to attend to configural patterns and physical elements rather than relational or conceptual information. However, changes to experimental methodology can alter their learning strategy to one based on the relationships between stimuli and “thereby reveal their concept-learning ability” (p. 119).

According to Sidman (1992), previous failures of non-humans to display generalised identity matching may have been caused by an irrelevant feature of the matching-to-sample procedure. Because sample stimuli are usually displayed in one display location and the comparison stimuli at two other display locations, subjects may come to identify stimuli not only by their physical characteristics but also by their location. In addition, evidence has been found for both colour and position preferences in pigeons’ matching performance, particularly during the early stages of task acquisition (Cumming and Berryman 1965).

Oddity preference effect

A number of authors have suggested that one reason for pigeons’ relatively poor performance in matching tasks is that they are particularly susceptible to the oddity preference effect (OPE), a predisposition to prefer stimuli that are relatively novel (see section 3.7.6.1.5). This phenomenon has been demonstrated in various species such as chimpanzees (Davenport and Menzel 1960), monkeys (Mishkin and Delacour 1975) and corvids (Wilson et al. 1985b), however the main focus has been on OPE in pigeons (e.g. Berryman et al. 1965; Wilson et al. 1985b; Zentall, Edwards, Moore and Hogan 1981). For example, Ginsburg (1957), Berryman et al. (1965) and Zentall and Hogan (1974, 1975) all found that (at least initially) pigeons perform better on an oddity than a comparable matching task. Wilson et al. (1985b) concluded that pigeons have “a marked preference for oddity” that “somehow interferes with [their] ability to display transfer of the matching or oddity rule” (p. 324).

According to Wright and Delius (2005), there appears to be a general belief that OPE is predetermined – an “initial preference for the odd stimulus” (Wilson et al. 1985a, p. 308) – however they claim that it is actually overlooked aspects of the experimental procedure that lead to the creation of OPE. One possibility is that pigeons frequently begin a trial by responding to the sample, an action which is then effectively extinguished due to non-reward, decreasing the possibility they will respond to the stimulus again when it appears as a comparison stimulus (Carter and Werner 1978). Whether OPE is inherent or a product of experimental procedures, it may help explain species differences in matching performance, particularly in pigeons.

In a contradictory argument, some authors claim there is little evidence for a predisposition to novelty in pigeons (Zentall, Hogan, Edwards and Hearst 1980) and in fact that pigeons “appear to be somewhat neophobic and are afraid of novelty” (Zentall 2000b, p 202). According to Zentall (2000b), this means the use of novel stimuli in matching/oddity transfer tests may lead subjects to avoid the novel stimuli and in turn skew the results unfavourably. (See D'Amato, Salmon and Colombo 1985; Oden et al. 1988; Pack et al. 1991 for examples of neophobia in other species).

Despite these purported hindrances, a number of experiments have demonstrated that pigeons can fully learn matching-to-sample under the ‘right’ experimental conditions (e.g. Wright 1997; Wright and Delius 2005). To address the problem of possible neophobia in pigeons, Zentall et al. (1981) conducted test trials using familiar stimuli that had been used in training as both correct and incorrect comparisons. The pigeons were successful and Zentall (2000b) claimed the results “suggest that pigeons use the identity relation to learn both matching and oddity” (p. 202).

Training set size

While pigeons have struggled with matching tasks using only a small number of stimuli, researchers have found that after training with a large number of stimuli for thousands of trials pigeons are able to acquire a generalised matching ability (e.g. Wright, Cook, Rivera, Sands and Delius 1988). Delius (1994) has suggested that the failure of many matching experiments with pigeons was largely due to underestimating the pigeon’s capacity and propensity for rote learning (see section 3.4.4.2.1), which would inhibit

concept learning (see also von Fersen and Delius 1989). According to Murphy and Cook (2008), pigeons often learn item-specific rules or configurations when tested with a limited number of stimuli (Carter and Werner 1978; Wright 1997; see section 3.7.6.1), interfering with relational learning.

Observing response effect

A number of authors have also demonstrated the importance of an observing response to the sample stimulus in pigeons (e.g. pecking at the stimulus) (Colombo, Cottle and Frost 2003; Zentall et al. 1974). Eckerman, Lanson and Cumming (1968), for example, found pigeons had more difficulty learning a simultaneous hue matching task without an observing response and showed serious disruption of an already established matching behaviour when the observing response requirement was removed. Wright (1997) found that as the number of pecks to the sample stimulus in a matching task increased, configural learning gave way to learning about the sample-comparison relationship. According to the author: “Pigeons making the most sample responses showed complete concept learning” (p. 119) (see also Wright 2001).

Hollard and Delius (1982) trained pigeons on both a matching and oddity task using a simultaneous matching procedure that included an observing response and correction trials (incorrect choices being followed by repetition of the same trial until a correct choice is made) during training. The training phase also used individually adapted schedules in selection and repetition of stimuli to facilitate acquisition. The pigeons were trained with white-on-black geometric shapes and were able to match novel stimuli even when the shapes were rotated by 45, 90, 135 or 180°. (Observing responses have also been used in matching experiments with other species, for example, capuchin monkeys, Tavares and Tomaz 2002).

Differential reinforcement

Another experimental parameter that appears to enhance matching-to-sample performance in pigeons is the use of differential reinforcement (previously discussed in regards to conditional discrimination, see section 3.2.3). In a differential reinforcement procedure each correct comparison choice is associated with a different outcome (a procedure also shown to improve performance in other species such as rats, Carlson and

Wielkiewicz 1976). For example, Linwick, Overmier, Peterson and Mertens (1988) found pigeons that performed near chance on a same outcome procedure with a 4-second retention interval were able to perform well above chance using differential reinforcers with a 32-second retention interval. The effect has been demonstrated in experiments when the differential reinforcement varied in hedonic value (e.g. food versus water, Honig, Matheson and Dodd 1984; wheat versus corn, Edwards, Jagielo, Zentall and Hogan 1982) and when the differential reinforcement was not hedonically different (e.g. different feeder locations, Friedrich and Zentall 2011; different coloured lights and lights versus tones, Miller, Friedrich, Narkavic and Zentall 2009). This suggests the effect is not merely the result of different behaviours elicited by the different reinforcers (such as pigeons showing increased pecking to stimuli linked with food vs. non-food, Zentall, Sherburne and Steirn 1992) being used as an additional cue.

3.7.3.2 Oddity

The inverse of matching-to-sample is non-matching, or oddity-from-sample, in which the S+ stimuli is that which does not match the sample (Irle and Markowitsch 1987). This type of experiment is often conducted using successive stimulus presentation in a similar manner to successive matching experiments. However, oddity can also be tested using simultaneous stimulus presentation where the subject must select the *different* stimulus from a number of *same* stimuli (Langworthy and Jennings 1972). However, oddity differs from the paired comparison same/different procedure in that the subject is selecting the *odd* stimulus from among a group of *same* stimuli, rather than comparing two (or more) stimuli to determine if they are *different* (or, alternatively, not *same*).

Oddity is a commonly investigated relational categorisation task and has been conducted using a wide variety of species (Bailey and Thomas 1998; Thomas 1996). For example, it has been demonstrated in birds (e.g. Benjamini 1983; Blough 1989; Lombardi et al. 1984; Pastore 1954; Wright and Delius 1994; Zentall and Hogan 1974), goldfish (Goldman and Shapiro 1979), rodents (Bailey and Thomas 1998; Langworthy and Jennings 1972; Nakagawa 1993; Wodinsky and Bitterman 1953), dolphins (Herman and Gordon 1974) and primates (Bernstein 1961; Davis, Leary, Stevens and Thompson 1967; Levine and Harlow 1959; Moon and Harlow 1955; Thomas and Boyd 1973;

Thomas and Frost 1983; Thomas and Kerr 1976; Shaffer 1967; Strong and Hedges 1966).

As with matching-to-sample, not all species appear to master the oddity task equally well. Strong and Hedges (1966) compared cats, raccoons, chimpanzees and rhesus monkeys on an oddity problem and found that neither cats nor raccoons achieved a 90% criterion within the maximum number of sessions allowed. Both the rhesus monkeys and chimpanzees were able to achieve criterion using identical training procedures, with the chimpanzee needing the fewest number of sessions. Other reports on cats have suggested they have difficulty mastering oddity problems (Boyd and Warren 1957; Warren 1960). Warren (1960), for example, found only one of five cats achieved good performance. Despite their success, even monkeys appear to be affected by perceptual factors in oddity learning experiments (Macphail 1982).

However, as with matching experiments, authors such as Macphail (1982) claim species difficulties with particular tasks can be due to procedural factors. Pigeons, for example, demonstrated improved oddity learning with changes to contextual variables (e.g. when an increased number of alternative (matching and incorrect) stimuli were presented along with a single odd stimulus, Zentall et al. 1980) and where “negative instances” (trials in which no correct response is possible) were interspersed among conventional trials (Zentall and Hogan 1978).

Similarly, early reports suggested rats were incapable of learning the oddity task (Koronakos and Arnold 1957; Oldfield-Box and Kay 1963). However, other studies found rats were successful using different experimental procedures, such as prior training on a serial reversal learning task using the same or similar stimuli (Wodinsky and Bitterman 1953), unconventional reinforcement such as intracranial stimulation or strychnine (Hudspeth 1964; Johnson and Levy 1968) or olfactory stimuli (Langworthy and Jennings 1972).

Despite claims that non-primate animals have successfully performed oddity problems on a ‘conceptual’ basis, some authors suggest that non-primate studies may have been influenced by confounding variables or be subject to competing interpretations (Bailey and Thomas 1998; Macphail 1982; Premack 1978; Steirn and Thomas 1990; Strong and

Hedges 1966; Thomas 1994, 1996; Thomas and Boyd 1973). For example, Langworthy and Jennings (1972) used ping-pong balls saturated with food odours to conduct a series of olfactory-based oddity problems in rats. The rats performed significantly better than chance, suggesting they had learned the ‘concept’. However Thomas (1996) argued that as the food reinforcers were available only under the odd ping-pong ball the rats might have been able to smell the food and choose the correct ball accordingly.

In a subsequent experiment, Thomas and Noble (1988) used a similar apparatus but modified the procedure to control for olfactory cueing. However, they were uncertain of their results because the rats only performed above chance on the second trial, leaving open the possibility they had simply mastered a learning set. This means that they had learned from their correct and incorrect choices in trial one and used that information appropriately in trial two. Using this interpretation, the rats could be said to be using a win-stay, lose-shift strategy (see section 2.2.2.1) – if they gain food (win) for choosing a stimulus in trial one they stay with that stimulus in trial two, if they aren’t rewarded (lose) for choosing a stimulus in the first trial they should shift to the alternate stimulus in the second trial. The authors suggested additional studies using more extensive training on each oddity problem, as Langworthy and Jennings (1972) had done, while maintaining the cueing controls might lead to more conclusive results.

When one of the authors conducted such a study (Bailey and Thomas 1998), they found that none of the rats exceeded chance on total correct responses on the first trials of the 60 transfer sessions (the criteria required by the authors). However, they found that one of the rats had two statistically significant near-perfect runs of correct responses on trial one during the early stages of the transfer sessions, leading the authors to conclude that he had used an oddity cue at the beginning of the experiment, before abandoning it in the later stages. Bailey and Thomas (1998) suggested that the rat may have changed strategy because the scents used began to be repeated (albeit in different combinations), with odours that had previously been correct now being incorrect, confounding first-trial performance. The ability of rats to remember odoriferous stimuli may also have affected the other rats overall performance, as well as a lack of motivation to utilise a conceptual strategy in the first trial when a learning set strategy provided rewarding results for the rest of each session. As to why only one rat showed significant first-trial correct responding, the authors noted that it was the only subject to investigate all the

stimuli before making a choice, leading them to suggest the introduction of a viewing period.

Macphail (1982) claims that because oddity problems can be solved in ways that do not require an oddity 'concept' (see section 3.7.6.1), it cannot be proved that non-humans possess a generalised oddity principle. However, others (e.g. Bailey and Thomas 1998; Strong and Hedges 1966; Thomas and Boyd 1973) have argued that successful performance on the first trial of a new oddity problem can be used as evidence that the solution is based on an oddity principle. Correct responding at levels considerably above chance on first trials of oddity problems has been found in a number of studies, including those with monkeys (Levine and Harlow 1959; Shaffer 1967; Thomas and Boyd 1973).

Similarly, while Benjamini (1983) claimed a careful analysis of the results and experimental procedures used in a number of oddity learning experiments with birds (Berryman Cumming, Cohen and Johnson 1965; Fried 1972; Ginsburg 1957; Pastore 1954; Zentall et al. 1974) made it difficult to state definitively that the birds had actually learned to respond to oddity rather than utilising other methods. For example, the performance of Pastore's (1954) canary could be attributed to formation of a discrimination learning set; Berryman et al.'s (1965) pigeons appear to have utilised a response sequence and Zentall et al.'s (1974) pigeons used positional cues. However, when Benjamini (1983) used more rigorous criteria (e.g. evaluation based on the first presentation of transfer trials, better experimental design) in testing oddity learning in ravens and gulls, he concluded that both species were "highly capable of oddity learning" (p. 191) and that the results were "the first unequivocal demonstration of oddity learning by birds" (p. 187).

Thomas (1996) has created even stricter requirements, arguing that only primates have demonstrated oddity concept learning under what he considers properly controlled conditions (see section 6.1.5). He claims he has yet to find a non-primate study that can withstand rigorous examination, although he says Langworthy and Jennings' (1972) rat study (above) came close. However the author blames this on methodological problems rather than a lack of capability in non-primates and suggests it is only a matter of time before a successful experiment (at least according to his criteria) is conducted.

3.7.3.3 Paired comparison same/different

Unlike matching and oddity, same/different categorisation using the paired-comparison same/different procedure has not been demonstrated in a wide variety of animals. It has been shown in a number of what are generally considered the more ‘intelligent’ primate species including monkeys (Bhatt and Wright 1992; Czerny and Thomas 1975; Flemming et al. 2007; Fujita 1983; Katz, Wright and Bachevalier 2002; King 1973; Wright and Katz 2006; Wright et al. 2003; Wright, Santiago and Sands 1984; Wright et al. 1983), baboons (Bovet and Vauclair 2001; Wasserman, Fagot and Young 2001) and chimpanzees (Premack 1971, 1976; Robinson 1955). However, many other species have struggled with the task, leading authors such as Premack (1978, 1983b) to suggest that it was unlikely any non-primate would be capable of same/different discrimination.

Wasserman et al. (1995) suggested that limiting factors in experimental procedure might have led investigators to underestimate the cognitive capacity of their subjects in same/different experiments. These include the overly restrictive use of only a few experimental paradigms (Lombardi et al. 1984; Macphail and Reilly 1989) or the use of only small numbers of simple stimuli (Santiago and Wright 1984). (See Wright 1992 and Zentall 1993 for further discussion).

As Wright et al. (2003) point out, many species that originally failed in same/different experiments have since succeeded using “procedures that better fit their disposition” (p. 184). One such example is the pigeon. Despite their proficiency in perceptual categorisation tasks (see section 3.4.3.1), early experiments with pigeons showed they had difficulty in performing both matching-to-sample (see section 3.7.3.1) and paired-comparison same/different categorisation tasks (Herrnstein 1985; Premack 1983b; Thompson 1995), leading some authors (e.g. Mackintosh 2000; Pearce 1991) to doubt whether a relational same/different ‘concept’ was within the cognitive abilities of pigeons.

Multi-element displays

According to Delius (1994), however: “most of the evidence denying the identity-oddity concept to pigeons must be dismissed ... as being due to the employment of patently

inadequate methods” (p. 37). Indeed, pigeons have now demonstrated paired-comparison same/different categorisation after training with multi-element visual stimuli. In one such study, Wasserman et al. (1995) exposed pigeons to a single slide containing 16 elements arranged in a 4 x 4 array. Pecks to one side key were reinforced if all the elements were the same; pecks to another side key were reinforced if all the elements were different. The pigeons were trained to 83% correct with 16 arrays of each kind and averaged 71% correct during the testing phase with novel slides. Young and Wasserman (1997) elaborated on Wasserman et al.’s (1995) design by randomly locating the 16 elements in a larger 5 x 5 array, effectively making the layout of each slide unique. Both acquisition and transfer were even more rapid than that found by Wasserman et al. (1995).

While not classified as same/different experiments, Honig and his colleagues have reported that pigeons are able to discriminate between ‘uniform’ and ‘mixture’ multi-element arrays (e.g. Honig 1991; Honig and Matheson 1995). In a series of experiments, pigeons were required to peck at one side of the screen when presented with uniform arrays (consisting of identical coloured squares) and on the other side when shown a mixture array (containing squares of two different colours in various proportions). Honig (1991) and Honig and Matheson (1995) found the pigeons could learn to discriminate between uniform (*same*) arrays and the various mixture (*different*) arrays. They concluded “it appears ... that Uniform arrays are distinctive to the pigeons” (Honig and Matheson 1995, p. 360). The uniform/mixture discriminations demonstrated by Honig (1991) and Honig and Matheson (1995) utilised only two items (two different coloured squares) and usually involved 36-element displays.

Cook and colleagues have also found that with multi-element stimuli pigeons are capable of learning the same/different discrimination across a wide variety of simultaneously presented visual items ranging from small, densely packed elements to more diffuse arrays of shapes, objects and photos (e.g. Cook 2002a, 2002b; Cook et al. 1995; Cook et al. 1997; Cook, Katz and Kelly 1999; Cook and Wixted 1997; Gibson, Wasserman and Cook 2006). The authors have found similar learning rates for these different stimulus classes (Cook 2002a; Cook et al. 1997) and suggested “that the same common discrimination framework or decision criterion is applied across all of these distinct types” (Blaisdell and Cook 2005, p. 68). In addition, the authors have found that

pigeons can transfer the discrimination not only to the same types of stimuli experienced during training (Cook et al. 1995; Cook et al. 1997), but also to a different range of stimuli (Cook et al. 1999; Cook et al. 2000).

Pigeons have also demonstrated same/different learning using an oddity-based variation on the multi-element procedure in which the *different* arrays contain only one non-identical item. For example, Cook et al. (1997) used 3 x 2 arrays of either six identical elements (*same*) or five identical elements and one odd element (*different*) of varying display types such as geometric shapes, digitised depictions of natural objects and black and white and colour photographs. Similarly, Gibson et al. (2006) successfully used a variation of the Wasserman et al. (1995) arrays containing either 16 *same* icons or 15 *same* and one *different* icon.

Meanwhile, Brooks and Wasserman (2008, 2010) created 16-item, multi-element stimulus arrays made up of mosaics, each containing 16 cells which could be filled with 16 possible luminance levels. The mosaics were generated randomly and without replacement to create trial-unique stimuli to help eliminate the possible role of individual stimulus memory through repeated presentation. The pigeons were successfully trained to 80% correct-choice performance, and testing a number of experimental manipulations led the authors to conclude that the pigeons were not using lower-level perceptual properties of the stimuli to perform the task.

The introduction of multi-element displays has been shown to enhance same/different performance in species other than pigeons. For example, Flemming et al. (2007) found rhesus monkeys initially failed in a paired-comparison same/different task in which they had to select the S+ relation (designated at the beginning of a testing session) when presented with a pair of images that was either identical or non-identical. The monkeys were able to successfully complete the task when the stimulus arrays were increased from two to eight elements.

Conditional rule

The introduction of multi-element displays is not the only experimental parameter shown to improve same/different performance. In Flemming et al.'s (2007) study

(above), once the monkeys had learned the task (either *same* or *different* for different subjects) they were unable to repeat that performance after the rewarded relation (S+) was reversed. To aid in S+ reversal learning, the authors introduced discriminative cues (background colours) to indicate which of the two relations was S+ for that trial (see section 3.7.4). Again, a change in the experimental procedure provided the information the monkeys needed to perform the task.

Training set size

Another example of changes in experimental conditions enabling a subject to succeed in same/different discriminations is increasing the number of training exemplars. According to Wasserman et al. (1995, p. 251): "... larger sets of training stimuli engender stronger generalisation performance in testing" (see also Wasserman 1993b; Wasserman and Bhatt 1992). For example, capuchin and rhesus monkeys that showed an initial lack of transfer in a same/different task using a small number of training stimuli succeeded when trained with a larger number of training exemplars (Katz et al. 2002; Wright 2010; Wright and Katz 2006; Wright et al. 2003) and a similar effect is seen in pigeons (Castro et al. 2010; Katz, Sturz and Wright 2010a; Katz and Wright 2006; Nakamura, Wright, Katz, Bodily and Sturz 2009; Wright 2010; Wright and Katz 2006). In addition, Schmidtke, Katz and Wright (2010) found the positive effect of increasing the training set was enhanced by the use of differential reinforcement (see section 3.7.3.1).

In fact, Delius (1994) argued that "the relative lack of evidence of same-different discrimination transfer to novel stimuli [in pigeons] may have been due to the use of too few training stimuli" (p. 33), a position echoed by Wright and Katz (2006). According to Castro et al. (2010), one common factor of successful same/different discrimination studies is the use of a relatively large pool of training stimuli (e.g. Blaisdell and Cook 2005; Flemming et al. 2007; Young and Wasserman 1997). They claim this is because more exemplars enhance categorical knowledge by providing more information about the category's generic features or by reducing the salience of features specific to each exemplar, or both. Prior studies in basic-level categorisation have found that even humans' ability to categorise novel stimuli improves as the number of training

exemplars increases (Homa, Cross, Cornell, Goldman and Shwartz 1973). (See below for further discussion of the effects of training set size).

Stimulus contact

Even a difference in testing procedure such as whether the subject touches the stimuli or not can have a big impact on the speed with which tasks are learned (the observing response effect is also seen in matching-to-sample studies, see section 3.7.3.1). Stimulus contact has been shown to enhance learning in primates (e.g. Harrison, Iversen and Pratt 1977; Katz et al. 2002; Meyer, Treichler and Meyer 1965; Neiworth and Wright 1994; Stollnitz 1965). Interestingly, in a test of same/different categorisation using capuchin and rhesus monkeys, Wright et al. (2003) found that while stimulus contact was required for rhesus monkeys to fully learn the same/different task, it was not necessary for capuchin monkeys. However, this difference in performance may be a function of the procedure rather than the particular species. In another experiment using a response lever procedure and no stimulus contact, rhesus monkeys were able to fully learn the same/different task (Wright et al. 1984). A study by Rumbaugh, Richardson, Washburn, Savage-Rumbaugh and Hopkins (1989) suggested that the positive difference in performance might be due to rhesus monkeys focusing on the effects of their hand's movement on the lever rather than on the hand itself.

Pigeons have also displayed improved performance with the introduction of stimulus contact in a variety of experimental paradigms. In the Gibson et al. (2006) experiment mentioned above, pigeons were initially unable to discriminate the displays of 16 *same* icons from the displays containing 15 *same* icons and 1 *different* icon (16S vs. 15S:1D). However, the pigeons were subsequently able to master the task after being required to locate and peck at the odd item in the 15S:1D displays. Cook et al. (1995) also reported rapid acquisition of a previously unsuccessful oddity-based same/different discrimination following the introduction of a peck requirement procedure.

In addition to using stimulus contact to improve attention, making the task choice by responding directly to the stimulus has also been shown to improve discriminative performance (Bitterman, Tyler and Elam 1955; Castro et al. 2010; Wodinsky, Varley and Bitterman 1954). Castro et al. (2010) surmised that when experimental subjects are

forced to respond away from the stimulus (such as by selecting one of two report keys), the intermediate step between observing the stimulus and receiving reinforcement slows learning of the correct response.

Number of stimulus elements

Despite these results, the introduction of methodological changes to improve performance in same/different experiments has not gone without criticism. One of the procedures that has attracted the most attention is the use of multi-element stimuli. It has been argued that multi-element stimuli may in fact introduce perceptual cues that subjects are using instead of relational or ‘conceptual’ ones. The contention is that the subjects in these experiments are using the greater comparative variance (entropy) of multi-element arrays or even mere perceptual regularity to perform the discriminations (Katz and Wright 2006; Katz, Wright and Bodily 2007; Vonk 2003) (see sections 3.7.6.2.2 and 3.7.6.2.3 for more detailed discussions of perceptual regularity and entropy). There is some evidence for this viewpoint. For example, in a pair of experiments examining the effect of the number of stimulus elements on same/different performance, the authors found that when the number of elements in the stimulus arrays was reduced, both pigeons and baboons were unable to perform the discrimination (Wasserman, Young and Fagot 2001; Young, Wasserman and Garner 1997). One way to reduce the possibility that these types of perceptual cues are being used in same/different discriminations is to conduct experiments using only two items to signify *same* or *different*, with two-item displays having the lowest possible entropy difference (Blaisdell and Cook 2005; Premack 1983b).

Initial reports that pigeons might be able to solve two-item same/different discriminations have been mixed. Wright et al. (1983) found that while monkeys were able to transfer a same/different discrimination to novel stimuli using a two-item, simultaneous procedure in which the stimulus relation was indicated by pressing one of two keys, pigeons were unable to do so. Even after nearly 20,000 training trials using 210 different pictures, the pigeons’ discrimination accuracy dropped from 80% to only 62% correct upon transfer to novel testing pictures.

In a similar procedure, Santiago and Wright (1984) trained pigeons to peck one key when presented with two identical colour pictures and another key when presented with two different colour pictures. The pigeons were able to transfer the performance to novel pictures, however, as with Wright et al. (1983) above, performance dropped from that seen during the training trials. According to Katz and Wright (2006), this performance was the first and best two-item same/different transfer in pigeons (before their study), however the drop in performance with the introduction of the transfer stimuli meant it was only “partial concept learning” (p. 84). Blaisdell and Cook (2005) also claimed there was evidence of item-specific learning during task acquisition, as well as the possible contribution of memorisation as the *same* and *different* stimulus pairs were presented in a fixed sequence through both the training and transfer trials.

Edwards et al. (1983) trained pigeons to make one response (pecking a key) when presented with a pair of matching shapes and another response (pecking a different key) when shown a pair of shapes that was different. To further differentiate the response keys, a correct response to each key was reinforced with a different outcome (i.e. access to peas or wheat) (see discussion of differential reinforcement in section 3.7.3.1). The authors claimed their study provided “evidence that pigeons can show reliable amounts of concept transfer” (p. 354), but acknowledged that at the same time “performance was primarily under the control of stimulus-specific associations” (p. 354). The pigeons were unable to transfer the discrimination to the first trial of novel (coloured) stimuli and showed evidence of item-specific, rather than relational, learning. The experimenters did demonstrate savings in subsequent acquisition (better performance on novel stimuli by subjects kept in the same rather than the reversed condition), suggesting “some contribution of a conceptual representation to the task” according to Blaisdell and Cook (2005, p. 68). However, Wilson et al. (1985b) found no evidence of relationally based transfer in pigeons using a similar procedure.

In contrast to these ambivalent results for pigeons on two-item same/different learning, Blaisdell and Cook (2005) have utilised a procedure that has garnered a more definitive outcome. A common aspect of simultaneous same/different experiments has been the requirement for the subject to make a different response to the presentation of two stimuli depending on whether they are the *same* or *different*. In Blaisdell and Cook’s (2005) experiment, the pigeons were simultaneously presented with two pairs of stimuli

– one pair containing identical coloured shapes, the other containing items that differed in both colour and shape – and were required to peck at the correct S+ stimulus pair. The pigeons were able to successfully transfer the discrimination to novel stimuli.

Blaisdell and Cook (2005) argue that requiring subjects to respond directly to the S+ stimulus rather than a separate response key may have led to greater attention being paid to the stimulus features (see above). In addition, they suggested the pigeons might have been helped by other procedural aspects of their experiment such as the use of two stimulus dimensions (colour and shape) being used, as well as the use of relatively simple geometric stimuli to encourage relational, rather than item-specific, learning. The experiment also used a large number of unique training exemplars. According to the authors, this may have decreased the possibility for memorisation and increased the birds' need to pay attention to relational information, in contrast to the smaller training sets employed by Santiago and Wright (1984) and Edwards et al. (1983) (see above).

Despite Blaisdell and Cook (2005) using a large number of different displays, Wright and Katz (2006) criticised the study because those displays were made up of too few unique training and transfer items resulting in insufficient variation and the potential for only partial concept learning. According to Wright and Katz (2006), even humans require variation in the exemplars to adequately learn rules (e.g. Chen and Mo 2004). However, as Blaisdell and Cook (2005) point out, even though their displays were composed of combinations of items from a set of only six different shapes and six different colours, when combinations of *same* and *different* pairs are taken into account there were 32,400 unique displays available for use.

Wright and Katz (2006) attempted to address what they saw as a flaw in Blaisdell and Cook's (2005) study and instead used an increasing training set of unique photos to test pigeons for two-item same/different learning. They found that while the pigeons were initially unable to perform the discrimination using smaller training sets, they were finally able to meet the authors' criteria for "full" concept learning (transfer equivalent to baseline performance and both above 80%) using a 256-item set size. This result was contrasted with the performance of two species of monkey in the same experiment that were able to succeed using a 128-item set size. (Another two-item same/different

experiment by Katz and Wright (2006) using pigeons showed increasing the training set size from 8 to 1024 items improved transfer performance from 51.3% to 84.6%).

Wright and Katz' (2006) findings led them to conclude that pigeons require a larger training set than some other species to fully learn a two-item same/different task and that previous failures by pigeons in these types of experiments could be attributed to the use of too few exemplars. The authors stress that the pigeon's need for more training exemplars "does not necessarily mean that pigeons are cognitively deficient in comparison with nonhuman primates in their ultimate ability to learn an S/D abstract concept" (Katz and Wright 2006, p. 85). According to Delius (1994), the use of too few training stimuli would enable pigeons, with their prodigious memory (see section 3.4.4.2.1), to respond in a rote fashion during training. This would inhibit concept learning and make them more sensitive to the novelty of the transfer stimuli, thus degrading their performance (the same phenomenon proposed for matching, see section 3.7.3.1). (Interestingly, Wright et al.'s, 1983, early study with pigeons failed using a 210-item set, see above).

Castro et al. (2010) took into account prior research on same/different discrimination and designed what they believed might be "the most effective task for pigeons to exhibit strong learning and transfer of a same-different concept" (p. 24). They used a combination of procedural elements that had previously been associated with improved same/different performance – prior training with multi-element stimuli, simultaneous presentation of stimuli, a conditional discrimination rule, an observing response requirement, direct responding to stimuli and a large training set size. The authors found that while choice accuracy declined when the number of icons in the arrays dropped to 4 and 2, it was still significantly above chance.

Similar experimental innovations have been utilised with other species to demonstrate two-item simultaneous same/different learning. A comparable direct response procedure to that used by Blaisdell and Cook (2005) was employed by Chausseil (1991) to show two-item simultaneous same/different learning in coatis (a relative of the raccoon). The coatis were presented with two pairs of shapes (two *same* and two *different*) and were reinforced for selecting the S+ pair. They were then able to transfer that performance to novel shapes. They were also able to respond correctly to stimuli of different design to

the training stimuli (e.g. increased number of items per array, items contiguous to each other, use of hue/brightness as the cue). A similar procedure was also used successfully with chimpanzees (Robinson 1955), where the subjects were trained using three-dimensional geometric shapes and were able to transfer the discrimination to household objects.

Rhesus monkeys in Flemming et al.'s (2007) study (see above) were initially unable to extract relational information from a pair of clipart images, but were able to perceive relations with the introduction of multi-element (eight-item) arrays. However, they were unable to reverse the discrimination until a discriminative cue was used to facilitate rule-switching (see section 3.7.4). Once these two factors (increased elements and discriminative cues) were introduced, the monkeys were then able to perform the discrimination with lower-item arrays, even back down to the critical two-element pairs. Flemming (2011) again used a conditional background cue, as well as trial-unique stimuli and a large training set, to test capuchin monkeys on a two-item same/different task. He found two of the capuchins succeeded in the two-item task without prior training with a multi-element array, while four additional capuchins succeeded with four-item displays.

Finally, Fujita (1983) showed Japanese monkeys, who had previously struggled with matching-to-sample tasks using a small training set (Fujita 1982; see Fujita 1983 for more examples), were able to transfer a two-item same/different task using a training set of only two different stimulus items by using simple stimuli (colours) and a variable-interval reinforcement schedule (in which a response is rewarded after an unpredictable amount of time has passed).

Three-dimensional stimuli

Another procedural innovation aimed at facilitating two-item simultaneous same/different learning was used by Keddy-Hector et al. (unpub.) in a study with pigs. Instead of the usual two-dimensional stimuli, the authors used three-dimensional stimuli to represent *same* and *different*. The pigs were able to select one of two different symbols depending on the object relation displayed using both artificial and naturally occurring objects and transfer that performance to novel objects and novel

combinations. According to the authors, the use of three-dimensional stimuli may be more salient for animals. (Another factor that may have contributed to the pigs' success in the Keddy-Hector et al. (unpub.) study was the use of stimulus contact with the objects at the beginning of each trial, see above).

Three-dimensional objects were also used in successful simultaneous same/different experiments with dolphins (Mercado, Killebrew, Pack, Macha and Herman 2000). Bovet and Vauclair (2001) used three-dimensional objects (food and non-food items) to demonstrate simultaneous same/different categorisation in baboons, claiming it "facilitated" performance (p. 474). Peterson, Meagher, Chait and Gillie (1973) even suggested that the use of only two-dimensional stimuli may inhibit animals' categorisation abilities. Weinstein (1941) found relatively comparable matching-to-sample performance between rhesus monkeys and three-year-old children using three-dimensional stimuli, but a large difference in ability favouring the children when two-dimensional stimuli were used.

Functional same/different

Finally, aside from using low-entropy, two-item stimuli, another way to rule out the use of low-level perceptual mechanisms in a same/different task is to use stimuli which contain no perceptual cues to sameness or difference. Bovet and Vauclair (2001) demonstrated that non-language trained baboons were able to identify pairs of items as *same* or *different* based on functional criteria (i.e. food versus non-food items) and transfer that learning to new exemplars (see section 3.5, associative categorisation). For example, they had to classify as *same* an apple and a banana or a padlock and a cup and as *different* an apple and a padlock – meaning they had to identify as *same* items that were perceptually different. The authors claimed their subjects had mastered "conceptual identity" and that the task was more difficult than perceptual *same/different*. Because it was based on the use of "abstract relations not only between objects, but also between concepts" (p. 470), the authors claimed it was equivalent in difficulty to conceptual matching (see section 3.7.5).

A number of factors assisted in the baboons' performance in Bovet and Vauclair's (2001) study. They had previously been successfully trained in functional (food vs. non-

food) categorisation (Bovet and Vauclair 1998, see section 3.5.2) and perceptual simultaneous *same/different* categorisation using food and non-food items (Bovet and Vauclair 2001, experiment 1, see above). The authors also suggested the baboons performance was facilitated by the use of three-dimensional stimuli: “It is likely that the use of 3-D stimuli made the function of the objects more salient (Bovet and Vauclair 2000) and, therefore, augmented the rapid generalisation from a few training objects to novel food and nonfood objects and facilitated the demonstration of conceptual identity” (Bovet and Vauclair 2001, p. 474).

3.7.3.4 Cross-modal same/different

An interesting variation of the same/different task is to utilise stimuli of different sensory modalities within the same experiment. The results of cross-modal relational categorisation experiments in animals have been mixed.

A number of primate species have demonstrated the ability to match stimuli in one sensory modality to the same stimuli in another modality. For example, Cowey and Weiskrantz (1975) used edible and inedible shapes presented first in darkness and then in the light to demonstrate cross-modal matching from touch to vision in rhesus monkeys, while Davenport and Rogers (1970) showed chimpanzees and orangutans were able to use touch to select an object from between two different objects that matched a visually presented object and transfer the performance to novel stimuli. Hashiya and Kojima (2001) showed a chimpanzee could acquire an audio-visual matching-to-sample task, in which a sample sound had to be matched to a photograph that corresponded to that sound.

Learning the same/different task in one modality and then transferring it to another has been less successful. There is evidence that, at least in some circumstances, the ‘identity’ concept required for relationally based matching-to-sample seems to be limited to the modality and even to the general class of stimuli with which it was developed. Monkeys can successfully transfer a matching performance in the visual modality to novel stimuli after training on as few as two exemplars (D’Amato, Salmon and Colombo 1985). However, without extensive training in the new modality, it does not extend to audition (D’Amato and Colombo 1985) or to touch (Milner 1973) or even

to other classes of visual stimuli (D'Amato and Colombo 1989; D'Amato, Salmon and Colombo 1985). D'Amato et al. (1986) queried whether this limitation is due to the fact that the matching concept is not well-articulated or because irrelevant contextual cues gain stimulus control to an unusually strong degree in animals.

Similarly, Young and Harlow (1943) reported a high level of generalisation of the oddity solution by rhesus monkeys using test stimuli that were similar in at least one physical dimension to the training stimuli. However, when Meyer and Harlow (1949) tested rhesus monkeys on oddity problems in which the test stimuli differed markedly from the training stimuli, the monkeys were unable to generalise their oddity performance (Benjamini 1983). A similar result was observed in Benjamini's (1983) testing of oddity learning in ravens and gulls, however, the author suggested that this phenomenon was due, to some extent, to the restriction of stimulus variety in the experimental situation.

Despite these poor results on immediate cross-modal transfer of same/different discrimination, the fact remains that, with training, monkeys can perform the task in more than one modality (see also Wright, Shyan and Jitsumori 1990). This supports Herman et al.'s (1989) argument against the idea of "modality specificity", in which advanced, or even simple, cognitive skills are largely restricted to each species' dominant sensory modality. Their study showed bottlenosed dolphins, considered an "auditory specialist", could perform approximately equally well on a visual matching-to-sample task as they did on auditory-based problems. Similarly, visually dominant pigeons are able to learn auditory, as well as visual, same/different tasks (Cook and Brooks 2009). Dolphins have also demonstrated the ability to perform matching-to-sample in three different modalities – vision, passive listening and active echolocation (Herman, Pack and Wood 1994).

3.7.3.5 Language-based same/different

While the vast majority of same/different experiments are conducted using the type of matching-to-sample, oddity and paired-comparison procedures described above, a number of experiments have been designed based on human language principles. One of the more unambiguous demonstrations of same/different learning in animals, and that

which seems to mostly closely resemble the language-based human expression of identity relations, is found in experiments in which arbitrary symbols are used to indicate relational concepts. Premack (1971, 1976) demonstrated that chimpanzees can learn to use tokens representing *same* and *different* and place them between objects manifesting the corresponding relationship. The chimpanzees are then able to choose the appropriate token when novel pairs of objects (either the same or different) are presented.

It is worth noting, however, that authors such as Edwards et al. (1983) argue that the use of response keys representing *same* and *different* used in more conventional same/different experiments mirrors Premack's use of tokens as symbols which act as an "arbitrary stimulus that represents a class of conceptually related stimuli" (Edwards et al. 1983, p. 350). Zentall, Edwards and Hogan (1983) describe their experiments (see Edwards et al. 1983 in section 3.7.3.3), in which they trained pigeons with a variation of Premack's symbol procedure using response keys with shapes, hues and lights serving as stimuli, as: "Teaching pigeons the 'words' same and different" (Zentall et al. 1983, p. 285). The authors used a number of experimental techniques to enhance stimulus discriminability (e.g. observing responses, differential reinforcement, differential spatial positions and redundant stimulus cues, see section 3.7.3.3). Despite the somewhat ambiguous nature of their results (see section 3.7.3.3), the authors argued that their results suggested that: "Pigeons appear capable of using the symbols 'same' and 'different' to categorise new exemplars of the concepts in a manner qualitatively, if not quantitatively, similar to that of language-trained chimpanzees" (Edwards et al. 1983, p. 354).

Even more evocative of human-like same/different learning is the performance of an African Grey parrot called Alex. After previously being trained to verbally identify the stimulus properties of particular objects in response to queries from the experimenter (e.g. "What colour?" – "blue", "What shape?" – "four-corner") (Pepperberg (1983), Alex was then trained with groups of objects to verbally respond with the correct category label (e.g. "colour" or "shape") in response to the questions "What's same?" and "What's different?" (Pepperberg 1987) or even report "none" to the same questions when objects were totally dissimilar or identical respectively (Pepperberg 1988). Alex

was able to transfer the performances to new combinations of training stimuli and to novel stimuli.

3.7.4 Same/different conditional discrimination

This type of experiment combines two separate cognitive skills – the ability to categorise stimuli based on whether they are the same or different (see section 3.7.3) and to implement ‘if-then’ (if this happens then do that) conditional reasoning (see section 3.2). According to Thomas’ (1980, 1986, 1996) hierarchy of learning abilities (see section 1.3.2.1), the addition of the conditional discrimination procedure requires a higher level of learning ability or ‘intelligence’ than relational categorisation alone and sits at level seven of Thomas’ eight-level ordinal scale. According to Thompson and Oden (1996): “An even more complex variation of a same/different discrimination is the conditional S/D discrimination task” (pp. 151-152). There has not been an extensive history using this type of experimental procedure; however it has been tested using both the matching/oddity and the paired comparison same/different paradigms.

Spaet and Harlow (1943) combined conditional discrimination and oddity problems to show rhesus monkeys could learn to choose the odd item among brass doorbell buttons or T-shaped objects on a yellow tray, and choose either of the non-odd items on a black tray. However, the large number of trials taken to master the task (4320-6840 trials) led Thomas and Kerr (1976) to suggest that the monkeys most likely learned the specific configurations.

Thomas and Kerr (1976) also combined a conditional discrimination with an oddity task; however they used a one-trial procedure (i.e. using non-repeating stimulus configurations) to eliminate the possibility of configuration learning. They took three adult squirrel monkeys that had previously successfully acquired a one-trial oddity problem and superimposed a tray-brightness, stimulus-response contingency. Responses to the odd objects were rewarded on a white tray and responses to the non-odd objects were rewarded on a black tray, with the objects being randomly selected from a stimulus pool of 124 wood forms and plastic toys on each trial. The monkeys were all able to achieve criterion performance of 90%, leading the authors to conclude they were utilising a “conceptual” solution.

Edwards, Miller and Zentall (1985) used only two shapes to train pigeons to respond on the basis of either *same* or *different* in a simultaneous matching task based on the presence of two different light levels in the conditioning chamber. Transfer tests were conducted with two colour stimuli resulting in a weak but significant evidence of transfer. Delius (1994) considered the result was “remarkable” considering the small number of training stimuli. According to Delius (1994), the conditional variant was likely to be responsible for promoting rule learning.

Burdyn and Thomas (1984) trained squirrel monkeys to select a pair of objects that were the same when presented with a single, specific triangle shape and to select a pair of objects that were different when presented with a single, specific heptagon shape. In the second part of the experiment, the authors used symbolic cues – “conceptual triangularity” as the cue for sameness and “conceptual heptagonality” as the cue for difference – with the triangles and heptagons being selected randomly on each trial from a pool of about 120 different variations of each shape. New pairs of objects were used on each trial.

While the squirrel monkeys successfully learned the task, Burdyn and Thomas (1984) were unsure whether they had demonstrated conditional reasoning (“if a triangle is presented, then choose the ‘sameness’ pair”) or conjunctive reasoning (“a triangle and a ‘sameness’ pair go together; therefore, choose the ‘sameness’ pair when you see a triangle”). Although the paper was titled as “conditional discrimination”, the authors acknowledged that either tactic would have solved the problem. Conjunctive reasoning (used in tandem with a categorisation problem) is also at level seven of Thomas’ hierarchy (Thomas 1980).

More recently, Flemming et al. (2007) have demonstrated that rhesus monkeys are able to perform same/different conditional discriminations using background stimulus colours to indicate whether to choose *same* or *different*. The stimulus panels contained two rows of clip-art images – one row of identical images and one row of all different images. When the background of the panel was black, the *different* row was the rewarded stimulus, when the panel was pink, the *same* row was rewarded. In this case, the authors did not set out to directly test the same/different conditional discrimination; rather they used the conditional cues to enable the monkeys to reverse a previously

learned same/different discrimination. Flemming (2011) used the same conditional procedure to demonstrate two-item same/different learning in capuchin monkeys (see section 3.7.3.3).

Castro et al. (2010) showed pigeons could discriminate simultaneously presented arrays of 16 *same* and 16 *different* icons when the correct choice was conditional on the colour of the stimulus background, demonstrating “nearly perfect” transfer to novel testing arrays. The pigeons were also able to perform the task using 24-, 20-, 12- and 8-icon arrays, although accuracy declined with 4- and 2-icon arrays. In a further study, Castro and Wasserman (2010) found that varying the size and spatial organisation of the stimulus icons had almost no impact on conditional same/different discriminative performance, suggesting learning was not tied to the particulars of the training stimuli. The authors suggested this might be result of using a large pool of multidimensional, colourful stimuli, making any one particular perceptual dimension less relevant.

3.7.5 Same/different second-order relationships

While not tested in this study, it is worth mentioning the final level of Thomas’ (1980) hierarchy of cognitive abilities that also involves same/different discriminations – second-order same/different relationships (also called relations-between-relations or relational matching). This task involves a form of analogical reasoning, requiring the subject to judge whether the relationship between one pair of stimuli is the same as, or different from, the relationship between another pair. One way in which this ability is tested is by seeing whether an animal can match a pair of identical objects with a different pair of identical objects instead of a pair of non-identical objects. Likewise, a non-identical pair should be matched with a different non-identical pair and not an identical pair. Basically, subjects are shown a sample pair of items that are either the same or different and must select the choice pair that is related in the same way (e.g. ‘if AA, choose BB, not CD; if AB, choose CD, not EE’) (Flemming et al. 2007).

This type of task is even more complex than same/different because it involves not just the relationship between similar or dissimilar elements, but also the relationship between relationships (Fagot, Wasserman and Young 2001; Pearce 1997; Thompson and Oden 2000; Tomasello and Call 1997). According to Thompson (1995, p. 211),

second-order same/different tasks are “fundamentally more complex than either physical matching or paired comparison S/D tasks.” Flemming et al. (2007) described second-order same/different relationships as “...one conceptual task for which some researchers propose a major difference in the abilities of some animals and those of others ... [the] ability to reason analogically, the highest degree of abstract conceptualisation” (p. 55). Premack (1983a, 1988) argued that among non-humans only language-trained chimpanzees are capable of analogical reasoning and there is some experimental support for this position.

There is convincing evidence that analogical reasoning has been demonstrated in the language-trained chimpanzee Sarah using tokens of different shapes, sizes and colours and plastic symbols to represent *same* and *different* (Gillan et al. 1981; Premack 1976, 1983b). Sarah was able to correctly identify whether the relationship between one pair of stimuli was the same as or different from the relationship between another pair of stimuli (e.g. AA is the same as BB). She was also able to complete analogous same/different relationships by selecting the correct stimuli (e.g. AA is the same as B?). (Impressively, in addition to figural analogy problems based on same/different relations such as size, colour and markings, she was also able to solve conceptual analogy problems using household objects in which the relations were functional and spatial).

Chimpanzees with and without language training have been directly compared on a simultaneous second-order same/different task in which the subject is presented with two pairs of stimuli and is required to indicate the relationship between them (e.g. AA and BB or, alternatively, AX and BY are both *same*, while AX and BB are *different*) (Pearce 1997). Utilising this experimental design, Premack (1983b) and Premack and Premack (1983) found language-naïve chimpanzees were unable to successfully complete the task while language-trained chimpanzees performed the discrimination fairly easily.

Other experiments suggest it may be some aspect of training with abstract symbols, rather than language training itself, that encourages relational matching (Shettleworth 1998; Thompson and Oden 1996). Thompson, Oden and Boysen (1997) found language-naïve chimpanzees could match *same* and *different* object pairs spontaneously. However, the four of the five chimpanzees in the experiment that mastered the task had

previously had training in the use of numerical problem solving and symbolic tokens, while the fifth that lacked the prior training failed. A similar result is found in human children. Gentner (2003) found five-year-olds are able to complete an analogical reasoning task easily, but three-year-olds (who appear unable to referentially label real world objects) fail the task. However, when aided by the presence of labels, the three-year-olds' performance is comparable to that of the five-year-olds, suggesting labels play a critical role in relational matching (Flemming et al. 2007).

Flemming et al. (2007) had promising results with language-naïve rhesus monkeys, who demonstrated the ability to “label” the relations in conditional paired-comparison same/different discriminations by performing the discriminations bi-directionally – both choosing the correct relational pair in the presence of the colour cue and choosing the correct colour in the presence of the corresponding relation (see section 3.7.4). This led the authors to speculate that the monkeys were using the cues as representational symbols or tokens in a similar manner to chimpanzees who then manifested successful relational matching performances (Premack and Premack 2003; Thompson and Oden 2000). Despite this, the monkeys were unable to learn a paired-relations matching-to-sample task using trial-unique stimuli, leading the authors to concede that bidirectional discrimination did not necessarily elevate the discriminative cues to the level of symbols and that there was a qualitative difference between the relational matching task demonstrated by language-trained chimpanzees and simply re-coding relations symbolically.

Despite the evidence supporting Premack's (1983a) contention that language training (and possibly abstract symbol training) is a prerequisite for analogical reasoning, subsequent studies have suggested he may have been premature. While not directly testing relational matching, Spinozzi (1993) found that not only could non-language or token trained chimpanzees perceive second-order relationships as infants, but older chimpanzees could actually construct them by spontaneously sorting objects according to second-order relations – that is, they were able to construct similarity-difference relations between groups of objects.

Similarly, Oden, Thompson and Premack (1990) had suggestive results with non-language trained infant chimpanzees. The authors found the young chimpanzees could

spontaneously perceive second-order same/different relationships. The chimpanzees were allowed more than five minutes to handle a pair of objects that was either the same (AA) or different (WX). They were then given a new object pair, which was either the same relation experienced in the first session (BB) or the alternative relation (YZ). The relation experienced in the first session affected handling times in the second session. Despite demonstrating the ability to detect second-order same/different relations, however, the infant chimpanzees were unable to actually match object pairs based on their relationship in a relational matching-to-sample task despite extensive training efforts. Human children also fail to match same/different second-order relationships before the age of about five years (House, Brown and Scott 1974; see above) but, like the infant chimpanzees in Oden et al.'s (1990) experiments, can perceive those relationships in preference-for-novelty tests at around 29 weeks of age (Tyrrell, Stauffer and Snowman 1991).

Smith et al. (1975) found that two language-naïve adult chimpanzees were able to master an actual relational matching task. However, Thompson and Oden (1996) claim the chimpanzees may have been utilising non-relation configurational cues such as symmetry or complexity. They also claim that because the experiment used differential reinforcement, only trial-one data from the testing phase (which was not reported) was relevant – despite the fact that the majority of relational categorisation studies do not have this requirement.

Fagot et al. (2001) determined non-language trained baboons could successfully discriminate relations between relations in a delayed relational matching-to-sample task using 16-item arrays. However, the performance on the *different* arrays deteriorated as the number of items in the arrays decreased, while the performance on the *same* arrays remained high regardless of icon number. According to Flemming et al. (2007), these results showed that for the baboons the task remained entropy dependent (see section 3.7.6.2.3); based more on a general perceptual sense of the different amounts of variation in the arrays rather than a cognitive ‘concept’ of *same* versus *different*. A similar procedure was used to demonstrate relational matching in pigeons (Cook and Wasserman 2007) and, although they did not test for it, the authors acknowledged that it was likely the pigeons’ performance would similarly degrade with lower-item arrays.

More conclusively, language-naïve orangutans and gorillas have demonstrated second-order relational matching based on shape and colour (Vonk 2003). The subjects were able to correctly select the matching *same* stimuli even when the incorrect stimuli were a closer visual match to the sample stimuli. They were also able to match stimuli according to what dimension was shared between objects pictured in the same stimulus. The author suggested the experiments showed that “language or symbolic token training is *not* a necessary condition for the acquisition and instrumental use of concepts pertaining to the relationship between items” (p. 85).

According to Vonk (2003), the fact that their subjects succeeded while chimpanzees without language or symbol training failed (Premack 1983b; Premack and Premack 1983; Thompson et al. 1997) may have been due to species differences but was more likely due to differences in the experimental procedures or insufficient testing in chimpanzees. Vonk (2003) claims studies have indicated that non-language trained chimpanzees and monkeys “may have greater capacities for making conceptual judgments than was previously believed” (p. 86).

Finally, second-order same/different relationships have not yet been convincingly demonstrated in non-primates, leading authors such as Tomasello and Call (1997) to suggest that this cognitive ability may be unique to primates. Further testing of this ability in non-primates is required – a good candidate would be a successor to Irene Pepperberg’s language-trained African Grey parrot Alex (now deceased), who was able to demonstrate a relatively sophisticated understanding of relationships by being able to verbally identify the physical property of a group of objects that was either the same or different (Pepperberg 1987) (see section 3.7.3.4).

3.7.6 *Same/different categorisation theories*

While there is now considerable evidence that a number of species are able to perform same/different categorisations, authors such as Fetterman (1996) and Thompson (1995) have pointed out that a key shortcoming of this type of research in animals is the failure to identify how the subjects were able to accomplish the task.

A number of theories have been put forward to account for both matching/non-matching and paired comparison same/different performance in animals. As many authors agree with Roitblat (1984, p. 85) that: “The processes controlling delayed matching-to-sample may be very different from those controlling simultaneous matching or oddity”, the theories that deal specifically with matching and oddity have been discussed separately from theories accounting for same/different categorisation in general.

3.7.6.1 Matching/non-matching theories

It is worth noting that matching-to-sample and oddity-from-sample may be solved using different mechanisms, at least in some species. Skinner (1950) predicted that since matching and oddity appeared to be opposites, it should logically follow that it would be no more difficult to acquire one task than the other. However, this has not always proved to be the case, even in experiments conducted using similar experimental procedures. For example, while the goldfish in Goldman and Shapiro's (1979) experiment showed no systematic differences in the acquisition of matching and oddity, Cumming and Berryman (1965) found pigeons in a similar experiment demonstrated marked differences between the two tasks. The pigeons' matching performance started at chance level accompanied by strong position and then small colour biases followed by fairly rapid task acquisition to well above 90% accuracy. In contrast, oddity performance began above chance level (suggesting a preference for oddity, according to the authors) then rose more gradually to a maximum of about 90%.

In addition, matching and non-matching can themselves be learned using different strategies. Katz, Bodily and Wright (2008) even found pigeons using both configural and conditional strategies (see below) in the same matching experiment.

3.7.6.1.1 *Conditional discrimination*

Matching/non-matching tasks, which are usually carried out using successive presentation of stimuli, have proved a popular method of testing same/different relational categorisation. However, matching/non-matching tasks have also been subject to the same criticisms that have been levelled against successive testing methods generally: that is, that they can be solved using conditional discrimination rather than

identity (see section 3.2). A number of authors refer to matching-to-sample only as a conditional discrimination task (e.g. if the sample is A1, choose discriminative stimuli A1) and not in terms of same/different categorisation testing. Roitblat et al. (1990) describe delayed matching-to-sample as a conditional discrimination combining two discrimination problems – a successive discrimination to identify the sample stimulus followed by a simultaneous discrimination among the comparison stimuli to determine which one matches the sample. According to Goldman and Shapiro (1979), three-key matching procedures “are examples of conditional discriminations in which the centre sample stimulus determines which discrimination is appropriate” (p. 260) while Hanggi and Schusterman (1995) refer to match-to-sample as “a sequential form of the conditional discrimination” (p. 544).

Similarly, oddity-from-sample can be solved using a conditional discrimination. Acquisition may be accounted for in two ways – avoidance (e.g. if the sample is A1, avoid choosing discriminative stimuli A1) or approach (e.g. if the sample is A1, choose discriminative stimuli B2 or B3, whichever is available) (Carter and Werner 1978). Experiments conducted by Berryman et al. (1965) favour an approach strategy in oddity experiments with pigeons while Zerbolio and Royalty (1983) found evidence of an avoidance learning strategy in matching and oddity testing in goldfish.

In support of the conditional discrimination explanation of matching/non-matching, Shettleworth (1998) points out that pigeons trained using only a small number of stimuli do not match novel samples but apparently memorise conditional rules, such as: “if the sample was red, choose red” – the multiple-rule model of conditional discrimination (see section 3.2.4.4). Only after training with a large number of stimuli for thousands of trials are they able to acquire a generalised matching ability (Wright et al. 1988). Furthermore, pigeons do just as well in symbolic matching, in which the sample stimuli are arbitrarily associated with one or more different stimuli through reinforcement (Zentall et al. 1989; see section 3.7.3.1).

Indeed, a number of experiments have supported the view that matching/oddity tasks are simply examples of conditional discriminations (e.g. Berryman et al. 1965; Carter and Eckerman 1975; Cumming and Berryman 1961). However, Macphail (1982), while acknowledging that oddity can be solved using conditional discrimination, claimed that

genuine matching or oddity learning could be guaranteed by demonstrating immediate (trial 1 of transfer trials) transfer to novel stimulus configurations. He claimed that performance had been successfully demonstrated (80% or better) in chimpanzees, rhesus monkeys, cebus monkeys and squirrel monkeys (Moon and Harlow 1955; Strong and Hedges 1966; Thomas and Boyd 1973). In addition, oddity tasks conducted using the simultaneous method in which there is no sample stimulus are not subject to sample-specific cues and conditional interpretations (Schrier and Thompson 1980).

Sidman et al. (1982) claim: “We cannot tell by looking at a subject’s conditional-discrimination performance whether or not it involves true matching to sample” (p. 24). According to Sidman and Tailby (1982), calling a conditional discrimination performance matching-to-sample requires proof that the subject displays not only conditionality, but also equivalence. This can only be determined by further testing to prove that the relation possesses all three properties of an equivalence relation:

- i) **Reflexivity** (identity; $A = A$), e.g. if the sample is green, the subject selects green (and this can be generalised to novel exemplars).
- ii) **Symmetry** (bidirectionality; if $A = B$, then $B = A$), e.g. if a subject has learned to select vertical when the sample is green they should select green when the sample is vertical.
- iii) **Transitivity** (mediated associativity; if $A = B$ and $B = C$, then $A = C$), e.g. if a subject has learned to select vertical when the sample is green and select triangle when the sample is vertical, they should select triangle when the sample is green.

(adapted from Sidman et al. 1982)

While strong evidence for reflexivity transfer in animals has been reported (e.g. Wasserman et al. 1995; Young and Wasserman 1997; Zentall et al. 1981; Zentall and Hogan 1974, 1975, 1976, 1978), the evidence for the other two requirements is less conclusive (Zentall 1998). In a series of experiments Sidman et al. (1982) found that monkeys and baboons were unable to solve a symmetry-based problem that five-year-old children could solve and monkeys were also unable to display transitivity when tested. These results echo findings with pigeons and primates that have shown limited ability to perform in symmetry and transitivity tests (D’Amato, Salmon, Loukas and

Tomie 1985; Dugdale and Lowe 2000; Gray 1966; Hogan and Zentall 1977; Holmes 1979; Lionello-DeNolf and Urcuioli 2002; Richards 1988; Rodewald 1974; also see reviews by Dugdale and Lowe 1990; Hayes and Hayes 1992; Saunders, Williams and Spradlin 1996). However, Sidman et al. (1982) clarified that the lack of performance in previous experiments did not prove that animals were necessarily incapable of identity matching.

In fact, a number of studies have claimed to demonstrate symmetry, reflexivity and transitivity in non-human animals (e.g. sea lions, Schusterman and Kastak 1993, and macaques, McIntire, Cleary and Thompson 1987). However, as Dugdale and Lowe (2000) point out, other authors have criticised these studies, arguing that the tested relations were trained rather than emergent (see Dugdale 1988; Dugdale and Lowe 1990; Hayes 1989 and Saunders 1989 for critiques of McIntire et al. 1987, and Horne and Lowe 1996, 1997 and Lowe and Horne 1996 for critiques of Schusterman and Kastak 1993).

Manabe et al. (1995) claim they were able to demonstrate stimulus equivalence in the budgerigar “of the same general type” (p. 125) as that described by Sidman and his co-workers. In one part of the experiment, the birds were trained to make high- or low-frequency calls in response to particular colour stimuli. They were then trained in a form-to-colour matching-to-sample task using the same colours. The birds spontaneously made the correct frequency ‘colour’ call in the presence of the form that had been paired with that colour. Manabe et al. (1995) examined the possibility that the relations they found might be the result of some indirect aspect of the experimental training. However, they argued that because one of their experiments showed evidence of bidirectional spontaneous relations (i.e. if $A = B$ and $B = C$, then $A = C$ and $C = A$): “It is hard to avoid the conclusion that something more than standard conditioning processes underlies the emergent relations demonstrated in these experiments” (Manabe et al. 1995, p. 126).

3.7.6.1.2 Relative novelty

The second criticism of matching as a test of same/different is that it can be solved using relative novelty rather than identity (see section 3.7.2.1.5). A basic tenet of

habituation theory is the ability to determine whether a stimulus has been encountered before. Babies, for example, look less persistently at stimuli they have recently seen than at stimuli they have not seen before. That is, they recognise a stimulus as being either the same as or different from one recently viewed. A similar type of habituation to recurring stimuli and orienting or arousal responses to novel stimuli has also been found in a wide variety of non-human animals, including both vertebrate and invertebrate species (Peeke and Herz 1973). Novelty preference has been demonstrated in both monkeys and children using visual paired-comparison (VPC) tasks (which replicate the successive matching/non-matching procedure), which usually involve the subject looking a picture for sufficient time to habituate, and then being presented with the same picture paired with a novel picture (Wright and Delius 2005). Typically they look more at the novel picture than the familiar picture (e.g. Fagan 1974; Pascalis and Bachevalier 1999; Zola et al. (2000).

Novelty and familiarity have proved salient ‘concepts’ for pigeons, the subjects of the majority of matching-to-sample experiments (see section 3.7.3.1), with experiments showing rapid acquisition (e.g. Macphail and Reilly 1989). Shettleworth (1998) also points out that pigeons perform well in experiments in which they are reinforced for responding to a novel slide the second time it appears, but not the first.

A number of authors have pointed out the potential for transfer of matching-to-sample performance to be based on familiarity and novelty rather than identity (e.g. Oden et al. 1990; Thompson and Oden 1996). Shettleworth (1998) argues that the delayed matching paradigm, in which the subject reacts first to the sample and then to the comparison stimuli, is merely a test of relative novelty which requires the subject to determine: “‘Which did I just respond to?’ rather than ‘Are these two things the same?’” (p. 225), or, in the case of oddity, “‘Are these two things different?’” (See also Wilson et al. 1985a).

Premack (1983b) agrees, arguing that in the successive task the subject “‘simply reacts to whether or not it has experienced the item before ... ‘Old/new’ or ‘familiar/unfamiliar’ may be more suitable labels for this case than ‘same/different’” (p. 127). Zayan and Vauclar (1998) state that in matching experiments: “... a subject may

simply recognise that a matching comparison stimulus is familiar rather than explicitly judge it to be identical to the sample” (p. 89).

According to Delius (1994), while this type of generalised, passive detection of familiarity and novelty may form the basis for more sophisticated mechanisms, cognitive scientists require a more active and explicit detection of identity/oddy relations to assert same/different categorisation. However, Zentall (2000b) argues that even if matching experiments are based on familiarity, it makes no difference: “... although it may seem more parsimonious to attribute the transfer of matching and oddity to relative familiarity and novelty, such an account is conceptually indistinguishable from generalized identity” (p. 202).

3.7.6.1.3 Exclusion effect

Another potential problem with matching as a same/different task is that it can be mediated by factors such as the exclusion effect rather than identity (Thompson 1995). The exclusion effect occurs when the comparison stimuli consist of an S+ stimulus and a familiar S- stimulus. In these circumstances, the subject can respond correctly not by matching but by excluding the familiar S- stimulus because it has previously been associated with another sample (Schusterman, Gisiner, Grimm and Hanggi 1993).

3.7.6.1.4 Configural theory

Pearce (1997), a proponent of configural discrimination theory (see section 3.1.4.2.1.ii), suggests a plausible account for matching can be made using configural learning rather than same/different categorisation. There are a limited number of configurations of sample and comparison stimuli that make up a typical matching problem. In order to solve the problem, the subject merely has to associate the correct response with each configuration (a similar theory was discussed as the configuration model of conditional discriminations, see section 3.2.4.1). One example of this can be found in Johnson and Levy’s (1968) oddity learning experiment with rats, in which the authors suggested the rats had learned specific configurations rather than an oddity principle. Similarly Wright (1997) found evidence of configural learning in pigeons in a matching-to-sample task. However, as Pearce (1997) himself points out, the configural account cannot account for

experiments in which the subjects have responded correctly to novel stimuli on the first trial before they have had the chance to associate the configurations of those stimuli with the correct choices (e.g. Herman and Gordon 1974; Kastak and Schusterman 1994; Mishkin et al. 1962; Nissen et al. 1948; Oden et al. 1988; Wilson et al. 1985b).

3.7.6.1.5 Oddity preference effect

It has been suggested that the oddity preference effect (OPE) discussed earlier (see section 3.7.3.1) may account for oddity transfer. Wilson et al. (1985a) concluded that: “When pigeons are transferred to novel stimuli, they characteristically revert to their oddity preference, and so it seems that even birds that have previously learned to ignore their preference may revert to it with novel stimuli” (p. 308). This suggests that any transfer to a novel stimulus may be due to OPE rather than a ‘higher order’ or relational comparison (Wright and Delius 2005). Indeed, Berryman et al. (1965) found evidence of OPE affecting performance in pigeons taking part in a simultaneous oddity problem, with the pigeons beginning the experiment at levels well above chance and showing less of a position preference effect than that seen in simultaneous matching experiments. However, when Wright and Delius (2005) examined the impact of OPE on oddity transfer, they found that while OPE might make some limited contribution to performance, it was far too small an effect to account for high levels of transfer. Wright and Delius (2005) also designed a series of oddity tests using procedures designed to counter the effects of OPE. They were able to demonstrate novel-stimulus transfer equivalent to training performance and claimed, “... these birds have fully learned the abstract concept of oddity” (p. 431).

3.7.6.2 General same/different theories

3.7.6.2.1 Control by absolute stimulus features

Another criticism of many same/different experiments is that the subjects may be responding on the basis of absolute stimulus features. One example is the brightness differences in the stimuli, particularly in experiments using black and white shapes. However, a number of experiments have demonstrated that animals can do more than merely select the stimulus with the odd or matching brightness. These experiments have shown successful transfer using *same* and *different* stimuli of the same brightness using

mirror images (Hollard and Delius 1982), matching stimuli of different sizes (Lombardi and Delius 1990) and comparison shapes in reverse contrast (from white-on-black to black-on-white) as well as comparison shapes in outline (Lombardi and Delius 1988).

3.7.6.2.2 *Low-level perceptual mechanisms*

Another possible alternative to relational learning in same/different experiments is the use of low-level perceptual mechanisms. One procedure that lends itself to such criticism is the use of multi-element stimulus displays (see section 3.7.3.3). While there is evidence that perceptual processes play an important role in ‘conceptual’ behaviour (e.g. Cook et al. 1995; Wasserman and Astley 1994), some scientists have gone further and suggested that the subjects of multi-element same/different experiments are *only* demonstrating a low-level perceptual mechanism. Katz et al. (2007) suggested that a large number of items introduced the possible role of “global perceptual features” (p. 83) such as “linear orderliness” (Mandler 2004, p. 139). Mackintosh (2000) remarked that “an obvious difference between a 4 x 4 array of As and a 4 x 4 array consisting of 16 letters A to P each occurring once, is that the former has a regular texture and the latter does not” (p. 132).

Indeed, Wasserman himself points out the possibility that the grid arrangement of the stimulus elements in the Wasserman et al. (1995) experiment (see section 3.7.3.3) may have allowed for a solution based on the greater orderliness of the *same* versus *different* stimuli (Young and Wasserman 1997) – an effect which may be emphasised when more items are included in the array (Vonk 2003). However, both Young and Wasserman (1997) and the authors of a similar multi-element array study (Cook et al. 1995, see section 3.7.3.3) have argued that because transfer was not perfect their subjects must have been doing more than merely responding to the overall texture of the stimuli and were making a same/different judgment at a higher “conceptual” level (Cook and Wixted 1997; Young and Wasserman 1997).

To test this proposition, experiments with pigeons (Young and Wasserman 1997) and baboons (Wasserman, Fagot and Young 2001) were conducted using disorderly arrays created by randomly placing 16 icons in an incompletely filled 5 x 5 grid instead of a completely filled 4 x 4 grid. Both studies showed that spatially displacing the stimulus

items to disrupt the regularity of the columns and rows had no effect on performance. Young and Wasserman (2001a) and Brooks and Wasserman (2008) also demonstrated that performance was unaffected by disarranging or rotating stimulus items.

Vonk (2003) argues against these findings as evidence for non-perceptually based same/different discrimination in non-humans, claiming that perceptual regularity can be present in an array “even when items are randomly arranged” (p. 78). However, Vonk (2003) concedes that more convincing evidence is found in experiments in which perceptual regularity could not be a factor. Young and colleagues used lists of successively presented stimuli that were either all the same or all different and found pigeons were able to determine whether the list consisted of *same* or *different* stimuli even though they could not respond until the last stimulus was presented (Young, Wasserman and Dalrymple 1997; Young, Wasserman, Hilfers and Dalrymple 1999). Similarly, Wright and Katz (2006) argued against the symmetry/regularity hypothesis on the basis of similar list-memory experiments with monkeys (Wright et al. 2003).

Further evidence against a low-level mechanism like orderliness was also demonstrated in the pigeon (Young and Wasserman 1997) and baboon (Wasserman, Fagot and Young 2001) experiments mentioned above. Both studies found blurring the icons in multi-element displays had a large adverse effect on performance – an effect that should not have occurred if alignment was the only factor being used to make the discriminations (see also Young, Wasserman and Ellefson 2007).

Katz et al. (2010b) tested whether repetition of stimulus features (translation symmetry) was responsible for same/different performance in pigeons when only two items were used. The authors used a successive procedure in which one stimulus was presented and removed then, after a delay period, a second stimulus was presented that was either the same or different and the pigeons were required to respond appropriately to each condition. Delay intervals from 0 to 6 seconds were used to make any emergent features like translation symmetry “imperceptible” (p. 36). Transfer trials were conducted after each increase in delay interval. The authors found there was “no evidence of the precipitous performance decline or default strategy that would be predicted by translational symmetry” (p. 35). However, due to the successive nature of the experiment, it is open to other interpretations (see section 3.7.2.1.2 and 3.7.2.1.5).

A number of other experiments have also shown that at least some species are able to perform same/different categorisation without reference to low-level perceptual differences between the *same* and *different* stimulus presentations. For example, Pepperberg (1987) showed an African Grey parrot could respond accurately to questions such as “what is same?” between objects when the objects differed in colour, shape or material (see section 3.7.3.4). Similarly, Bovet and Vauclair (2001) showed baboons were able to classify pairs of objects as *same* or *different* based on a functional (food versus non-food) rather than perceptual basis. Both the *same* and *different* object pairs were perceptually different, discounting the use of perceptual cues (see section 3.7.3.3).

3.7.6.2.3 High-level perceptual mechanisms

Another theory about how animals perform same/different discriminations also resulted from the multi-element experiments conducted by Wasserman and his colleagues. They found that increasing the number of items in a display made the same/different categorisation task “more obvious” (Young and Wasserman 1997, p. 168). The authors attempted to quantify this effect in terms of a measure from information theory – entropy. Entropy is a mathematical measure of display variability that is calculated using the number of stimulus categories in a display. When all the items are the same, entropy is zero. When all the items are different, entropy is maximal for the number of items. As the number of unique items rises, so does the entropy value. So, the higher the number of different items, the higher the entropy value for the *different* stimulus and the greater the difference between it and the (zero-value) *same* stimulus. According to this theory, the more items used in a multi-element display, the greater the entropy difference between the *same* and *different* arrays and the more “obvious” the discrimination.

Young and Wasserman (1997) suggest their entropy theory is the reason why pigeons have experienced difficulty in same/different experiments using 2-item discriminations (e.g. Edwards et al. 1983; Santiago and Wright 1984) while 16-item discriminations such as that used by Wasserman et al. (1995) and Young and Wasserman (1997) have proved more successful. They suggested it was not the absolute number of items in the display that simplified the task, rather it was the fact that a larger number of items led to

an increase in the maximal amount of variability (entropy) in the *different* displays. For example, both a 16-item and a 2-item *same* array have an entropy value of 0.00. However, a 16-item *different* array has an entropy value of 4.00 compared to a 2-item *different* display with an entropy value of 1.00. So, in a 16-item task, the subject must learn to discriminate between entropies of 0.00 and 4.00 while in a 2-item task they must discriminate between entropies of 0.00 and 1.00 – “presumably a much more difficult task”, according to Young and Wasserman (1997, p. 168).

Young and Wasserman (1997) analysed pigeons’ performance on multi-element stimulus arrays. When they were presented with stimuli of intermediate degrees of entropy (i.e. mixed arrays containing both a number of the same and different icons) the pigeons didn’t treat all the mixed displays as *different*; instead they tended to identify mixed displays with relatively few non-identical items as *same* and mixed displays with a relatively high number of non-identical items as *different*. This led Young and Wasserman (1997) to suggest that pigeons are sensitive to a spectrum of stimulus variability rather than just a dichotomous same/different discrimination. Castro and Wasserman (2010, p. 170) claimed pigeons “did not categorise the stimuli into ‘same’ vs. ‘different’, but that they dimensionalised the stimuli into ‘low variability’ vs. ‘high variability’ ...” Studies have shown that baboons and monkeys also respond to mixed arrays proportionally, rather than as an all or nothing decision (Fagot et al. 2001; Smith, Redford, Haas, Coutinho and Couchman 2008; Zentall, Wasserman, Lazareva, Thompson and Rattermann 2008; see also section 3.8.2.1).

Based on their findings with pigeons, Young and Wasserman (1997) went further and suggested that entropy might be the single cue that accounts for pigeons’ (and possibly other non-humans’) same/different discrimination performance. “Pigeons, and perhaps other species, may be translating the human concept of same/different into minimal versus maximal entropy” (Young and Wasserman 1997, p. 168). If indeed this was the case, a universal entropy-based explanation for non-human same/different discrimination could cast doubt on the ability of non-humans to perform relational (or conceptual) categorisation (but see section 3.8.2.1).

Gibson et al. (2006) described entropy as a “single relational cue” and Young and Wasserman (1997) used the term “relational sensitivity”, however the use of the term

relational could be misleading. While sensitivity to entropy appears to involve something more than just responding to a low-level perceptual cue such as uniformity, it can be argued that it does not rise to the level of relational categorisation.

Entropy involves the extraction of a sense of the variability of a group of items that is relatively difficult to detect with only a few items and becomes more apparent as the number of items increases. Relational identity, on the other hand, is independent of the number of items (provided there is more than one) and involves the ability to compare individual items and make same/different judgments. Vonk (2003) describes entropy detection as a simpler perceptual process which provides a way for subjects to solve same/different problems “without necessarily having acquired concepts for ‘sameness’ and ‘difference’” (p. 77).

Gibson et al. (2006) decided to examine the possibility, arising from Young and Wasserman’s (1997) findings, of an entropy-based unidimensional account of same/different learning. According to this theory, subjects set a decision criterion along the spectrum of possible entropy values allowing them to discriminate *same* from *different* displays (Cook and Wasserman 2006). This account would also explain oddity-based same/different discriminations in which the *different* displays contain only one non-identical item (e.g. Cook et al. 1997; Zentall et al. 1980); albeit the entropy decision criterion for the *different* displays would be much lower.

Some evidence for this unidimensional interpretation can be found in the contrasting results of two same/different experiments using 2-item displays. Cook et al. (2003) found pigeons readily acquired the discrimination, while Young, Wasserman and Garner (1997) found that pigeons failed to master it. Because the Young, Wasserman and Garner (1997) 2-item experiment was conducted after extensive training to discriminate 16-item same/different displays, Gibson et al. (2006) speculated that the pigeons had adopted a relatively high entropy decision criterion for selecting *different* during the 16-item training and found it difficult to then utilise a more difficult low entropy decision criterion during the 2-item experiment. However, it is worth noting that the Cook et al. (2003) study was conducted using successively presented stimuli, leaving open the possibility that more prosaic mechanisms were utilised (see section 3.7.2.1.2 and 3.7.2.1.5).

More compelling evidence for an entropy-based explanation for non-human same/different discrimination is found in the fact that some species that initially struggled with two-item simultaneous same/different discriminations with low entropy differentials were able to succeed in the task when multi-element stimuli with relatively higher entropy differences were used (see section 3.7.3.3). Pigeons (Wasserman, Frank and Young 2002; Wasserman, Young and Nolan 2000; Young, Wasserman and Garner 1997) and baboons (Fagot et al. 2001; Wasserman, Fagot and Young 2001; Wasserman, Young and Fagot 2001), for example, appear to rely heavily on the amount of variety in a display to discriminate *same* from *different* and their performance deteriorates as the number of items in the displays is decreased. In addition, Castro et al. (2010) showed that the amount of entropy in a display also affected reaction times in pigeons, with longer reaction times for lower entropy displays. Even humans appear to be sensitive to entropy in same/different tasks (see section 3.8.2.1).

However, some later experiments have cast doubt on a unidimensional entropy-based explanation that would account for all same/different discriminations. Cook et al. (1997) conducted same/different experiments in which four different types of displays were used concurrently – differing in configuration (texture vs. visual search organisation), type of elements (small and large coloured shapes, pictures of birds, flowers, fish and humans) and the processing demands required by their global-local element arrangement. The pigeons were able to discriminate all four display types at the same rate and transfer all of them to novel stimuli. The authors suggest the results show that “no single or simple perceptual attribute shared in common across the displays seems sufficient to account for these transfer data” and that a likely explanation is “that the pigeons developed and used a single generalised same-different rule applied to all displays simultaneously” (pp. 428-429).

Specifically, Cook et al. (1997) claim an entropy-based account of their experiment was unlikely because the entropy value for one of the *same* displays (1.00) was actually larger than that of any of the *different* displays of the other three display types (0.59-0.65). If the pigeons were using entropy to make decisions they should have found discriminations using the higher-entropy *same* displays much harder to learn and that was not the case. The authors also trained pigeons specifically with *different* displays of

three different levels of entropy. A unidimensional entropy model predicts that accuracy should be greatest with the higher-entropy display, but the results did not bear this out.

Gibson et al. (2006) directly tested the unidimensional entropy approach by simultaneously training pigeons to discriminate displays of 16 *same* icons from displays of 16 *different* icons (16S vs. 16D) and displays of 16 *same* icons from displays of 15 *same* icons and one *different* icon (16S vs. 15S:1D). An entropy-based account suggests that learning to discriminate between low (16S) and high (16D) entropy displays should adversely affect learning to discriminate between two kinds of low entropy displays (16S and 15S:1D). However, the pigeons were able to learn and transfer performance in both tasks (albeit requiring an observing response to the odd item in the 15S:1D displays).

Another experiment suggests that while entropy may be useful for learning a same/different task, it can give way to more relationally based methods. Flemming et al. (2007) found rhesus monkeys that were unable to perform a two-item same/different discrimination succeeded when the number of items in the stimulus arrays was increased to eight items, leading the authors to suggest that their subjects' initial conceptual knowledge "may better be described as a 'uniformity versus chaos' distinction" (p. 61). However, in contrast to the results with pigeons and baboons (Wasserman, Young and Fagot 2001; Young, Wasserman and Garner 1997) mentioned above, after the higher-entropy training the monkeys were able to perform lower-entropy discriminations using stimulus arrays of six, four and even two items. Flemming et al. (2007) suggested this performance indicated that, unlike the pigeons and baboons, the monkeys were not constrained by entropy by the end of the experiment. They contended that entropy may have been required only to facilitate learning of the task rules, at which point the monkeys were able to generalise the performance to displays of any number of elements using a conceptual knowledge "which quickly generalises to a 'same versus different' distinction in the way that we more broadly conceive it" (p. 61).

The contrasting findings of Flemming et al.'s (2007) monkey study with those conducted with pigeons (Young, Wasserman and Garner 1997) and baboons (Wasserman, Young and Fagot 2001) may be due to procedural variations in the

experiments or point to genuine differences in the way different species utilise perceptual information to solve these types of tasks. Differences can be found even in the way different species fail in a task. Young et al.'s (1997) pigeons' decrease in performance was primarily due to an increase in errors in response to the *different* arrays while Wasserman, Young and Fagot's (2001) baboons showed an increase in errors on both *same* and *different* trials.

Further to Flemming et al.'s (2007) findings of entropy being used only in the learning phase in rhesus monkeys, even more striking evidence against a universal entropy account of same/different categorisation is found in experiments in which researchers have demonstrated simultaneous same/different discriminations with pigeons, capuchin monkeys and great apes starting with pairs of items and skipping the high-entropy phases (e.g. Blaisdell and Cook 2005; Flemming 2011; Katz and Wright 2006, Wright and Katz 2006; see section 3.7.3.3).

Gibson et al. (2006) posited an alternative theory to the unidimensional entropy account, suggesting that the nature of the same/different training causes pigeons to process different attributes of the same/different arrays. Wasserman and Young (2010, p. 17) suggested that "different experimental tasks may prompt organisms to deploy different mechanisms to solve them". Training with 16-item arrays containing all identical or all non-identical icons (e.g. Wasserman et al. 1995; Young and Wasserman 1997) led pigeons to respond to a quantitative dimension of entropy, while training with arrays containing all identical or single-odd-item arrays (e.g. Cook et al. 1997; Zentall et al. 1980) led pigeons to learn about the more qualitative properties of *sameness* and *differentness*. Similarly, Flemming (2011) theorised that experimental methodology, such as the use of simplified stimuli (e.g. Blaisdell and Cook 2005) or large sets of trial-unique stimuli (e.g. Flemming 2011), could encourage subjects to focus less on the perceptual features of stimuli and allow more relationally guided behaviour to emerge. In both these experiments, subjects were not limited by entropy like the subjects of many previous studies and were able to successfully learn and transfer two-item same/different discriminations.

Perhaps the most telling evidence against a unidimensional entropy theory of same/different discrimination is found in experiments designed so that there are no

entropy cues at all for subjects to use. As discussed in section 3.7.6.2.2, Young and colleagues experiments using successive presentation of ‘lists’ of *same* or *different* stimuli shows convincingly that even if entropy has been used by pigeons in previous multi-element experiments, they are able to perform same/different discriminations without reference to entropy-infused stimuli (Young, Wasserman and Dalrymple 1997; Young et al. 1999; see also Cook et al. 2003 above). Similarly, as discussed in section 3.7.6.2.2, Alex the African Grey parrot’s ability to correctly label “What is same?” about a group of objects (colour, shape or material) (Pepperberg 1987) and Bovet and Vauclair’s (2001) functionally based same/different experiment with baboons obviously do not rely on entropy-based cues.

3.7.6.2.4 Relational categorisation

A common theory put forward by experimenters to explain their subject’s ability to categorise on the basis of *same* and *different* is that the animals understand the relationship between the stimuli (e.g. “respond *same*” for paired comparison same/different tasks and “match like with like” for matching tasks) (Thompson 1995).

However, as can be seen by the absolute theories described above, many authors continue to resist relational explanations for complex discriminations in non-humans. Often this can be interpreted as a laudable attempt to follow Lloyd Morgan’s canon that: “In no case may we interpret an action as the outcome of the exercise of a higher psychical faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale” (Morgan 1894, p. 53). There is also the possibility that because the ability to utilise relational information in problem solving is considered a more ‘advanced’ process, they prefer to ascribe more prosaic absolute methods to animals. This attitude is reflected in the blanket statements of some authors about the impossibility of non-human animals using relational information to solve categorisation problems (see section 3.8).

Wilson et al. (1985a) tried to test for relational learning, contending that a relational explanation could be offered for matching and oddity performances if two criteria were met – firstly, matching and oddity discriminations were learned faster than a comparable non-relational conditional discrimination and, secondly, positive transfer

was shown when subjects were shifted from one matching or oddity discrimination to another. However, the authors claimed the pigeons in their experiment (at least using their particular experimental paradigm) did not meet these criteria, casting doubt on claims of relational learning in pigeons.

Despite this resistance, the results of numerous same/different ‘concept’ learning experiments (see section 3.7.3) have led even an absolute theorist such as Pearce (1997) (see section 3.1.4.2.1) to acknowledge that relational processes may be used to solve these types of discriminations. Pearce (1997) has allowed that matching experiments in which animals respond correctly on the first trial with novel stimuli (e.g. Levine and Harlow 1959; Shaffer 1967; Thomas and Boyd 1973) indicate “at least some species, therefore, seem capable of solving discriminations on the basis of relational information” (pp. 125-126). In addition, ‘simple’ absolute theories such as conditional discrimination and relative novelty cannot account for successful performance in categorisation using simultaneous same/different procedures. As discussed in section 3.7.3.3, a number of primate and non-primate species have demonstrated simultaneous same/different performances that have not so far been explained by perceptual or procedural factors. Katz and Wright (2006), for example, claim the impressive transfer results of their two-item same/different experiment “help to establish (or at least indicate) that the pigeons are basing their judgments on the relationship between the items of each pair and not some other cue(s) that may happen to covary with this relationship” (p. 84).

Elmore, Wright, Rivera and Katz (2009) demonstrated that even when pigeons failed to transfer a simultaneous same/different task to novel stimuli, they could show evidence of relational learning. Similarly, Wright and Katz (2009) showed that monkeys and pigeons who were unable to transfer a two-item same/different task to novel picture stimuli using a small training set (see section 3.7.3.3) could still show evidence of relational learning by performing well with novel combinations of training pictures and inverted pictures, a test they should have failed if they had learned the task item-specifically (e.g. if-then or configural learning).

In the final analysis, it seems likely that both relational and absolute discrimination theories could prove valid depending on the situation – for example, different animals

could perform the same tasks using different methods or the same animal could utilise different methods depending on the task being undertaken (see sections 3.7.6.2.3, 6.4.4 and 6.4.5). It is also possible that the testing procedure itself may influence how animals undertake these types of experiments. While absolute theories have proved most effective at predicting the results from successive discriminations, relational theories have been found to better explain the results of simultaneous discriminations (Mazur 2002). As discussed in sections 3.7.2.1.5 and 3.7.6.1.2, both Premack (1983a) and Shettleworth (1998) claim that the only true test of same/different categorisation is when the stimuli are presented simultaneously. Similarly, there are a number of competing theories as to how matching/non-matching tasks can be performed (see section 3.7.6.1), whereas there is more support for a relational account of paired comparison tasks (Pearce 1997; Shettleworth 1998).

3.7.6.2.5 Concept learning

While there is considerable endorsement for relational explanations for at least some types of same/different experiments, more contentious is the popular application of the term ‘concept’ to these and other types of categorisation experiments – an issue that will be addressed in section 3.8.

3.8 Concept learning

Do animals exhibit conceptual behaviour? C. Lloyd Morgan asked this question in 1894 and after more than a century comparative psychologists are still arguing (Wasserman et al. 1988). Numerous authors have claimed conceptual ability accounted for the successful performance of animals in experiments at each of the three levels of categorisation described in this chapter – perceptual, associative and relational. However, there is continuing debate about whether concepts can be attributed to animals and even about what is meant by animal concept learning.

3.8.1 Definitions

*Few terms have been used in psychological and epistemological theory in as many different senses as ‘concept’ and its derivatives.
(Herrnstein 1990, p. 137)*

Considering the large and diverse body of literature relating to categorisation and concept learning, there is a surprising lack of consensus about both the definition of the term ‘concept’ and to what processes it should be applied. Even in the field of human psychology, there is little agreement about the precise definition of a concept. While most authors would ascribe to a loose definition in which a human concept is viewed as knowledge that facilitates the categorisation process (Barsalou 1991, 1992), this knowledge is often portrayed as existing independently of behavioural and environmental factors. Many human studies focus on the knowledge on which conceptual behaviour is presumably based rather than the role of experience in creating and maintaining that behaviour (Zentall et al. 2002).

Obviously, it is impossible to investigate directly whether animals possess this type of ‘knowledge’. However, instead of speculating about hypothetical knowledge structures, it is possible to take a more operational approach and instead examine “what individuals are doing when they are said to behave conceptually and how they came to behave that way” (Zentall et al. 2002, p. 238). A variation of this idea was put forward by Lea (1984b), who argued that the use of terms such as ‘concept formation’ and ‘conceptualisation’ when referring to complex categorisation experiments could be interpreted on two levels – what was being categorised and how the subject achieved the categorisation.

To claim conceptualisation in non-humans on the basis of Lea’s (1984b) first level – what is being categorised – suggests that animals learn a ‘concept’ in the sense that they learn (by whatever mechanism) to group stimuli into open-ended categories based on human concepts defined by the experimenter, e.g. people, trees, fish etc (see section 3.4). According to Zayan and Vauclair (1998, p. 89): “It is generally assumed that reference to ‘concepts’ is made only to emphasise ‘the fact that the categories are usually defined in terms of a human language concept’ (Watanabe et al. 1993, p. 353).” While some authors would argue that applying the term ‘concept’ to these types of

cognitive abilities is semantically misleading (see section 3.8.4), in principle this is a fairly conservative interpretation that would be widely accepted based on the preponderance of experimental evidence.

Conceptualisation in non-humans according to the second level – how the categorisation is achieved – is more controversial. In the period following the publication of the type of open-ended perceptual categorisation experiments discussed in section 3.4.3, there seemed to be two fairly disparate schools of thought. Many early animal categorisation experimenters claimed virtually all their subjects' performances were due to human-like conceptual abilities (see section 3.8.3.1), while other authors refused to believe that animals could ever use concepts in a similar manner to humans (see section 3.8.2.1).

More recently, however, information gleaned from experiments designed to examine how, rather than merely whether, animals perform open-ended categorisation tasks seems to have encouraged both schools of thought to move away from such extreme positions. A number of authors in the anti-animal concept school have acknowledged that some species, under particular circumstances, might be capable of using human-like concepts (see section 3.8.2.2), while many scientists in the pro-animal concept arena have become more circumspect about exactly what types of experimental performances can truly claim to be conceptually mediated (see section 3.8.3).

3.8.2 Arguments against animal concept learning

3.8.2.1 Exclusive to humans

The idea that abstract conceptual behaviour is the exclusive province of humans is an old one, dating back at least as far as the famous English philosopher Locke, who stated: "... the power of *Abstracting* is not at all in [nonhuman animals]; and ... the having of general *Ideas*, is that which puts a perfect distinction betwixt Man and Brutes; and is an Excellency which the Faculties of Brutes do by no means attain to" (Locke 1690/1975, p. 159) (see also Descartes 1637/1994 and Morgan 1894 for similar views).

The idea that the ability to form and use concepts is exclusively human is one that is still held by many scientists (e.g. Davidson 1985, 1999; French 1995; Huber 2001; Lea

1984b; Pearce 1997; see sections 1.2 and 3.7.1). One reason for this could be the importance of abstract concepts in human development and adult cognition (Wright et al. 2003). For example, in children the abstract concept of ‘sameness’ plays a critical role in cognitive development (e.g. Daehler and Bukatko 1985; Piaget and Inhelder 1969/1966). In adults, James (1950/1890, p. 459-460) called it “the very keel and backbone of our thinking” and “the most important of all the features of our mental structure”. Deacon (1997) went so far as to label the capacity to determine abstract relations, such as those that seem to unite many categories, as the essence of what it means to be human (see Zentall et al. 2002).

This type of viewpoint was challenged by the deluge of perceptually based animal ‘concept’ experiments that arose from Herrnstein and Loveland’s (1964) perceptual categorisation study with pigeons (see sections 3.4.3 and 3.8.3.1), as well as the many associatively and relationally based experiments that have claimed conceptual explanations (see section 3.8.3). However, some authors reject a conceptual interpretation of these experiments out of hand; claiming that because the ability to form concepts is so closely linked with language it must be uniquely human.

Chater and Heyes (1994), for example, argue that concepts can only be defined using language and so only humans are capable of forming them. According to Chater and Heyes (1994, pp. 236-237), “concepts can be ascribed only to language-users” because “we simply do not know how to turn the claim that nonlinguistic animals have concepts into an empirically substantive question.” Huber (2001) acknowledges the difficulty of proving conceptual behaviour is *not* involved in categorisation tasks, but still claims the idea of a concept is too entwined with natural language to even examine the possibility in non-humans. He views categorisation as occupying a middle ground between simple discrimination and conceptualisation, which he defines as the “linguistic manipulation of classes of objects, events or ideas by using symbolic representations and by attaching to them verbal names” (Chapter 1, online). Huber (1995) further argues that the influence of language theory on the problem of categorisation is misleading. Rather than linking categorisation with symbolic manipulation and acquiring logical rules, the author argues that there are much simpler and older mechanisms at work in terms of perception and even in common-sense knowledge.

Thompson (1995) is a proponent of the humans-only view of concept learning, but expands the criteria to include our closest relatives, chimpanzees. According to Thompson (1995, p. 213), in ‘conceptual’ tasks such as second-order same/different relations and mirror-mediated self-recognition tasks, “there appears to be a fundamental distinction between humans and chimpanzees on the one hand and other non-human primates on the other hand ... with the possible exception of chimpanzees, no one species ... exhibits the full range of conceptual knowledge ...”

Many authors consider these views to be anthropocentric. For example, Zentall et al. (2008), after reviewing numerous studies they claim provide evidence of perceptual, associative and relational ‘concept learning’, concluded: “We cannot say that nonhuman animals have cognitive capacities that are equivalent to those of adult humans; but, we do believe that there is now good evidence that many species of animals are likely to have some of the same conceptual abilities that have typically been reserved exclusively for humans” (pp. 38-39).

A variation of this argument is that rather than animals being able to perform a ‘high-level’ human task that instead many of the processes involved in human conceptualisation are in fact relatively basic, perceptual mechanisms. According to Goldstone and Barsalou 1998, p. 232): “Concepts usually stem from perception, and active vestiges of these perceptual origins exist for the vast majority of concepts.” A number of human cognition researchers have suggested that making a distinction between ‘low-level’ perceptual processes and ‘high-level’ conceptual processes might be misleading; rather that there is a continuum from perceptual to conceptual (Castro et al. 2010; Goldstone 2004; Goldstone and Barsalou 1998). Castro et al. (2010) surmise that conceptual processes arise when perceptual processes become less bound to the perceptual specifics of stimuli.

One possible perceptual mechanism that has been suggested as common to both humans and animals in solving same/different concepts is that of entropy. As discussed in section 3.7.6.2.3, animals such as pigeons and baboons have been shown (in some, but not all, circumstances) to utilise perceptual variability (entropy) to solve same/different tasks. A number of studies have shown that humans also can and do use entropy to solve same/different discriminations. Young and Wasserman (2001b) found a minority

of college students used entropy to solve a same/different task, while reaction times and choice accuracy suggested that the majority of students were sensitive to entropy (Castro, Young and Wasserman 2006; Young and Wasserman 2001b). According to Castro and Wasserman (2010, p. 170): “All organisms – even humans, who are capable of using language – may rely on variability when solving a same–different discrimination; so, the perception of variability may truly be the substrate of abstract conceptual thinking ...” (see also Wasserman, Young and Cook 2004).

However, it is also worth noting that even if humans and animals do both use entropy, they may not do so in exactly the same way. Fagot et al. (2001) compared the performance of humans and baboons tested on similar relational matching tasks of varying degrees of entropy and found that while both species were influenced by entropy, the performance of the humans was far superior, both in terms of learning speed and choice accuracy. While species differences over the suitability of the experimental methodology may account for some of this discrepancy (see section 1.3.1), the study also showed that humans and baboons responded differently to varying degrees of entropy. Humans responded *same* only to arrays with a very low degree of entropy while baboons also responded *same* to higher-entropy arrays, showing a more gradual transition from *same* to *different* and a more inclusive criterion for *same*. A similar effect was seen in a same/different task with humans and monkeys (Smith et al. 2008), with the authors describing the performances as qualitative, categorical and rule-based in humans versus quantitative, continuous and similarity-based in monkeys.

Castro et al. (2010) suggested that rather than a dramatic discontinuity between species, the disparity was due to different species setting different decision criteria along a continuum of variability, with humans having an entropy cut-off point close to 0.00, while other species set the cut-off point higher so larger increments in variability are required to report *different* (see also Cook and Wixted 1997; Fagot et al. 2001; Smith et al. 2008). Fagot et al. (2001) hypothesised that this difference may be due to the more restrictive definition of *same* in humans engendered by language use, leading the authors to conclude that “entropy detection may underlie same-different conceptualisation, but that additional processes may participate in human conceptualisation” (p. 316).

3.8.2.2 Language-trained animals

The view that concepts are uniquely human because they are inherently language-based was given an interesting twist with the advent of language-trained animals. In a series of publications, David Premack claimed animals could learn abstract concepts if, and only if, they had had language training (Premack 1978, 1983a, 1983b, 1988; Premack and Premack 1983). (It is worth noting that Premack (1983b) considered second-order same/different tasks (see section 3.7.5) as “abstract” while perceptual, associative and basic same/different tasks were not). In one of these experiments Premack (1983b) found language-naïve chimpanzees were unable to solve a second-order same/different problem that a language-trained chimpanzee was able to solve fairly easily. Premack and others have argued that animals without language training probably rely on “a more image-based code or on the recognition of a small set of relevant features” (Fabre-Thorpe et al. 1998, p. 303). While seeming to allow animal concept learning, the language-training exception still meant that animals without specialised training provided by humans were still incapable of conceptualisation.

Huber (2001), who argues against concepts in non-humans (see section 3.8.2.1), is also willing to make an exception for language-trained animals. He bases this on the belief that it is language itself, not being human, that is the prerequisite for concept learning. The author goes on to cite the example of the language competencies of great apes (Ristau and Robbins 1982) as “clearly involving far more than mere categorisation” (Chapter 1, online). Similarly, Savage-Rumbaugh et al. (1980) claimed that language training was the decisive factor that enabled two chimpanzees to acquire functionally based “concepts” in their associative categorisation experiment (see section 3.5.2) while a third, non-language trained chimpanzee failed. The failure of cebus monkeys to transfer a matching task to other modalities led D’Amato and Colombo (1989) to suggest that the ability to construct symbolic representations of same/different afforded by language training “may prove a necessary prerequisite for an abstract matching concept” (p. 236).

Despite this support for language-based concept learning, there is some debate surrounding whether animals can in fact learn a human-like language. In a chapter examining animal language training experiments, Wynne (2001, p. 161) claims that “in

reality it is unlikely that anything approximating a human language capacity has been demonstrated in any non-human species” and that “many of the claims made on behalf of these animals have been exaggerated”. Further, Chater and Heyes (1994) claim that while the performance of language-trained animals such as Premack’s chimpanzee (Premack 1971, 1976) and Pepperberg’s parrot (Pepperberg 1987) (see section 3.7.3.4) is impressive, the fact that it is impossible to know what the animals mean when they use words like “same” and “different” means this type of experiment does not provide proof of animal concepts as it “does not indicate how, if at all, the animal defines or conceives of the stimuli to which it is exposed” (p. 232).

Whether animals can learn language or not, other researchers have come to believe that language is not an essential prerequisite for conceptualisation. Allen (1999, p. 39), for example, claims that “it would be a mistake to think that [language] is the only basis for conceptual representation available”, while Herrnstein (1990, p. 155) states: “Language is a sufficient condition to permit the inferring of concepts, but it is not also a necessary one”. Smith et al. (2008) questioned whether the explicit (i.e. qualitative and rule-based) responding seen in human same/different conceptualisation is linked by representational necessity to language or is the result of the vast majority of neuroscience research using human participants. The authors wondered whether there were non-linguistic forms of explicit cognition that animals might use, such as symbolic, semantic or Boolean.

A number of authors have set out to test Premack’s claims about the necessity of language training in conceptual behaviour. Thompson et al. (1997) demonstrated that language-naïve chimpanzees were able to perform a second-order same/different problem similar to that used by Premack (see Premack 1983b) (although they only extend the conceptual umbrella to include chimpanzees with symbol use training). Burdyn and Thomas (1984) also argued against Premack’s assertions regarding simultaneous same/different requiring language-training in animals, pointing out that their experiments had demonstrated “the squirrel monkey’s ability to make conceptual, simultaneous same-different judgements. None of these monkeys had language training ...” (p. 412). Similarly, Edwards et al. (1983) asserted that the results of their same/different experiments (see section 3.7.3.4) showed that “pigeons can show reliable amounts of concept transfer under conditions analogous to those described by Premack

(1976) as being able to qualitatively distinguish humans and language-trained chimpanzees from other animals” (p. 354).

3.8.2.3 Requires a unique mental structure

Scientists in the mentalist tradition of human psychology have more stringent requirements than simply having language as a prerequisite for conceptual abilities. Examples of such requirements include verbal expression of a rule, the ability to mentally manipulate (and discuss) the concept and the possession of a unique mental structure that is active only when an example of that concept is presented externally or is active internally. While Lea (1984b) argues that the first two requirements are obviously unhelpful when dealing with animals, as well as being obscure, he agrees with the necessity of the third.

The use of a unique mental structure requires that the concept should be more than the sum of its component features, or component instances – that is, it does not rely solely on perceptual similarity. To use Blough’s (1984) example, if a subject is taught an instance of ‘person’ as a tall man in a white coat it would generalise to another instance, such as a short woman in a maroon sweater, and would generalise in this particular way, not to all white objects or all objects of a certain height. The traditional test of concept discrimination – transfer to novel stimuli – is inadequate to determine whether this unique mental structure is being used to perform the discrimination as such transfer can be accounted for by methods based on perceptual similarity, such as feature learning (see section 3.4.4).

A number of experiments have been conducted specifically to test whether conceptual behaviour can be demonstrated according to Lea’s (1984b) criteria. Vaughan and Herrnstein (1987) tested pigeons with a tree/no tree categorisation task. The experiment used two concurrently available variable-interval schedules of reinforcement, with the alternating schedules signalled by slides either containing trees or not. In most natural categorisation experiments, one category is associated with reinforcement and the other with non-reinforcement. Here, both categories (tree/non-tree) were correlated with equal levels of reinforcement. Despite this, the pigeons were able to categorise the stimuli and transfer the performance to novel stimuli. Their results led the authors to claim that: “To

the extent that a class may be construed as a concept if it is superordinate to the exemplars drawn from it, as Lea (1984[b]) has argued it may, the present results suggest that pigeons can conceptualise, not merely categorise” (p. 15).

According to Bhatt and Wasserman (1989), Lea’s (1984b) requirement that concepts be mediated by a unique mental structure can be interpreted as a demand for categorisation based on secondary stimulus generalisation – that is, the formation of equivalence classes of stimuli grouped together by mediating associations rather than just by perceptual similarity. One way to test for equivalence classes is to use pseudocategories (see section 3.5.2). Bhatt and Wasserman (1989) conducted a series of experiments to test whether categorisation training led to the formation of equivalence classes in pigeons and found that: “The lack of evidence of secondary generalisation implies that our pigeons failed to meet Lea’s (1984[b]) criterion for conceptual behaviour” (p. 213).

However, other authors such as Vaughan (1988) and Wasserman et al. (1992) used different experimental procedures and claimed they were able to demonstrate equivalence class formation. According to Wasserman et al. (1992): “Each study found clear evidence that new categories of functionally equivalent stimuli were formed, thereby supporting the view that much of the richness and complexity of human conceptual behaviour is to be found in the behaviour of nonhuman and nonverbal animals” (p. 379).

Huber (2000) agreed that the grouping of stimuli according to their reinforcement history may be interpreted as the formation of a “functional concept” (p. 252) according to Lea’s (1984b) definition and that “it is reasonable to speak of the formation of nonsimilarity-based or superordinate concepts” (p. 253), however he believed that because the results can be explained in terms of mediated or secondary generalisation they should not be described as conceptualisation in a human sense.

3.8.3 Arguments for animal concept learning

As discussed above (see section 3.8.2), trying to determine whether animals have concepts based on requirements for facilitating knowledge, language and mental structures is a self-defeating task. According to Zentall et al. (2002, p. 239), “concepts,

defined largely in terms of abstract knowledge, provide a slippery foundation for an experimental analysis.” However the authors point out that it is possible to “recast the notion of knowledge in terms of necessary and sufficient conditions for conceptual behaviour” (p. 239). Many experiments have been conducted using a variety of criteria to determine if animals are behaving conceptually.

3.8.3.1 Perceptual categorisation as concept learning

Despite the ongoing controversy, comparative psychologists have a long history of ascribing human-like conceptual abilities to non-humans and one type of study that has attracted a lot of these claims is perceptual categorisation. The label ‘concept’ began to be applied regularly, and fairly broadly, to animals about 90 years ago (e.g. Bingham 1913). By the 1920s and 1930s a number of experiments indicated rats could be trained to select a triangular stimulus despite differences in form (e.g. scalene or isosceles), brightness, orientation or background (e.g. Fields 1928, 1929, 1932; Lashley 1938a). This was taken as evidence that rats could acquire the “abstract idea” or “concept” of triangle (Fields 1932; Washburn 1926) (see Chater and Heyes 1994). This use of the term was supported by one of the early definitions of conceptual behaviour provided by Keller and Schoenfeld (1950) who proposed a fairly liberal definition which was largely the same as that for categorisation – that conceptual behaviour is demonstrated when an organism responds similarly to members of one class of stimuli and differently to members of other classes. Their definition stresses generalisation and discrimination: “... when a group of objects gets the same response, when they form a class the members of which are reacted to similarly, we speak of a concept” (p. 154) and “Generalisation within classes and discrimination between classes – this is the essence of concepts” (p. 155).

In 1964 Herrnstein and Loveland claimed their pioneering perceptual categorisation experiment using person/non-person visual stimuli (see section 3.4.3.1) demonstrated pigeons possessed “greater powers of conceptualisation than are ordinarily attributed to animals” (p. 549) and that “the evidence for a concept is incontrovertible” (p. 551). Following Herrnstein and Loveland’s (1964) experiment, an increasing number of animal perceptual categorisation experiments were conducted and broad definitions of concept learning continued to be offered. Malott and Siddall (1972, p. 3), for example,

declared: “When an organism makes the same response to all members of a given stimulus class, we term this behavior conceptual”, while Zentall and Hogan (1975, p. 233) asserted: “Concept learning involves making a common response to those members of a class of stimuli that have certain specifiable characteristics.” According to Schrier and Brady’s (1987) study of categorisation of humans in slides by rhesus monkeys: “On the basis of the available evidence, a concept interpretation appears to fit the facts better than one based on simple stimulus generalisation” (p. 142). Morgan et al. (1976) even claimed pigeons could learn the “concept” of the letter ‘A’.

The application of the word ‘concept’ to examples of perceptual categorisation by non-humans continues. In a 1998 textbook on animal cognition, Roberts classified categorisation in non-humans as “concept learning” based on perceptual similarity (perceptual concept learning), relationships between stimuli (relational concept learning) and common associations (associative concept learning). Mazur (2002) used the terms categorisation and concept formation interchangeably. He also said that while the distinction between discrimination and concept formation was not always clear-cut, the most important difference was that while discrimination experiments use only two stimuli (S+ and S-), concept formation experiments use many stimuli divided into a positive group (S+) and a negative group (S-).

The label ‘concept’ is even still applied to categorisations of relatively basic stimuli. Wynne (2001) defined a concept as an abstract or perceptual category, a grouping together of items that share common features or functions. He even defined ‘triangles’ as a simple concept, as did Sappington and Goldman (1994) in testing the “concept of triangularity” in horses. In their study testing categorical discrimination of direction in frequency-modulated tones with Mongolian gerbils, Wetzel et al. (1998) described the stimuli as an “ascending-descending concept” (p. 29). According to the authors: “Categories are concepts formed by the brain suitable to classify perceptual objects into members and non-members of a category” (p. 36).

3.8.3.1.1 Transfer tests as proof of perceptual concept learning

In response to criticism that animals were merely memorising in the early perceptually based ‘concept’ experiments, authors began to require proof that the categorisation

extended beyond the training stimuli by testing for transfer to novel stimuli. As mentioned in section 3.8.3, this is an example of using demonstrable behavioural criteria, rather than more theoretically based requirements such as knowledge, language or mental structures (see section 3.8.2), to determine whether a performance is conceptually based. “The *behavioural evidence* that an animal perceives, or has learned, a natural object concept ... is an animal’s ability to transfer its performance spontaneously to novel exemplars of the category ...” (Thompson 1995, p. 176).

As Herrnstein et al. (1976) explained, since conceptual behaviour permits organisms to categorise open-ended classes of stimuli, differential responding to both old and new members of the categories being studied should be a requirement of concept learning. Many perceptual categorisation experiments (e.g. Bhatt et al. 1988; Lubow 1974; Malott and Siddall 1972; Siegel and Honig 1970) have asserted that the ability to categorise perceptual stimuli and extend the classification to novel members of the category was sufficient evidence to prove conceptualisation. According to Hanggi (1999, p. 250): “A necessary test before attributing an ability such as concept or category formation is that of novel stimulus presentation.”

Despite the continued support for animal perceptual categorisation as ‘concept’ learning, there has also been considerable criticism. Wasserman et al. (1988), for example, have queried whether successful transfer to novel stimuli is sufficient to demonstrate categorisation, let alone concept learning. According to the authors, a number of studies that have used novel-stimulus transfer to demonstrate ‘conceptualisation’ have in fact been successful because the subjects simply couldn’t tell the difference between the training and transfer stimuli (although the authors claimed their own study was designed to avoid this pitfall). “... true conceptual generalisation can be said to have occurred if and only if the testing stimuli differ discriminably from the training stimuli” (Wasserman et al. 1988, p. 244).

Huber (2001) claims it is anthropomorphic to only require transfer to prove concept learning and points out that studies like Herrnstein and Loveland’s (1964) did not adequately examine the possibility that the successful performance of the ‘concept’ task was due to some visual clue in the slides or non-visual property of the experimental procedure. “... evidence for anything more interesting than pure picture memorization is

not per se indicative of the acquisition or use of a ‘complex visual concept’” (Huber 2001, Chapter 1, online). A number of critics (e.g. Allen and Hauser 1991; Davidson 1999; Stephan 1999) claim that perceptual categorisation experiments such as those conducted by Herrnstein and colleagues “do not show that the participating animals master any concepts at all” (Stephan 1999, p. 82). According to Davidson (1999), the ability to discriminate certain things from others is insufficient evidence of having a concept. “A creature does not have the concept of a cat merely because it can discriminate cats from other things in its environment” (p. 82).

Troje et al. (1999) said that in the early period of animal categorisation experiments, researchers such as Lubow (1974) and Poole and Lander (1971) were largely influenced by human cognitive psychology, “often leading to questionable interpretation of the original findings in terms of human language concepts” (p. 354). Watanabe et al. (1993) agreed, suggesting the use of the term “concept” in the titles of early papers (e.g. Herrnstein and Loveland 1964; Lubow 1974; Poole and Lander 1971) was “premature” (p. 356).

Even among those who conducted the early experiments, there has been some circumspection about making conceptual claims for results that may in fact demonstrate more prosaic abilities. As mentioned previously, Herrnstein and Loveland (1964) made fairly ambitious claims about the pigeon’s conceptual ability for their pioneering perceptual categorisation experiment (see section 3.8.3.1). In fact, when Greene (1983) replicated the ‘person’ experiment almost 20 years later, it was discovered that the pigeons were using “conceptually irrelevant” features in the slides as well as the “conceptually relevant” features of the people instances (see section 3.4.4.6). Presumably in light of such evidence, Herrnstein later refined his use of the umbrella term ‘concepts’ and created a hierarchy of discrimination levels (see section 1.3.2.1). He used this new system to re-label his 1964 study as an example of open-ended categorisation rather than conceptualisation (while allowing for the possibility that some perceptual categorisation experiments may still demonstrate conceptualisation) (Herrnstein 1990).

More recent articles, such as Wright et al. (2003), claim that perceptually based categorisation does not demonstrate a concept in the true sense of the word and consider

a term such as category learning would be more appropriate for these types of experiments. As Zayan and Vauclair (1998, p. 89) point out: “As noted by Herrnstein (1990) and Thompson (1995), the operational distinction between open-ended categories and concept is difficult to make, especially since the role of conceptual mediation is difficult to assess, given the still imprecise nature of the mechanisms that control categorical behaviours.”

Lea (1984b) goes further and suggests that because all the theories put forward to account for transfer in perceptual categorisation experiments rely on the novel stimuli bearing some form of similarity to, or sharing common elements with, at least one training stimulus, successful open-ended categorisation can be accounted for by perceptual discrimination and generalisation processes. He argues that categorisation cannot be considered unequivocally conceptual unless the categories are held together by relationships that do not depend solely on physical similarity. Hanggi (1999) agreed, asserting that: “For true conceptualisation, one must have representations that transcend perceptual features” (Hanggi 1999, p. 250).

An interesting example of perceptually based categorisation that claims to demonstrate a concept according to this criterion is a cross-modal study conducted by Martin-Malivel and Fagot (2001) with baboons. One of the two subjects was able to match pictures of baboons and humans with relevant audio recordings. According to the authors: “Clearly, cross-modal effects cannot be accounted for by the feature, prototype or exemplar theories, which posit that categorisation is exclusively controlled by the perceptual characteristics of the stimuli. Alternatively, our results cannot be explained to satisfaction by the ‘secondary stimulus generalisation’ account ... We propose that [the subject] developed amodal abstract concepts of the human and baboon categories, and referred to these concepts while responding in the task” (p. 212).

3.8.3.1.2 Feature learning as concept learning

In response to criticisms of the earlier experiments (see section 3.8.3.1.1), a number of perceptual categorisation studies were conducted in the late seventies using simpler, more carefully specified sets of stimuli (e.g. Cerella 1979; Lea and Harrison 1978; Morgan et al. 1976). These studies indicated that pigeons were ‘merely’ associating

pictures, and/or the features they contained, with reward (Mackintosh 2000) leading to the increasing popularity of non-conceptual categorisation theories such as feature learning (see section 3.4.4.4).

However, other psychologists incorporated the new ideas into their conceptual framework and considered feature learning sufficient criteria for saying an animal had acquired a concept. It is from this tradition that the term “higher order concept formation” (e.g. Lubow 1974) arises. According to this idea, because even simple discriminations involve feature learning, complex discriminations must involve some more elaborate type of concept (Lea 1984b).

Honig and Stewart (1988) argued that, for animals, “concepts are discriminated accretions of characteristics typical of a particular class that control the same patterns of behaviour” (p. 550). According to the authors, while humans tended to adopt a template model for concepts (analogous to the exemplar model, see section 3.4.4.3), it was possible that for animals conceptual discriminations “may be based on stimulus generalisation between instances of the same class on the basis of specific, punctate features” (p. 550). The authors further suggested that a feature-based definition of animal conceptualisation meant a broader range of stimulus classes could be defined as concepts for animals. In a functional sense, an animal’s discrimination of more commonly posited perceptual experimental ‘concepts’ such as humans, fish or trees (see section 3.4.3) might not be very different from its discrimination of individuals, or, as in the case of Honig and Stewart’s (1988) study, geographic locations.

There is some support in human psychological literature for a purely feature-based view of conceptualisation. According to Thompson (1995), feature-based concept theories include the early classical view – that all members within a category share a finite set of necessary and sufficient features – and more recent theories based, respectively, on probabilistic feature analysis and the retention of multiple exemplars (Smith and Medin 1981).

Even if a feature-based definition of conceptualisation were accepted, a number of authors have recently begun to cast doubt on whether animals do in fact form concepts using feature learning. Support for a more parsimonious feature account comes from a

number of feature learning experiments that have shown persistent reliance on irrelevant features of a target concept. As mentioned in section 3.4.4.4.1, the monkeys in D'Amato and Van Sant's (1988) 'person present' experiment showed persistent errors to slides containing patches of red while pigeons in Greene's (1983) re-evaluation of Herrnstein's experiments found similar background control of categorisation performance.

D'Amato and Van Sant (1988) argue it is extremely difficult to distinguish between stimulus generalisation and the formation of an abstract concept because both are based to some degree on physical similarity. "Transfer to new positive exemplars might arise from the animal's abstracting a variety of relevant features from previous positive instances and assembling them into an abstract representation, such as a prototype, which would qualify as concept-mediated transfer. Or it might be due to 'mindless' generalization from a specific relevant or even irrelevant feature of previously encountered positive exemplars" (p. 52).

Further support for this view was found by analysing subjects' misclassifications in a number of studies. Experimenters have sometimes found better performance on stimuli rated by the experimenters as intermediate to poor examples of the concept being tested (eg. Herrnstein and De Villiers 1980). Huber (2001) suggests that this indicates the subjects may have been responding to factors other than the experimenter's intended concept. According to Huber (2001), such experiments demonstrate that animals do not learn about the defining features of a concept and ignore all other features, rather they "learn about any feature that occurs with some positive probability on trials and are followed by a specific psychological consequence (e.g. food)" (Chapter 3, online). Thompson (1995) believes it shows the subjects' choices were determined by "the specific range of exemplars experienced during training and not by the particular features of a prototype" (p. 188).

Alternatively, experiments by Schrier and Brady (1987) and Schrier et al. (1984) have shown a reduction in concept-learning performance by monkeys on exemplars rated as 'poor' by experimenters. However, the authors also considered this evidence against human-like concept learning in their subjects. "... if our monkeys had a unitary concept similar to our own, we would ... have expected them to do better than they did at

categorising *intermediate-to-poor* and most *poor* slides, which humans do readily ...” (Schrier and Brady 1987, p. 142).

Another group of psychologists claim that, even if categorisation performance is solely controlled by relevant features, feature learning is still insufficient evidence of concept formation. Huber (2001) cites as evidence for this view a number of experiments (Jitsumori 1993; Lea and Ryan 1983; Von Fersen and Lea 1990) in which the total number of possible features belonging to the stimuli were predetermined and it was demonstrated that responding had come under the control of those features. According to Huber (2001), because experiments such as these show that a clearly specified feature model is able to adequately explain categorisation performance then “it would be superfluous to ascribe to pigeons the formation of a concept” (Chapter 3, online).

3.8.3.1.3 *Do pictures represent real objects?*

Recently a more fundamental question than the necessity of language or a unique mental structure has been raised in the debate over whether animals possess human-like concepts of perceptual categories such as ‘person’ and ‘tree’, or are merely able to categorise stimuli based on those concepts using more prosaic means. In simple terms, at issue is what animals see when they look at experimental slides. Do they in fact recognise the objects and scenes depicted in slides as representations of real objects and scenes or do they merely see an array of shapes and colours? The importance of this question cannot be underestimated in light of the fact that most of the research on natural animal ‘concept learning’ has used colour photographs as discriminative stimuli (Watanabe 1993).

Some authors have pointed out that experimental slides are designed to suit the optical abilities of humans and there may be biological reasons why an animal might not perceive a picture in the same way as a human. Birds, for example, perceive ultraviolet wavelengths invisible to humans and their presence or absence in slides may affect how they discriminate between them. Many animals also have a higher flicker fusion frequency than humans (e.g. Adret 1997) so videos might be perceived as a succession of individual frames rather than uninterrupted motion. Based on these kinds of biological grounds, whether animals perceive experimental stimuli as representations of

real objects may depend on both the species and the type of stimuli being used (Shettleworth 1998).

D'Amato and Van Sant (1988) argue that continuing attempts to identify concepts in animals using photographs may be futile because animals may have highly developed concepts that cannot be revealed by two-dimensional photographs. And, even when an animal does classify slides in the same way as a human, that doesn't mean it has formed the same concept as different species have been shown to use different means to achieve the same result.

The most commonly used subject of perceptual 'concept learning' experiments, the pigeon, has been extensively tested on the correspondence between images and reality with mixed results (see Bovet and Vauclair 2000; Fetterman 1996; Shettleworth 1998). On the negative side, there is evidence that pigeons don't recognise anything special about pictures of real objects. For example, pigeons are relatively unaffected by stimulus distortions such as inversions and mirror images that disrupt discriminations in people and monkeys (Phelps and Roberts 1994). Pigeons also learn serial lists made up of colour photographs and random kaleidoscopic images with equal ease, while humans find the kaleidoscopic images more difficult to remember (Wright, Cook et al. 1990; Wright, Santiago, Sands, Kendrick and Cook 1985). These types of experimental results led Fetterman (1996) to suggest that: "There is not a great deal of evidence that nonhuman animals, especially pigeons, perceive pictorial stimuli in the same way humans do" (p. 8).

This uncertainty over whether even the concept learning 'poster' animal in fact perceives experimental stimuli as representations of real objects casts doubt over whether at least some animals can in fact discriminate on the basis of either supposedly pre-existing concepts such as 'tree' (Herrnstein et al. 1976) and 'person' (Herrnstein and Loveland 1964) or learn a new concept based on depictions of unfamiliar objects such as 'fish' (Herrnstein and de Villiers 1980). According to Watanabe et al. (1993), in these early 'concept' experiments "there is no implication that their subjects in any sense recognise the pictures as representations of real objects" (p. 356). The fact that pigeons do equally well categorising on the basis of stimuli depicting non-realistic

images such as squiggles (Vaughan and Greene 1984) and dot patterns (Watanabe 1988) offers some support for this view.

However, there is evidence that animals can perceive pictures as real objects. A number of studies have shown that monkeys can spontaneously respond to pictures as if they were the real objects (e.g Kyes, Mayer and Bunnell 1992; Rosenfeld and van Hoesen 1979) and even jumping spiders court mates and attack prey they see on television (Clark and Uetz 1990). Other studies involving associatively based training have also shown object-picture equivalence. For example, monkeys can recognise familiar group members in slides Dasser (1987) and baboons can transfer from real objects to cut-out pictures in a food/non-food categorisation task (Bovet and Vauclair 1998). In a more specific test, Davenport and Rogers' (1971) demonstrated that photographically naive chimpanzees and orangutans can proficiently match objects with colour and black-and-white photographs and perform fairly well with silhouettes and line drawings.

Even pigeons, despite some experiments casting doubt on their ability to perceive pictures as real objects (see above), have demonstrated object-picture correspondence in some studies. For example, Looney and Cohen (1974) showed an upright silhouette of a pigeon was better at producing reinforced conspecific attack behaviour than an inverted silhouette, an outline of a pigeon or a piece of coloured paper. In more direct studies, Cabe (1976), Delius (1992), Lumsden (1977) and Watanabe (1993, 1997) found pigeons were able to transfer categorisations between pictures and solid objects and "see the pictures as representations of real objects" (Watanabe 1997, p. 188). Wilkie, Willson and MacDonald (1992) conducted a review of a number of studies and claimed: "Our review of the evidence suggests that animals such as pigeons likely do see photographs as corresponding to the natural stimuli" (p. 91).

In addition to conflicting experimental results such as those above, some studies even seem to provide evidence for both positions regarding animals' perception of two-dimensional stimuli within the same experiment. Cole and Honig (1994) showed pigeons were able to more quickly find food in particular locations in a room after being positively reinforced on pictures of those locations compared to pigeons that were reinforced on pictures showing room locations that did not contain food. However, when the experiment was reversed (with pigeons being trained in the room and tested

on the pictures), the differential performance disappeared. Another example of a mixed result from investigations of picture-real life correspondence was found by Vandenheede and Bouissou (1994), who discovered that sheep respond appropriately to slides of conspecifics but not to slides of humans. Similarly, chickens react to images of conspecifics and predators as if they were the real thing, apparently on the basis of shape and motion, however they find insufficient detail in slides and videos to recognise other chickens individually (Patterson-Kane, Nicol, Foster and Temple 1997). Monkeys, on the other hand, do recognise familiar group members in slides (Dasser 1987).

Despite the mixed results, experiments have demonstrated that at least some animals in some situations do treat experimental stimuli in the form of slides and videos as corresponding to the real objects. However, merely being able to categorise pictures of objects does not automatically mean that an animal is treating the pictures as representations of, or equivalent to, real objects. According to Bovet and Vauclair (2000, p. 143), “the establishment of some equivalence between the real object and its pictorial representation is dependent upon both the stimulus’ dimensions and experimental and/or motivational conditions.” In addition, Watanabe et al. (1993) point out that even if animals do recognise pictures as representations of objects, and use concepts to make category discriminations, “we do not know that their concepts are identical to those of the experimenter” (p. 357).

3.8.3.2 Associative categorisation as concept learning

As mentioned previously, associative categorisation has received much less attention than perceptual and relational categorisation. Consequently, there has been little discussion of whether non-human associative categorisation constitutes concept learning – do animals have a concept of ‘food’, for example. One example is that of Savage-Rumbaugh et al. (1980), who claimed two of the chimpanzees in their associative categorisation experiment (see section 3.5.2) had “acquired a concept of ‘food’ and ‘tool’ that was functionally based, generalisable, and symbolically encoded. (p. 923). Similarly Dasser (1988a, 1988b) refers to monkeys having a “social concept” because they can correctly identify mother-offspring pairs (see section 3.5.1).

However, as with perceptual categorisation, the fact that more prosaic explanations for these types of experiments have been put forward, such as language training and mediated generalisation (see section 3.5.3), casts doubt on conceptual mechanisms (although it has been suggested that the secondary stimulus generalisation demonstrated in pseudocategory experiments can itself be used as evidence of Lea's (1984b) conceptual requirement of a "unique mental structure", see section 3.8.2.3). Pearce (1997) goes so far as to say that the possible role of mediated generalisation, in which perceptually dissimilar items are categorised based on a pre-existing or artificially created common response, means that "it remains an open question as to whether or not success by animals in solving any categorisation problems ever implies the possession of a concept" (p. 124).

3.8.3.3 Relational categorisation as concept learning

The increasing popularity of experiments based on relationships between stimuli has led a number of authors to a new definition of concept learning. This definition rejects the use of the term 'concept' when applied to perceptually based experiments because they can be solved on the basis of the absolute properties of the stimuli themselves (Lea 1984b). Instead, they reserve the term concept for tasks that can only be solved using the relationship between stimuli (see section 3.6.2). According to Vonk (2003, p. 77): "Researchers investigating natural concept formation in non-human species have had difficulty disentangling the role of conceptual versus perceptual processing. Because the concept of how environmental stimuli are related is independent of their physical properties, some of the strongest evidence for 'abstract' concept formation comes from researchers examining the extent to which non-human species can understand the relationships between items."

There is considerable support for the idea of relational categorisation providing evidence of concept learning. Benjamini (1983), in reference to his experiment demonstrating oddity learning in ravens and gulls, said: "It may be defined also as a form of 'abstract learning' or 'concept formation', assuming that these terms refer to transfer which can not be explained by (a) stimulus generalisation along physically definable dimensions or (b) non-specific transfer effects" (p. 187). Many other authors have described same/different categorisation in terms of concepts (e.g. Cook et al. 1995;

Cook et al. 2003; Fagot et al. 2001; Flemming et al. 2007; Hoeschele et al. 2012; Santiago and Wright 1984; Wasserman et al. 1995; Wright 2010; Wright and Katz 2006; Wright et al. 2003; Young, Wasserman and Dalrymple 1997). The description of relational categorisation as conceptualisation is not limited to same/different experiments. Jaakkola et al. (2005), in a study of relative numerosity, described bottlenose dolphins as “understanding ... the concept of numerically ‘less’” (p. 296) while Avargues-Weber et al. (2011) claimed their honeybees had displayed “above/below conceptual learning” (p. 904).

A number of authors have also made clear conceptual distinctions between perceptually and relationally based categorisations (e.g. Monen, Brenner and Reynaerts 1998). In his later writings Herrnstein (1990) defines stimuli grouped according to some principle of perceptual similarity as open-ended categories, while stimuli grouped based on criteria other than perceptual similarity are called concepts. Avargues-Weber et al. (2011, p. 898) stated that: “Relational rules such as ‘same’ or ‘different’ ... are considered as a form of abstract conceptual cognition as they involve learning beyond perceptual generalisation.” Wright et al. (2003) claimed that while perceptual categorisation should more accurately be referred to as category learning, “sameness” is an abstract concept because it transcends stimuli features and instead depends on the relationship between stimuli: “Abstract concepts are rules about relationships (e.g. identity) among stimuli” (p. 184). Similarly, Tavares and Tomaz (2002) defined conceptual learning as “the ability to solve problems by using an abstract rule” (p. 132).

As with other forms of categorisation, transfer to novel stimuli is considered evidence of conceptual behaviour. Wasserman et al. (1995) claimed for the pigeons in their experiment that “accurate choice responding in the presence of [novel stimuli] constituted the prime evidence of same-different conceptualisation” (p. 249). Wright and Katz (2006) stated: “In our opinion, a subject that has learned an S/D concept ought to be able to perform as accurately with novel stimuli as with training stimuli (p. 235) and Katz et al. (2007) maintain abstract-concept learning “involves judging a *relationship* between stimuli based on a rule ... The rule is considered to be abstract when it can be applied to novel stimuli” (p. 80). Tavares and Tomas (2002, p. 132) said “the critical test for assessing concept formation is the presentation of new stimuli items”, while Wright and Lickteig (2010, p. 274) stated: “Transfer to novel stimuli is

very strong evidence that subjects have learned the relationship among stimuli and the abstract concept”. Similarly, Giurfa et al. (2001) claimed for their subjects that: “Because the bees continue to choose the appropriate matching (or non-matching) stimulus even in new situations, we conclude that they can form and use a concept of sameness ... and difference ... in making their choices” (p. 932).

3.8.3.3.1 Matching/non-matching as concept learning

The most common testing procedures for same/different categorisations are matching/non-matching and paired comparison same/different, both of which can be conducted using simultaneous or successive presentation of stimuli (see section 3.7.2.1). While many authors have claimed same/different conceptualisation on the basis of delayed matching/non-matching tasks (e.g. Giurfa et al. 2001; Zentall and Hogan 1974; Zerbolio and Royalty 1983), a number of authors have raised questions about whether procedures such as matching/oddity and the use of successively presented stimuli can be mastered using means other than relational information, let alone concept learning (see section 3.7).

Some authors have even distinguished between simultaneous same/different and matching-to-sample as representing different types of concepts, referring to subjects of match-to-sample studies as having displayed a “matching concept” (Colombo et al. 2003; Wright 1997). Tavares and Tomaz (2002), in a delayed matching/non-matching to sample study in capuchin monkeys, stated: “Success in these tasks have been interpreted as ‘concept’ learning, since the rule that allows subjects to make a correct choice is the concept ‘matching’ or ‘non-matching’, regardless of the physical properties of the various stimuli presented in each problem” (pp. 131-132). However, Thompson (1995, p. 209) claims that due to the problems of interpretation, “results from MTS [matching-to-sample] studies are often difficult to evaluate with respect to the investigators’ claims that their animals do or do not have a matching concept”.

As discussed in sections 3.7.2.1.5 and 3.7.6.1.2, Premack (1983a, 1983b) believes that when stimuli are presented successively, as in a delayed matching-to-sample task, that the resultant performance has “relatively little to do with same/different. The animal simply reacts to whether or not it has experienced the item before” (p. 354). Similarly,

Shettleworth (1998) argues that subjects in successive matching-to-sample experiments may be responding according to “Which did I just respond to?” rather than ‘Are these two things the same?’” (p. 225). According to Premack (1983a, 1983b), a true same/different judgement requires that the stimuli be presented simultaneously.

3.8.3.3.2 Paired-comparison same/different categorisation as concept learning

Even when stimuli are present simultaneously, not all authors are willing to ascribe conceptual meaning to relational categorisation. Mandler (2004, p. 140), for example, stated: “Whatever the pigeons are responding to does not appear to be anything like a human concept of same-different.” Similarly, in examining studies by Cook et al. (1995) and Wasserman et al. (1995) using multi-element stimuli (see section 3.7.3.3), Shettleworth (1998) wonders whether the successful findings in fact reveal a true “*same/different* concept” or are merely evidence of a low-level perceptual mechanism. According to Shettleworth (1998, p. 227), “the line between abstract concepts and direct perception of relationships may not be easy to draw”. Animals may have an implicit knowledge of abstract relationships contained in a specific perceptual module, yet be unable to access it to make explicit discriminations. For example, biological motion (Thompson 1995) and connectedness (Hauser 1996) could arguably be described as either abstract concepts or as higher-order properties that are perceived directly (Shettleworth 1998). (See also section 3.7.6.2 for discussion of possible non-conceptual explanations for simultaneous same/different categorisation).

However, both Cook et al. (1995) and Wasserman et al. (1995) argue that their subjects must have been doing more than merely responding to perceptual cues in their studies because transfer was not perfect. They claim the pigeons must have processed the individual elements and then made a same/different judgment at a higher, conceptual level: “This generalization decrement suggests that the birds did discriminate specific icons in the visual arrays as well as their relation to one another” (Wasserman et al. 1995, p. 252).

According to Wasserman et al. (1995), the results of studies such as theirs and those of Cook et al. (1995), Edwards et al. (1983) and Santiago and Wright (1984) demonstrate that “... it is becoming increasingly clear that the pigeon is capable of evidencing

advanced forms of conceptual behaviour ... thus arguing against Premack's (1983[b]) earlier conclusion that, among nonhuman animals, only language-trained chimpanzees can show same-different conceptualisation" (p. 252). Similarly, Cook et al. (1995, p. 259) claim: "The conceptual behaviour engaged in by our pigeons suggests that these animals may indeed be capable of forming generalised same-different concepts."

A number of authors have argued that even if animals make use of a more concrete perceptual mechanism like entropy (see section 3.7.6.2.3) to solve same/different discriminations, it does not mean they are utilising methods that are non-conceptual (e.g. Fagot et al. 2001; Wasserman et al. 2002; Zentall et al. 2008). Further, it has been argued that humans also utilise some common perceptual mechanisms in performing same/different conceptualisation (see section 3.8.2.1).

Other authors are willing to acknowledge same/different categorisation as concept learning, but only when the task involves second-order same/different relationships. In examining the results of experiments by Oden et al. (1990) studying second-order same/different tasks in chimpanzees (see section 3.7.5), Thompson (1995) acknowledges that recognising second-order same/different relationships and being able to actually match object pairs based on their relationship are both solved using relational features. However, he claims the difference between the two tasks reflects the difference between recognition and discrimination, "with the term 'conceptual' reserved for the latter ability only" (p. 213). According to Flemming et al. (2007, pp. 55-56): "Successful performance on a relational matching-to-sample task provides the necessary evidence that an animal has the most heightened degree of abstract conceptualisation."

3.8.3.4 Conceptual hierarchies

While a number of authors describe animals as either having or not having concepts, others have elaborated on their definitions of animal concepts by describing levels of complexity in conceptual behaviour. Malott and Siddall (1972) claimed experiments demonstrating the acquisition of basic or easily defined concepts such as triangularity showed the acquisition of a "simple concept", that is, "one in which the stimulus properties can be easily specified" (p. 3). Experiments using more complex stimuli that could not be easily specified, such as 'person/non-person' (Herrnstein and Loveland

1964), showed acquisition of a “complex concept”. Wright et al. (2003) describe perceptual concepts as “natural concepts” and relational concepts as “abstract concepts” and claim that: “Judgments of relationships that transcend individual features of the stimuli can be considered higher order learning, and therefore abstract-concept learning can be considered higher order” (p. 184).

Similarly, Wasserman et al. (1995, p. 252) claimed “conceptual behaviour appears to involve relatively concrete basic-level (Bhatt et al. 1988) and higher-order (Wasserman et al. 1992) categories as well as much more abstract stimulus relations (Cook et al. 1995; Edwards et al. 1983; Santiago and Wright 1984; the present results)”. Vonk and MacDonald (2004) examined levels of abstraction in “natural concept formation” (p. 3) in orangutans, the levels comprising discriminating between orangutans and humans/other primates (concrete level), primates and other animals (intermediate level) and between animals and non-animals (abstract level).

Flemming et al. (2007) view conceptual behaviour as a “continuum”, asserting that “there is little debate over whether non-human animals exhibit at least basic conceptual abilities”, but claimed that some abilities, such as analogical reasoning, were at the “highest degree of abstract conceptualisation” (p. 55). Burdyn and Thomas (1984, p. 411) claimed: “Class concepts are the ‘elements’ of conceptual knowledge (behaviour), and relational concepts are higher order concepts based on relations (conjunctive, etc.) among such elements. There are two types of class concepts, absolute and relative, as distinguished by the *necessity to compare* stimulus choices in order to affirm that an exemplar is a member of a class.”

Thomas (1986) defined concept learning as discrimination based on some common characteristic shared by a number of stimuli. In his learning-intelligence hierarchy, Thomas (1980) placed conceptual abilities at the top end of his eight-level scale of task complexity – ranging from the most basic (absolute or relative class concepts) to the highest degree of abstract conceptualisation (relations between relations, or analogical reasoning) (see section 1.3.2.1). In 1996 he refined his hierarchy further by using an operational distinction to distinguish between the two most basic “conceptual” abilities. According to Thomas (1996), categorisation based on the physical attributes of the stimuli is an “absolute class concept”. Using this definition, the features that determine

an object's class membership are inherent in the object. For example, the defining features of a tree are inherent in each tree. Conversely, Thomas (1996) defines a "relative class concept" as one in which the defining features are not inherent in the objects but are relative among the objects, such as which object is odd, larger or which set of objects manifests fewer. The operational distinction between the two is whether the subject must compare the stimuli to determine which one manifests the concept – relative (requires comparison) versus absolute (no need to compare).

3.8.4 Conclusion

The diversity of views described above shows that there is still no definitive answer to C. Lloyd Morgan's (1894) question asked at the beginning of section 3.8 about whether animals exhibit conceptual behaviour and which, if any, categorisation tasks can be used as evidence of conceptual abilities. While animals have demonstrated that they can solve categorisation problems based on perceptual, associative and relational concepts defined by human experimenters, it is still uncertain whether they use concepts in same manner as humans to solve them (Monen et al. 1998; Watanabe et al. 1993).

In a 1998 textbook on animal cognition, Roberts defined concepts in human cognition as "mental categories into which people place experiences of the world" and claimed "analogs of most forms of human conceptualisation can be found with other species" (p. 335). At least in his earlier writings (see section 3.8.3.1.1), Herrnstein suggested that animal concepts may differ in degree, rather than kind, from those of humans. "There has been reluctance to assume that the sorting done by human beings is of the same nature as that done by animals. Given the large difference in degree between the concepts of man and animals, a difference in kind has long seemed plausible ... But ... our findings show that an animal readily forms a broad and complex concept when placed in a situation that demands one" (Herrnstein and Loveland 1964, p. 551). In a comprehensive review of animal 'concept learning', Zentall et al. (2008, p. 13) concluded that, "not only are nonhuman animals capable of acquiring a wide variety of concepts, but that the underlying processes that determine concept learning are also likely to be quite similar".

However, as D'Amato and Van Sant (1988) point out, research has shown that different species often rely on different means to achieve the same result (see section 3.7 for examples). In the same manner, just because an animal classifies stimuli into the same categories as a human, doesn't mean that it has formed the same concept or utilised the same methods. A number of authors are willing to use the term concept regarding animal categorisation, but clarify that it is not necessarily the same as a human concept. In their study of categorisation of humans in slides by rhesus monkeys, Schrier and Brady (1987, p. 142) stated that "... to say that a concept is involved does not imply that it is like the one we have." Similarly, Huber (2000, p. 253) argued: "The notion that some patterns of animal categorisation correspond to human concepts does not necessarily imply that the content or structure of the animal and human concepts are identical." Chater and Heyes (1994) claim that in reviewing the status of research on "animal concepts", they found the results indicated that "... an animal cannot have the same concept SAME, or the same range of SAME concepts, as a human, but leave intact the claim that animals can be ascribed some sort of SAME concept" (p. 231).

As mentioned earlier (section 3.8.1), one of the main problems in the debate about concept learning in animals is that of semantics – what abilities are being claimed for non-humans when the word "concept" is used. One solution would be to define the term when it is used in a particular experiment, as Thomas and Kerr (1976) did: "Conceptual behaviour, as defined here, refers to selective responses to stimuli which are consistently correct in terms of predetermined and discoverable reinforcement contingencies but which do not depend upon prior experience with the specific stimuli presented on a given trial" (p. 335).

Other authors have suggested that the term should not be used at all. Huber (2001) claims the concept debate is "fruitless" because the present definition of a "concept" is based on the human experience. The author claims that even if animals do use something more than perceptual mechanisms to perform complex categorisations, there is currently no plausible account of what animal concepts might involve (such as clusters of features or something more abstract or knowledge-based). In their review of animal concepts, Chater and Heyes (1994) state that "we have assumed that cognitive terms are useful in comparative psychology only to the extent that they can be used in

the same way in discussion of humans and animals, and we have argued that ‘concept’ is not such a term” (pp. 235-236).

One possibility would be to find a new term that more clearly spells out exactly what abilities are being tested in experimental studies. Lea (1984b) proposes the use of the term “concept discrimination experiments” for studies of the type pioneered by Herrnstein and Loveland (1964) to emphasise that the stimuli concerned are defined in terms of a concept (albeit the experimenter’s) while leaving open the question of whether the subject uses a concept to make the discrimination (e.g. Ghosh, Lea and Noury 2004). Shettleworth (1998) goes further and omits the use of the word concept altogether, arguing that perceptually based experiments, at least, should be referred to operationally as “category discriminations” leaving open the question of whether the animals have learned a concept in any sense. As mentioned in section 3.8.3.1.1, Wright et al. (2003) favour the use of the term category learning for experiments based on perceptual mechanisms: “Abstract concepts are easily confused with so-called ‘natural’ concepts (e.g. trees, water, fish), which use the same term ‘concept’. Although in one sense subjects do learn the concept of a category of items, the terms would be less confusing if such learning was referred to as category learning” (p. 184).

While some type of semantic clarification may prove valuable, it does not address the central issue of whether in fact animals use human-like concepts to perform categorisations or employ some other means. Despite writing decades ago, Premack (1983a) sums up the current understanding of non-human conceptualisation by describing it as “shrouded in mystery” and attesting that: “... how any species forms concepts or, indeed, what is a concept, is largely unknown” (p. 357). Cheney and Seyfarth (1990) agree that the notion of a concept when applied to animals is “inherently vague”. “We may be able to agree that a concept is something more than a collection of individual exemplars or even a prototype, but in many respects its precise features cannot help but remain elusive” (p. 89).

However, this uncertainty is insufficient reason to conclude that all animal categorisation involves nothing more than simple perceptual mechanisms. More than a century ago, many authors believed only adult humans were capable of conceptualisation (Morgan 1894). It has since been demonstrated that humans begin to

integrate new information into fairly sophisticated categories by 10 months of age (Younger and Cohen 1985). In a similar manner, further research may yet definitively demonstrate that at least some species are capable of using human-like concepts to perform some types of categorisation tasks.

3.9 Rationale

Having examined the experimental history and theoretical background of discrimination, conditional discrimination and categorisation, it is important to summarise the rationale behind the selection of the experimental tasks used in this study.

Previous experiments have already demonstrated that echidna's possess basic discrimination learning abilities (Buchmann and Rhodes 1978; Gates 1978; see section 2.2.2.4). The next step in order of complexity (according to hierarchies such as those proposed by Herrnstein, 1990, and Zayan and Vauclair, 1998; see section 1.3.2.1) would be to examine the echidna's ability to discriminate based on complex perceptual categories, such as person/no-person (Herrnstein and Loveland 1964), tree/no-tree (Herrnstein 1979) etc. However, for the purposes of this study, it was decided to move directly to the level of relational categorisation. There were a number of reasons for this decision.

Firstly, on a practical level, complex perceptual categorisations such as those demonstrated by Herrnstein and others (see section 3.4.3) use stimuli which require a relatively sophisticated visual apparatus to discriminate. As has been discussed previously, the echidna's visual system is much less effective than that of the most commonly used experimental subject, the pigeon (see section 2.1.4.1). Conducting Herrnstein-type experiments with an echidna might lead to the subject's performance being adversely affected by an inability to differentiate between stimuli. As Hodos (1986) points out, experiments designed to be similar to human intelligence tests can be biased towards animals with good pattern vision, leading to poor performance by species with lesser visual abilities. Because of this it was decided to use stimuli comparable to that used successfully in Gates' (1978) visual acuity study in which echidnas demonstrated the ability to discriminate shapes (circle/triangle,

horizontal/vertical lines) on black and white stimulus boards (see section 2.2.2.4). This type of stimulus has been used successfully in relational categorisation (and specifically same/different) experiments (see section 3.4).

A second reason for deciding to test relational rather than perceptual or associative categorisation was also motivated by biological reasons. As discussed in chapter 2.2, the echidna has an unusual and comparatively large and complex brain structure, including a surprisingly voluminous frontal lobe. While it is by no means certain that these anatomical anomalies are indicative of increased cognitive abilities or that structures such as the echidna's frontal cortex are functionally equivalent to those found in other animals or humans, their presence suggests that echidnas may be capable of 'higher-level' cognitive tasks and provides a strong inducement to conduct more complex testing. More specifically, it has been suggested that the prefrontal cortex may play a crucial part in abstract-concept learning such as same/different. "Among neural structures that play a critical role in abstract-concept learning, the prefrontal cortex (PFC) stands out" (Wright 2010, p. 250) (see also Freedman and Miller 2008).

Thirdly, in addition to the goal of performing cognitive experiments on a rarely tested and unusual species (see section 2.3), this study also attempts to add to the debate about cognitive evolution (see section 1.6). This has been accomplished by examining whether a phylogenetically and physiologically 'primitive' species can perform 'advanced' cognitive tasks.

Relational categorisation fulfils the requirement of a 'higher-level' cognitive task (see sections 3.7.6.2.4, 3.8.3.3, 3.8.3.4 and 6.2.2.1). While perceptual and associative categorisation can potentially be explained in terms of more prosaic associative learning mechanisms (see sections 3.4.4 and 3.5.3), there is considerable support for the idea that abstract relational learning requires more than just a sophisticated visual processing system. Many authors agree that relational categorisation constitutes a more complex and 'advanced' task than perceptual and associative categorisation. For example, Wright et al. (2003, p. 184) claim that: "Judgments of relationships that transcend individual features of the stimuli can be considered higher order learning ..." Similarly, Huber (2001, Chapter 2, online) believes that "the ability to learn relational or abstract concepts is more likely to provide evidence of intelligence" while Thomas (1996, p.

160) suggests that the distinction between the two level 6 abilities on his cognitive task hierarchy (see section 1.3.2.1) – absolute (perceptual) and relative (relational) categorisation – “may have profound implications in terms of the cognitive ability of different species”.

Furthermore, while perceptual categorisation seems to be fairly widespread, having been demonstrated in a wide variety of species from bees to primates (see section 3.4.3), the prevailing school of thought is that relational learning is a relatively uncommon cognitive ability fairly high up on the various hierarchical cognitive models. This makes testing for this type of learning in the echidna an interesting contribution to the existing literature – if the echidna can successfully perform same/different relational learning either a ‘primitive’ species is capable of a ‘higher-level’ task or perhaps the ability is more widespread than previously thought.

If the subject succeeded in the same/different task, it was decided to further test the abilities of the echidna with an even more supposedly difficult and rarely tested task. In accordance with Thomas’ (1980, 1986, 1996) hierarchy of learning abilities, it was decided to introduce the additional complication of a conditional discrimination to the same/different experiment to raise it to the level of an even more complex level 7 process (see section 1.3.2.1).

Finally, while there is considerable support for relational categorisation as a ‘higher-level’ ability, there is still no consensus about whether it constitutes concept learning, or even what cognitive processes that phrase implies. However, there seems to be greatest support for a definition that encompasses relational rather than perceptual or associative mechanisms (see section 3.8.3.3). Since a number of authors are of the opinion that concept learning is such a ‘high-level’ skill that they consider it the exclusive domain of humans (see section 3.8.2.1), it is suggestive that many other authors raise relational categorisation to the level of concept learning. If animals do indeed categorise on the basis of something resembling human concepts – a capacity that would certainly be considered a ‘higher-level ability’ – a more likely candidate would be found in the realm of relational categorisation in which animals must rely on something other than perceptual cues (Vonk 2003; see section 3.8.3.3). While this debate is by no means settled, the potential link between relational categorisation and some form of

conceptualisation is another reason to consider it a more likely candidate as an ‘advanced’ task and gives further impetus to the selection of relational learning for this experiment.

CHAPTER 4

GENERAL METHODS

4.1 Subject

4.1.1 Pitpa

The subject was a 13-year-old female short-beaked echidna (*Tachyglossus aculeatus aculeatus*) kept in captivity at Taronga Zoo in Sydney, Australia. The subject, named Pitpa (ARKS number 870143), was born in captivity and was parent-reared. She was identified by a blue and yellow plastic tag attached to a spine on her right-hand side towards the rear and a tattoo “8” located on her ventral side. Pitpa was weighed monthly throughout the course of the experiments and maintained an average weight of around 4.5-5kg. She experienced no major health problems during the experiments.

The nature of these experiments meant that the subject had to be comfortable with continual handling, not become stressed by a new environment and be outgoing and willing to explore new things. Zoo staff described Pitpa as easy to handle – she was often used for keeper talks to educate zoo visitors – as well as curious and interested in her surroundings. She was considered one of the zoo’s best “escape artists” with a long history of “jail breaks” from extremely secure enclosures, including one during the course of this experiment. These factors (apart from the escape) made Pitpa an ideal subject for these experiments.

The subject was housed in an off-exhibit 10 m x 10 m open enclosure with a substrate of plants, logs, leaf litter, bark and earth. She was maintained on a high-fat diet (see Appendix) and received 100 ml of food daily. She had free access to water at all times.

Pitpa was an experimentally naïve subject who had previously only experienced normal husbandry activities with zoo staff, as well as being used in animal education talks.

4.1.2 Use of single subject

4.1.2.1 Reasons for use of single subject

One of the problems with conducting studies with echidnas that require controlled laboratory-type settings is the difficulty in obtaining and maintaining subjects.

According to Gates (1973, p. 53): “Unfortunately, echidnas are not readily available; are sometimes difficult to keep in good health, and take some time to become accustomed to handling!”

As a protected species, it is difficult to get permission to take echidnas from the wild (a special licence must be obtained from the NSW National Parks and Wildlife Service) – a problem cited by Gates (1973, p. 10) in which only “borrowing” echidnas from other sources allowed his experiments to be concluded. Nicol (2003, p. 795) claims that the fact that echidnas are now “highly protected” is partly to blame for a reduction in echidna neuroscience studies. Echidnas, particularly those taken from the wild, can also be difficult to maintain in captivity. Gates (1973), for example, was forced to terminate one experiment when four out of five of the subjects died.

Habituating echidnas to handling can also be particularly difficult, as was the case with two of the potential subjects of this experiment. Echidnas, with their covering of long, sharp spines, are hard to handle even when co-operative. When they feel threatened they adopt defensive postures, such as digging themselves into the ground or curling up in a ball (see section 2.1.5), positions from which they cannot be forcibly moved without risk of injury to the animal (and the handler). Augee et al. (2006, p. 100) described the echidna as “a remarkably strong animal for its size” due to its musculoskeletal structure. Gates (1973, p. 88), in discussing the difficulty in restraining echidnas, described them as having “immense muscular power and body flexibility in extricating themselves from a wide range of situations”. Gates (1973) spent up to a month handling some of his subjects on a daily basis before he could commence testing and even then some animals “regressed” in later experiments. He gave up on one animal after seven weeks of daily handling were unsuccessful.

It was originally planned that this experiment would be conducted using more than one subject and the zoo provided three other echidnas – Rozelle, Cruegar and Cass – in addition to the final subject, Pitpa. Rozelle became ill and had to be removed. While Pitpa was handled regularly in her role in zoo education talks, Cruegar was not used to being handled and became stressed in the apparatus, either trying to get out or curling up in a corner, and paid no attention to the stimuli even when tempted with food. Cass was even less used to handling than Cruegar and buried himself as soon as someone

entered the enclosure. Attempts to habituate Cruegar and Cass were made for several weeks, however due to time constraints and ethical considerations in continuing to stress the animals; it was decided not to use those echidnas. Cruegar stayed in the enclosure for the duration of the experiments so Pitpa, who was raised with other echidnas, would not be socially isolated; Cass was put back into the zoo's main echidna population. The zoo's other 'tame' echidnas were needed for zoo activities and were not available for research.

4.1.2.2 Precedent for single-subject experiments

While the use of one subject is not optimal, it is more of an issue for studying natural behaviours than for this type of artificial cognitive testing. Rather than testing what a particular species *does* do, the objective of this type of study is to determine what members of a species *can* do. Abilities demonstrated by an individual show those abilities are within the capacity of that species – variation between individuals means some individuals may be less capable, others possibly more so. (See Hanggi 1999; Pepperberg and Brezinsky 1991).

This type of single-subject testing has an established history including a number of well-known experimental series such as Irene Pepperberg's cognitive experiments with Alex the African Grey parrot (e.g. Pepperberg 1983, 1987, 1988; Pepperberg and Brezinsky 1991), Kastak and Schusterman's equivalence studies using a single California sea lion, Rio (Schusterman and Kastak 1993, 1998) and a number of long-term primate language studies (e.g. of Washoe by Gardner and Gardner 1969 and of Kanzi by Savage-Rumbaugh and Lewin 1994). Other studies using single experimental subjects include matching-to-sample with a dolphin (Roitblat et al. 1990), analogical reasoning in the chimpanzee (Gillan et al. 1981), object-object relations in the chimpanzee (Tanaka 1996) and conditional discrimination learning in a harbour seal (Hanggi and Schusterman 1995).

As in these studies, the results here are applicable to the species as a whole in terms of demonstrating the capability of echidnas. Regarding the use of single-subject experiments, Hanggi (1999, p. 244) states: "A positive finding, regardless of the

training methods or history of the subject, implies that this aptitude is within the capacity of the species”. (See also Pepperberg and Brezinsky 1991).

4.2 Apparatus

The apparatus was a custom-built plywood y-maze variant, with dimensions as shown in Figure 1, which was located within the echidnas’ living enclosure.

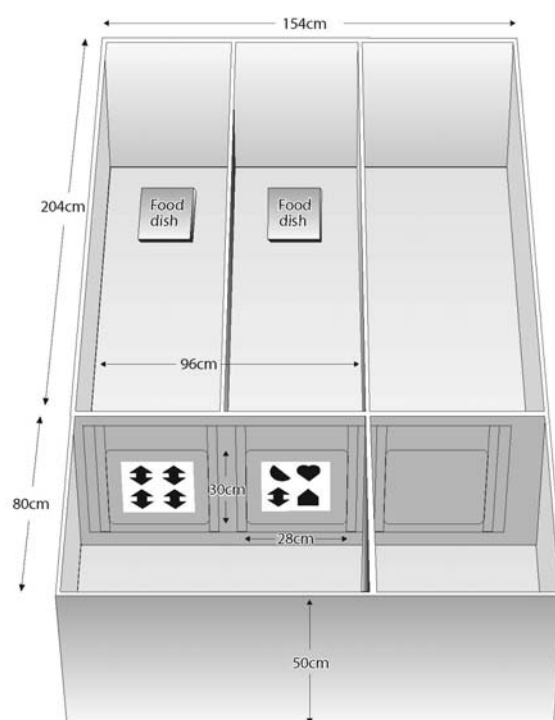


Figure 1: Three-dimensional diagram of the apparatus showing stimulus panels and covered food dishes



Figure 2: Photo of the apparatus situated in the enclosure at Taronga Zoo

The apparatus walls were of sufficient height, 50cm, to prevent an echidna from climbing out and a wooden floor stopped the subject both from digging out and from probing the ground for additional food. It was painted with several coats of non-toxic green paint to prevent deterioration in the outdoors. A number of small holes were drilled at the edges of the maze arms to provide drainage. The apparatus was built to provide a three-choice option, however the third arm was walled off for these experiments, as only two-choice testing was required.

At one end of the two-choice section of the apparatus was a 96cm x 80cm start box. The front wall of the start box contained two hinged swinging doors, on which the stimulus panels were fixed with Velcro, which the subject pushed through to enter one of the maze arms. The doors only swung one way, from the start box into the maze arms, so the subject could only choose to go through a door once per trial. Many same/different experiments are designed so the subjects must select the S+ stimulus at a location removed from the stimulus itself (e.g. pressing a lever, pecking a key) (see section 3.7.2.1). However this experiment uses a procedure similar to that used by Blaisdell and Cook (2005), Chausseil (1991) and others (see section 3.7.3.3), in which the subject is required to respond directly to the S+ stimulus. According to Blaisdell and Cook (2005), responding directly to the S+ stimulus may lead to greater attention being paid to stimulus features, a view shared by Castro et al. (2010, p. 36), who suggested “direct responding may facilitate discrimination learning”. The actual design using stimulus panels attached to push-through doors is similar to that used by Gates (1978) in his study of visual discrimination in the echidna and also by Sappington and Goldman (1994), who trained horses to push through stimulus panels to gain a food reward.

The back wall of the start box was removable. During testing it was in place to prevent the subject from leaving the apparatus or the other echidna in the enclosure from entering. When trials were not being conducted the back wall was removed and the swing doors tied open using elasticised straps to allow the echidnas free access to the empty apparatus. This was done so the subject would not be tempted to explore an unfamiliar environment during testing and be distracted from the task at hand.

Located at the end of each maze arm was a round metal food dish (12cm in diameter x 6cm deep) of the same type as those generally used to feed echidnas at the zoo. It was

important to control for olfactory cueing, particularly as echidnas have a very acute sense of smell (see section 2.1.4.2). A previous experiment testing oddity learning in rats (Langworthy and Jennings 1972, see section 3.7.3.2) was criticised for methodology which allowed for the possibility that the rats learned the problem simply by smelling where the food was located (Thomas 1996).

To prevent the echidna from detecting the smell of food inside the dishes, the food dishes were not located immediately behind the swing doors but at the end of relatively long maze arms (approximately two metres). In addition, each dish was covered with a 20cm x 20cm plywood lid. An earlier experiment conducted with other echidnas at Taronga Zoo (Quince 1998) had tested this method and concluded that the wooden lids prevented the echidnas from locating food in the dishes on the basis of olfactory cues. This was confirmed by a further study conducted using the same equipment (Burke et al. 2002). Anecdotally, it seems unlikely that Pitpa would have walked to the end of the maze arm and lifted the lid off the food dish on every trial if she could smell whether or not there was food in the dish.

4.3 Stimuli

4.3.1 General stimuli

Each stimulus consisted of a 21cm x 21cm laminated panel containing black-and-white figures created using Microsoft Publisher and printed with a laser printer (hp LaserJet 1000). Apart from the plain black and white stimuli used in Experiment 1, the panels contained a variety of geometric and irregular figures selected from Microsoft Publisher autoshapes which were deemed basic enough to be visible to the echidna from within the start box approximately 20-30cm away. This was the distance estimated by Gates (1978) to be the “choice” point at which echidnas were able to discern and discriminate visual stimuli in his examination of echidna visual capabilities. The stimulus panels in this study were slightly smaller than those used by Gates (1973) (which were 26cm x 26cm) due to restrictions imposed by the size of the apparatus swing doors, but were considered (and proved to be) discernible by the subject.

4.3.2 Same/different stimuli

For the same/different discrimination sections of this experiment (Experiments 4 to 7), it was decided to use relatively simple, black-and-white stimulus items rather than more complex visual stimuli such as photographs of natural scenes that are often used in same/different experiments with pigeons (e.g. Cook et al. 2000; Santiago and Wright 1984). In addition to concerns about the echidna's visual acuity (see below), the choice of stimuli was based on a number of objectives. Firstly, it would determine whether echidnas could categorise objects they had not previously encountered in their environment, suggesting an ability to adapt to a range of situations rather than just natural environments (Huber 1995). Secondly, the use of uncomplicated stimuli would also help avoid introducing confounding information found in pictures of natural scenes (Hanggi 1999). According to Vonk (2003): "With natural stimuli it can be difficult to de-couple the role of perceptual and conceptual processing" (p. 84). Complex visual stimuli have been found to lead to stimulus-based perceptual errors such as the subjects attending to irrelevant stimulus features. An example of this problem was seen in the "red patch" errors found in D'Amato and Van Sant's (1988) perceptual categorisation of "person present" experiments discussed earlier (see section 3.4.4.4.1). In particular, the use of black-and-white stimuli avoids the possibility of colour information interfering with the processing of other elements in the stimuli (Lamb and Riley 1981), as well as making allowance for the uncertainty surrounding the echidna's capacity for colour vision (see section 2.1.4.1).

The same/different stimulus items in this study were presented in multi-element arrays on panels made up of either all the same or all different items in a design popularised by Wasserman et al. (1995) (see section 3.7.3.3). The echidna's visual acuity was a consideration in determining the size, type and number of elements to be used per panel. Wasserman et al. (1995) used fairly small elements consisting of relatively complex line drawings and 16 elements per panel. However, as the echidnas' visual acuity is significantly poorer than that of a pigeon (Gates 1978; Hodos 1993; see section 2.1.4.1) it was decided to make the size of the stimulus panels and elements greater than that used by Wasserman et al. (1995). Wasserman and his colleagues used 7cm x 7cm displays and 1cm x 1cm elements, whereas this study utilised 21cm x 21cm panels and 6-10cm wide elements. It was also decided to employ only four elements per panel and

use simple, relatively easy to distinguish geometric shapes as stimulus items. The use of geometric shapes has proved a popular stimulus for categorisation experiments with a number of species, e.g. coatis (Chausseil 1991), pigeons (Blaisdell and Cook 2005), horses (Hanggi 1999) and primates (Vonk 2003).

Another consideration in selecting the number of shapes on each panel was the suggestion that the Wasserman et al. (1995) study may have been solved on the basis of a generalisable order-disorder rule due to the fact that the *same* arrays had a greater linear orderliness of rows and columns than that of the *different* arrays (see section 3.7.6.2.2). While later experiments indicated that pigeons were able to successfully perform the task using non-linear, disorderly arrays (Young and Wasserman 1997), the use of four rather than 16 items in the arrays for this experiment reduces the chance of this effect confounding the results. With only two items in any direction it is unlikely that perceptual grouping principles would organise the display into rows or columns (see Palmer and Rock 1994). Fewer items also reduces the likelihood of an entropy-based explanation for the subject's performance as fewer items means less difference in variability between the *same* and *different* arrays than with higher-item arrays (see section 3.7.6.2.3).

The shapes used on the stimulus panels were selected to include both regular and irregular shapes of different sizes and orientations to deter the subject from using perceptual cues such as uniformity, regularity or relative brightness in the same/different tests, a criticism that has been levelled at many other same/different experiments (Delius 1994). For example, both of the panels in Figure 3 below belonged to the *same* category.



Figure 3: Two of the *same* stimulus panels used in Experiment 4 demonstrating variation in both uniformity and relative brightness

As with Wasserman et al.'s (1995) study, the same shapes were used in both the *same* and *different* panels to control for item-specific cueing from individual shapes. For similar reasons, the six shapes used in the *same* panels for the same/different

experiments were each used the same number of times (four) in the six *different* panels. Each shape also appeared in different positions on the panel as far as was possible – three of the shapes appeared in all four positions, while the other three shapes appeared in three different positions and appeared in one of the positions twice.

4.3.3 Conditional stimuli

For the conditional phases of this study, the stimuli were designed to contain both the geometric shape elements discussed above and conditional cues in the form of the background colour of the panels. This is similar to the combined stimulus method designed by Lashley (1938b), which has also been called the “two-choice visual” conditional discrimination (Schrier and Thompson 1980) (see sections 3.2.2.1.4 and 3.2.3). As in this experiment, this method of using background colour as a conditional cue has been used to study both conditional discrimination (Lashley 1938b) and conditional same/different categorisation (Castro et al. 2010; Flemming 2011; Flemming et al. 2007).

4.4 Procedure

4.4.1 Scheduling

Echidnas hibernate for varying lengths of time from early winter to early to late spring (Grigg et al. 1992, see section 2.1.8) so the testing was conducted during the warmer months (November to April). Zoo staff had indicated the echidnas were generally active in the early afternoon coinciding with their usual feeding time so the trials were all performed at that time of day.

4.4.2 Pre-training

After several days familiarisation with the new enclosure, an initial preliminary training phase was conducted to teach Pitpa the experimental procedures. She was first taught to remove the lids from the food dishes. She successfully learned how to remove the lids (by placing her snout on the undersurface of the lid and pushing it up and off) after only a few attempts (see Figure 4).



Figure 4: Photo of Pitpa lifting off a food dish lid



Figure 5: Photo of Pitpa pushing through a swing door

The apparatus was then placed in the enclosure and left open for several days to familiarise the subject with the test area. Pitpa was then trained to push through the swing doors for a food reward in the maze arms (see Figure 5), with care being taken not to favour one arm over the other. When this was accomplished and the subject appeared comfortable using the apparatus, the test phase began.

4.4.3 General trial procedure

For all experiments, a trial consisted of the simultaneous presentation of one pair of stimuli – basically the two-choice simultaneous discrimination method described in Sutherland and Mackintosh (1971), also called a paired comparison task (see section 3.7.2.1.1). In the later same/different experiments (Experiments 4 to 7), the pair consisted of two multi-element arrays in a similar procedure to that used by Blaisdell and Cook (2005); Castro et al. (2010) and Flemming et al. (2007) in their same/different and conditional same/different studies (see section 3.7.4).

One session of trials was conducted per day. Testing was conducted every day starting at approximately 1pm. A number of sessions were cancelled due to heavy rain, lack of subject motivation (e.g. not looking at the stimuli, not interested in food and trying to get out of the apparatus), subject in torpor and on one occasion for minor veterinary treatment.

Because of the echidnas' tendency to sleep for some of the day or even enter torpor for short periods even in the summer months (see section 2.1.8), it was decided to begin

testing only when the echidna was awake and motivated. The session was initiated when the subject indicated a willingness to proceed. This was determined by observing the subject's behaviour – it was considered the subject was motivated when she displayed behaviours such as approaching and following the experimenter (often trying to climb up the experimenter's leg) and walking around the apparatus and trying to climb inside. Lack of motivation was considered indicated when the subject stayed buried in the enclosure after the experimenter entered, even when tempted with food.

After the apparatus was returned to testing configuration (back wall of the apparatus put in place and the swing doors lowered), the stimuli were attached to the swing doors. Food dishes with lids were placed at the ends of the maze arms, with the dish behind the correct stimulus containing 10ml of food, the other empty. For each day's session only one of the dishes was used to contain the food reward, the other remained empty so there was no possibility of even a small reward for an incorrect choice. The dishes were swapped between the maze arms so the dish containing food was always located behind the correct stimuli.

Initial testing with the subject showed a tendency to rush straight through one of the doors as soon as she was placed in the apparatus rather than examining both doors, possibly due to her lower position relative to the stimulus panels and the physical constraints on tilting her head upwards (see section 2.1.3). Due to this tendency, it was decided to include a viewing period as part of the experimental procedure. At the beginning of each trial the subject was lifted into the start box and held at the rear of the box centred between the two doors facing the stimuli at eye-level for approximately 3-5 seconds of viewing time.

One example of the advantage of a viewing period was shown in an experiment by Bailey and Thomas (1998), in which the only rat to show successful first-trial transfer in their study of olfactory oddity learning was the only one that investigated all of the stimuli before making a choice (see section 3.7.3.2). The decision to provide a viewing time was also based on sample identification theories such as the drift model of sample encoding (Roitblat 1984; Roitblat and Harley 1988), which describes how increasing sample durations allows a subject to more strongly encode a sample stimulus, and sequential sampling theory, which assumes that “the subject's confidence in its

identification of the stimulus grows monotonically with increasing numbers of looks ...” (Roitblat et al. 1990, p. 91). An observation period has also been used with other species such as pigeons (e.g. Gibson et al. 2006; Wright and Katz 2006) and rhesus monkeys (Katz et al. 2002; Wright and Katz 2006; Wright et al. 2003).

After the viewing period, the subject was placed straight down on the floor of the start box in the same central position between the two doors. The subject selected a door and pushed through into the arm behind. She then walked down the maze arm to the food dish, which either contained food if the choice was correct or was empty if incorrect. A choice was considered to have been made when the subject pushed through one of the doors. In common with Gates’ (1973) procedure, an error was not recorded if the subject approached, but did not push, the incorrect door. (On several occasions she headed for one door then ‘changed her mind’ and chose the other).

After Pitpa either ate the food or lifted the lid to discover an empty food dish, she was placed in a holding area (a large, empty plastic garbage bin in the unused third arm of the apparatus) during the inter-trial period while the food dishes and stimuli were changed. The echidna could not see over the top of the bin to observe in which maze arm the food was placed (see Figure 6).



Figure 6: Photo of Pitpa in the holding bin during the inter-trial interval

During the early experiments in this study, it was decided to use a correction trial procedure in which the subject repeated the same trial until a correct response was made (e.g. Burdyn and Thomas 1984; D’Amato, Salmon and Colombo 1985; Hollard and

Delius 1982; Santiago and Wright 1984). Wasserman et al. (1995, p. 250) described their use of correction trials in terms of the pigeons being “punished” for incorrect responses, however the rationale in this study was that it gave the subject the opportunity to make correct responses to previously incorrect selections and thus facilitate learning. According to Santiago and Wright (1984), the correction procedure can also “help remove response biases that otherwise develop” (p. 500).

During the correction trials (Experiment 1, Experiment 2 and the first part of Experiment 3) the stimuli and food dishes remained untouched for the next trial if the subject made an incorrect choice and continued in that configuration for each trial until a correct choice was made. The echidna was not moved to the holding area between correction trials and was merely taken back to the start box after she had exposed the empty food dish. When a correct choice was made the echidna was removed to the holding area and the stimuli and food dishes reset for the next trial. A correct choice was recorded only if the subject selected the S+ stimulus on the first trial of that configuration. During non-correction trials, which were used for the later experiments, the subject was removed to the holding area between each trial and the stimuli and food dishes reset for the next trial whether the choice was correct or not.

Under both correction and non-correction conditions, the session was concluded when 10 correct choices were made and there was no upper limit set on the number of trials it took the subject to reach that criterion. As 10ml of food was given per trial, the echidna’s entire daily allotment of food was consumed during the session and no supplementary feeding was given other than insects caught by the animal in the enclosure.

While some authors (e.g. Brodigan and Peterson 1976; Cumming and Berryman 1961; Edwards et al. 1983; Katz and Wright 2006; Wasserman et al. 1995) restrict the daily food intake of subjects during an experiment to ensure they are “kept hungry and therefore in a well-motivated state” (Gates 1973, p. 33) others do not deprive their subjects of food to enhance performance (e.g. Flemming et al. 2007; Tavares and Tomaz 2002). In this case, such a procedure was prohibited by zoo ethics regulations. However, the subject appeared quite food motivated throughout the experiment, except for periods where she had entered torpor. In fact, Tavares and Tomaz (2002) suggested

that not depriving subjects of food and water (in addition to conducting testing in the subjects' living area, as was also done here), may have led to better experimental outcomes in their study due to a reduction in stress. Like Pitpa, the capuchin monkeys in Tavares and Tomaz' (2002) experiments initiated testing, suggesting the process was not unduly stressful for them.

To control for position habit, the S+ and S- stimulus panels were randomly alternated between the left and right doors according to a randomisation schedule generated at www.randomizer.org. Measures were also taken to control for auditory cues, both from the noise of the Velcro on the stimulus panels and from the sounds of the experimenter and the dishes. Regardless of whether the panels had to be changed or not, both panels were removed and replaced for each trial. The experimenter stood in the same maze arm each time the food dish was replenished irrespective of which maze arm the food dish was located. In addition, both dishes and both lids were picked up and put down whether the dish containing food had to be swapped into the other maze arm or not. As discussed previously (see section 4.2) olfactory cues were also addressed through the use of distance and wooden lids on the food dishes.

4.4.4 Transfer trials

To determine whether Pitpa had learned the task and not just memorised the training stimuli, transfer trials using novel stimuli were conducted. This is considered by many authors as the best way to test for 'concept learning' (see section 3.8.3.3). "Most important, to demonstrate either categorisation or conceptualisation, it is imperative to show that discriminative responding occurs with untrained test stimuli rather than only with training stimuli" (Hanggi 1999, p. 250).

During the transfer trials, novel pairs of stimuli were introduced randomly throughout each session (using the randomisation schedule) to ensure the subject did not become confused about the task, leading to an overall deterioration in performance. According to Thompson (1995, p. 209): "Abruptly introducing all novel stimuli to an animal that has experienced only familiar ones during training can disrupt performance and thereby mask any evidence of conceptual learning." (See also D'Amato, Salmon and Colombo 1985; Mercado et al. 2000; Pack et al. 1991).

This approach has been utilised in pigeon same/different discrimination experiments from the Wasserman laboratories, where ‘warm-up’ trials are used before starting testing sessions (e.g. Gibson et al. 2006; Wasserman et al. 1995; Young and Wasserman 1997). In the Wasserman et al. (1995) study, for example, testing sessions began with 32 warm-up trials showing all the training stimuli twice; then two randomly selected training trials were shown followed by one randomly selected testing trial until all the testing stimuli were seen once. Each testing session was also separated by two retraining sessions procedurally identical to the training sessions.

The method of interspersing training and test stimuli used in this experiment is a variation on that used by Bhatt et al. (1988), in which repeating stimuli were shown in odd-numbered sessions and novel stimuli shown in even-numbered sessions in a pigeon perceptual categorisation experiment. It is similar to that used by Burke, Everingham, Rogers, Hinton and Hall-Aspland (2001) and Wetzel et al. (1998), in which novel and training stimuli were presented randomly in studies of sea lion perception and categorical discrimination of tone direction in Mongolian gerbils respectively. The procedure has also been used with chimpanzees (Robinson 1955) and monkeys (Fujita 1983).

Interestingly, Wasserman et al. (1995) utilised the multi-element facet of their experiment to test the effect of using previously trained elements (icons) in testing stimuli. In Part 1 of their study, the authors compared the results of using testing stimuli made up of icons from the training phase to testing stimuli consisting of all new icons. Contrary to their expectations, the authors found chance performance with the previously seen icons but significantly different from chance performance with the novel icons. In addition, there was a significant disparity between the results for *same* and *different* stimuli. On the novel icon arrays, the average accuracy to the *same* arrays was not significantly different from chance (46% correct), whereas the average accuracy to the *different* arrays was significantly different from chance (82% correct) – a trend that was reflected in each of the four testing sessions. Of the familiar icon arrays, average accuracy to the *same* arrays was below chance (28% correct), whereas average accuracy to the *different* arrays was significantly different from chance (75% correct) – a performance differential that was significantly different from chance.

The same/different performance anomaly was not observed in the second part of Wasserman et al.'s (1995) experiment in which all the testing icons were novel (in the sense that they had not previously been differentially reinforced). However, the authors suggest there were a number of confounding factors in Part 2 that might have influenced the result. There were twice as many training and testing stimuli in Part 2 (reducing the risk of memorisation according to the authors) and the pigeons had had prior experience with the experimental paradigm in Part 1. The subjects had also already seen the supposedly “novel” testing stimuli in Test 1 (although the authors point out that it was just four times each 28 days previously, the pigeon’s prodigious memory has been well documented – see section 3.4.4.2.1).

Regardless, the results of Wasserman et al. (1995) indicate that using novel stimuli containing previously untrained (and in the case of this study previously unseen) elements appears to be a more effective method of testing task generalisation than reusing training icons in the testing phase and thus the former method has been employed here.

Wasserman et al. (1992) and others have advocated for nondifferential food reinforcement on transfer trials (e.g. Gibson et al. 2006; Wasserman et al. 1995; Young and Wasserman 1997). They argue food should be given regardless of whether a choice is correct so that repeated testing can be conducted without the confounding influence of explicit training effects. However, it could be argued that this approach could be equally confounding, as the subjects would be effectively being trained to respond to incorrect stimuli during transfer trials. Another possibility is to provide no reinforcement at all during transfer trials; however the potential for experimental extinction of responding to test stimuli (Young and Wasserman 1997) and reduction of subject motivation would then arise.

In contrast, other authors (e.g. Flemming et al. 2007; Zentall and Hogan 1975) use differential food reinforcement during transfer tests – that is, only correct responses are reinforced with food rewards in the same manner as training trials. Zentall and Hogan (1975) claim this method enhances detection of the most sensitive measure of transfer in testing for ‘concept learning’ – that is, the rate at which a second problem is learned. This experiment has taken this approach.

4.5 Analysis of results

4.5.1 General analysis

The results of the experiments were analysed using two-tailed binomial tests and assessed against an alpha level of .05 to determine whether they were significantly different from chance (50% correct). The calculations were performed using the java applet: http://users.abo.fi/jtuomain/speech/z_score.html. Chi-squared tests were used to compare performance between blocks and between stimulus types and assessed against an alpha level of .05 using the Java applet:

<http://www.socscistatistics.com/tests/chisquare/Default2.aspx>.

4.5.2 Results across blocks

In order to minimise stress on the subject and reduce the chance of her losing interest, it was decided in conjunction with zoo staff to limit the number of trials conducted each day. Each day's session ended when the subject completed 10 correct trials, with the number of trials taken to reach that criterion ranging from 10 to 22 trials throughout the course of the study. However, analysing the data based on each daily session would utilise too few trials to provide a reliable assessment of the subject's performance. In addition, the echidna's behaviour could be expected to vary between days due to a variety of factors such as weather, temperature and food motivation, an issue exacerbated by the outdoor experimental setting. For these reasons, the session data was collated into blocks (usually of five sessions each) for analysis. Dividing the data for each experiment into blocks, rather than analysing the results of each experiment in its entirety, provided the opportunity to track changes in performance as each experiment progressed.

Collating the daily session data into blocks also provided a better basis for comparison with similar studies undertaken with other species. For example, in their seminal paper on same/different learning in pigeons, Wasserman et al. (1995) analysed their results using a daily testing session of 144 trials. Another well-known same/different study was conducted by Pepperberg (1987) under similar constraints to this one – working with a single subject (an African Grey parrot called Alex) who often had short session lengths

due to the subject's lack of motivation (p. 426). Pepperberg measured performance by aggregating the session data into a single block of 113 transfer test trials.

4.5.3 Task criteria

The criterion for the training phase of each experiment was two consecutive blocks significantly different from chance. For the transfer trials, the criterion was one block significantly different from chance and no significant difference between the training and transfer blocks. Katz and Wright (2006) stressed the importance of performance on novel stimuli being at least as good as the training performance. According to Katz and Wright (2006), transfer equivalent to baseline is important because anything less than this is partial transfer, implying there are multiple cues controlling behaviour.

Due to the time constraints on the availability of the subject, both in terms of how long the zoo would allow the subject to be off-exhibit and the fact that echidnas periodically enter torpor and sometimes true hibernation during colder weather (see section 2.1.8), it was decided to limit each experiment to a maximum of 20 sessions.

4.6 Ethics considerations

Ethics approval for the experiments carried out during this study was given by the Zoological Parks Board of NSW Animal Care and Ethics Committee. A number of measures were undertaken to enhance the welfare of the subject including:

- Providing a large, natural living enclosure containing trees, branches, artificial and natural shelters, water containers large enough to allow bathing and a sufficient dirt layer above the floor fencing to allow natural burrowing behaviour.
- Housing a second echidna in the enclosure to prevent social isolation.
- Monthly weighing to monitor the subject's health.
- Keeping a daily record of behaviour, feeding activity and physical appearance of the subject to help identify any problems.
- Immediate access to veterinary treatment when required.

CHAPTER 5

RESULTS

5.1 Experiment 1: Black/white discrimination

5.1.1 Introduction

This experiment was conducted in part to provide the subject with discrimination training and also to confirm the results of a study of visual acuity in the echidna by Gates (1973), which found that echidnas were capable of making a visual discrimination between black and white stimuli. Buchmann and Rhodes (1978) also demonstrated black/white discrimination in their study of instrumental reversal learning in the echidna; however the visual stimuli were combined with tactile cues.

It also provided the opportunity for an admittedly limited study of the echidna's long-term memory. It was originally planned that this series of experiments would be conducted during the Australian summer months (December – February) when echidnas are most active. However, during the first season of testing a number of the zoo's echidnas, including the planned subject of these experiments, developed a bacterial skin complaint that prevented them being available to participate until late March. Testing began after the familiarisation phase was completed, however after only six sessions the subject lost interest in food, and thus the trials, as the temperature dropped and she entered torpor (see section 2.1.8). When testing resumed seven months later in November, the same black and white stimuli were used and the experiment repeated.

5.1.2 Method

5.1.2.1 Stimuli

The stimuli were one black panel and one white panel as seen in Figure 7 (see also Figure 2).

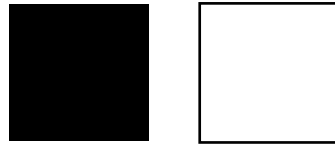


Figure 7: Stimulus panels for Experiment 1 – black/white discrimination, S+ = black

5.1.2.2 Procedure

Both Part 1 (conducted in March) and Part 2 (conducted in November) of the black/white visual discrimination experiment were carried out using correction trials, so the subject was shown the same stimulus configuration for each trial until a correct choice was made. However, a correct response was recorded only if the first choice was correct. The subject was shown 10 pairs of stimuli during each daily session and the number of correct choices out of 10 was recorded. The correct choice for this experiment was black.

Six sessions were conducted in Part 1 of the experiment, for reasons discussed in section 5.1.1, and 10 sessions were conducted in Part 2.

5.1.3 Results

5.1.3.1 Part 1 – March/April

While the results of Part 1 do not meet the target criterion of two consecutive blocks significantly above chance, examination of Figure 8 suggests the subject was learning the black/white discrimination before the experiment was stopped. For the purpose of analysis the results were grouped into two blocks of three sessions each. A two-tailed binomial test was conducted on the cumulative score of each block (number correct out of 30), with chance being 15/30. The results for both the first block (correct responses = 15/30, $z = 0$, $p > .05$) and the second block (correct responses = 20/30, $z = 1.83$, $p > .05$) did not differ significantly from chance.

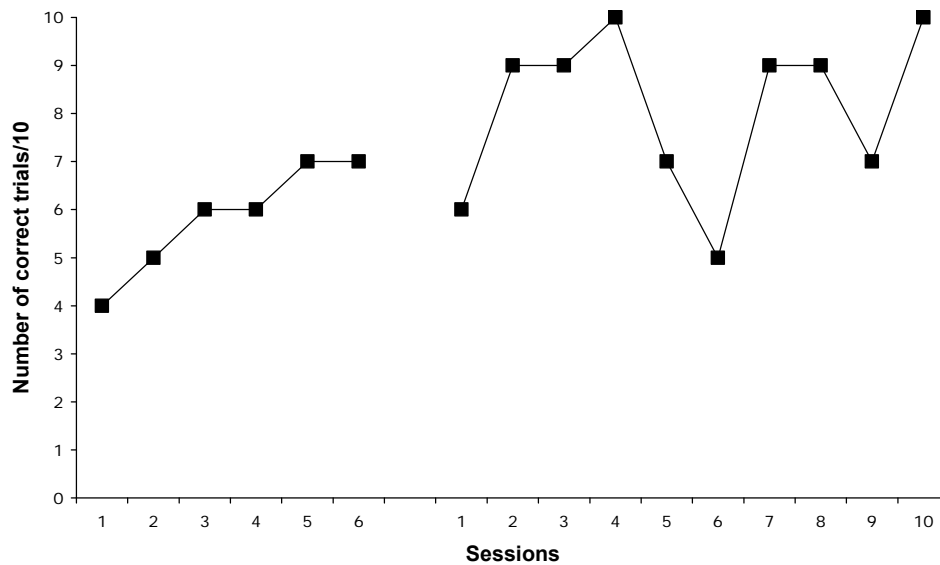


Figure 8: Number of correct responses to black/white discrimination task, S+ = black (correction trials). First six sessions show Part 1 of the experiment (March/April), the next 10 sessions show Part 2 of the experiment (Nov/Dec)

5.1.3.2 Part 2 – November/December

For analysis, the data were grouped into two blocks of five days each. When the blocks were analysed using a two-tailed binomial test on the cumulative score of each block (number correct out of 50, chance = 25/50), the results were fairly similar for each block. Both the first block (correct responses = 41/50, $z = 4.53$, $p < .001$) and the second block (correct responses = 40/50, $z = 4.24$, $p < .001$) were highly significantly different from chance, meeting the criteria for successful learning of this task.

Significantly different from chance ($p < .05$) for an individual session was calculated to be 90% (9/10 correct responses) using a two-tailed binomial test. The subject achieved that result or better on six out of the 10 sessions; including three consecutive days immediately following day 1 (see Figure 8).

5.1.3.3 Side bias

The results of both Parts 1 and 2 were then examined to determine how many times per session the subject chose either the right-hand or left-hand side (see Figure 9).

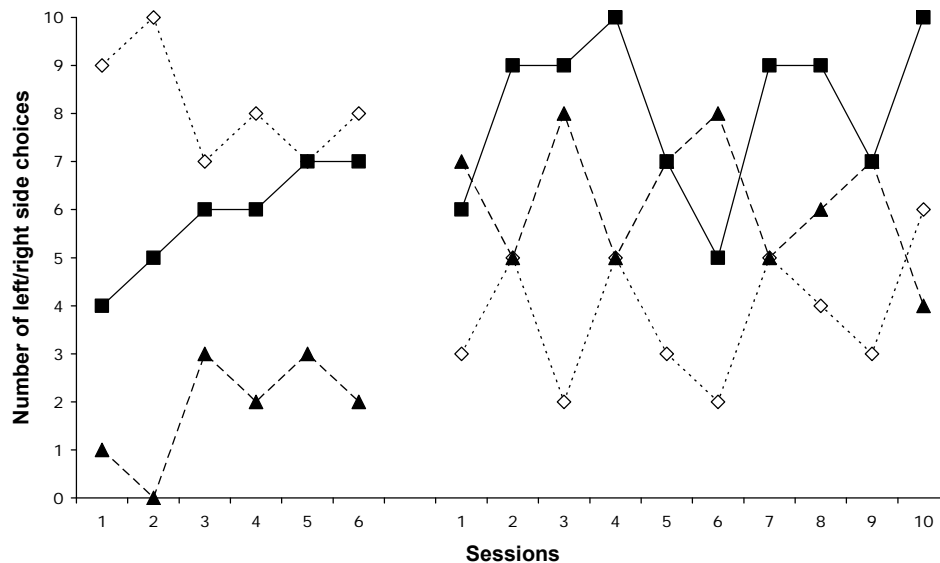


Figure 9: Number of left/right choices in black/white discrimination task, S+ = black (correction trials). ◇ = the number of left-hand choices, ▲ = the number of right-hand choices, ■ = the number of correct responses. First six sessions show Part 1 of the experiment (March/April), the next 10 sessions show Part 2 of the experiment (Nov/Dec)

Visual examination of Figure 9, which compares Pitpa's selection of the left-hand and right-hand maze arm during Experiment 1, indicates she had a strong tendency to a 'left' side bias during Part 1 of the experiment. During Part 2 of the experiment, conducted approximately seven months later, she seemed to show a (less pronounced) preference for the right arm.

5.1.4 Discussion

The results of this experiment confirm the findings of Gates (1973, 1978) by demonstrating that echidnas are capable of performing a visual discrimination between black and white stimuli. This would certainly be expected, as this ability seems to be extremely common among animal species (see section 3.1.3). Pearce (1997) claimed that, to his knowledge, no vertebrate has ever been shown to be incapable of solving discrimination problems and even a single complex cell, the protozoa *Paramecium*, can be trained to discriminate between two auditory stimuli (Hennessey, Rucker and McDiarmid 1979).

Although it is difficult to compare performances of subjects in different experiments due to discrepancies in apparatus and experimental procedure, it is interesting to note that the subject of this study was able to solve this discrimination with comparable

rapidity to the echidnas in Gates' (1973, 1978) study, which in turn was similar to that obtained with rats by Sutherland and Mackintosh (1971).

Gates (1973, 1978) conducted six daily sessions of 18 correct trials per session for a total of 108 correct trials. By session five, having experienced 72 correct trials in the previous four sessions, all three echidnas were achieving 90% or better (significantly above chance) in individual sessions. Pitpa was exposed to 60 trials in Part 1 of the experiment and then had a seven-month break. In Part 2, she had one session of 10 correct trials, then scored 90% or better in the next three sessions. Her performance deteriorated slightly during the middle sessions of Part 2, but improved again by the end of the experiment.

5.1.4.1 Side bias

It is a common finding in experiments where animals are required to choose between a number of stimuli that subjects initially show a positional bias before they solve the discrimination (e.g. Carter and Eckerman 1975; Cumming and Berryman 1961, 1965). Some authors have suggested that positional cues are more salient than visual cues (Sutherland and Mackintosh 1971) and the results of this experiment seem to support that view, with the subject showing a strong initial positional bias before learning to respond on the basis of the black/white stimuli.

A number of early authors (Krechevsky 1932, 1938; Lashley 1929) explained the side bias tendency by suggesting that when animals are presented with a discrimination they rapidly form a single hypothesis, such as 'choose right', which they discard when it proves inadequate and then choose another one, such as 'choose black', until they find one that is consistently rewarded. According to Krechevsky (1932, 1938), hypotheses could only be learned and tested one at a time and a position habit should form and dissipate before a discrimination is solved.

However studies such as that conducted by Turner (1968) have shown that animals can learn about the nature of the stimulus even when they are exhibiting a position habit. Turner found responding time was affected by the nature of the stimulus (in this case black or white), with the subjects gradually taking longer to choose the preferred

position to the incorrect stimuli and vice versa. Other studies also support Turner's conclusion (e.g. Bitterman and Coate 1950; Ehrenfreund 1948; Spence 1945) and the idea that discriminations are solved by testing one hypothesis after another has been generally discredited (Pearce 1997).

The results of this experiment also tend to support Turner's findings. Firstly, the overall speed with which the subject learned the discrimination suggests she was learning about the stimulus early in the experiment. In addition, while Figure 9 shows her performance tended to improve during sessions in which she exhibited reduced side bias, her accuracy showed gradual improvement throughout the experiment at the same time as her tendency to side bias was reducing. These results indicate she could learn about stimulus properties at the same time as she was testing a position habit.

5.1.4.2 Memory

While admittedly providing only limited data, the results also suggest some form of long-term memory retention has occurred (see Figure 8). In Part 1 of the experiment, the results showed the expected learning curve. On the first day of Part 2, conducted seven months later, the subject achieved a similar result to those observed on the final days of Part 1. The subject then scored significantly different from chance results (90% or better) for the individual sessions on days two, three and four. While a drop in performance can be seen during the middle two days, indicating the subject may have tried alternative strategies or been distracted by internal or external factors, in the final four days of the experiment the subject was again significantly different from chance on individual sessions on three out of four days. Anecdotally, it was also observed that very little retraining in the use of the apparatus was required after the seven-month interval.

These results are consistent with the findings of Buchmann and Rhodes (1978) on the echidna's long-term memory capability. In that study, three echidnas that had taken part in a study of instrumental learning were re-tested one month after the experiment ended. They rapidly achieved levels of performance comparable to those seen at the end of the original experiment.

However, the results of this study seem to contradict the finding of Burke et al. (2002). The echidnas in that experiment were unable to remember the location of a previously rewarding food location to employ either a “win-shift” or “win-stay” foraging strategy using a retention interval of 90 minutes, despite being able to do so at shorter retention intervals (two and five minutes).

As discussed in section 2.2.2.2, the contrasting results of long-term memory performance between this experiment and that of Buchmann and Rhodes (1978) and the Burke et al. (2002) study, suggest there may be different memory mechanisms at work in different tasks. Both this study and Buchmann and Rhodes (1978) used visual stimuli, while Burke et al. (2002) examined spatial memory. Like hummingbirds and rats (Gaffan and Davies 1981), echidnas may have only evolved a short-term spatial memory while also possessing an effective long-term visual memory. It is also possible the artificial spatial scale of the Burke et al. (2002) study may account for the subjects’ inability to remember locations at greater time intervals. It is also the case that Burke et al. (2002) was a working memory study in which the subjects had to remember locations that changed on a daily basis, making the task more difficult than a static spatial memory task. While outside the scope of this study, further experiments may help answer these questions and determine the extent of the echidna’s long-term memory capabilities.

5.2 Experiment 2: Shape discrimination

5.2.1 Introduction

Like black/white discrimination, shape discrimination has been successfully demonstrated in many species (reviewed in Sutherland 1961) including rats (Dodwell 1957), cats (Warren and Baron 1956), monkeys (Harlow 1944), sheep and calves (Baldwin 1981), goats (Baldwin 1979), horses (Sappington and Goldman 1994), pigeons (Towe 1954), chickens (Bingham 1913) and the octopus (Sutherland 1958).

Gates (1973) conducted the only other known shape discrimination testing in echidnas and claimed his experiment suggested that echidnas were able to discriminate between a circle and a triangle. However, his results were not entirely conclusive. Two of his

subjects were able to learn the discrimination in fewer than the criterion 500 trials, one showed no sign of learning in 500 trials and the other was terminated at 360 trials because it lost weight and refused to eat in the discrimination box.

This study attempts to repeat Gates' (1973) experiment and either support or challenge his findings. This study also used a circle and a triangle as the stimulus shapes – firstly to replicate Gates (1973), but also because circle/triangle is the most commonly tested shape discrimination (Sutherland 1961) and because those shapes were considered fairly easy to distinguish, particularly considering the echidnas limited visual acuity (see section 2.1.4.1).

5.2.2 Method

5.2.2.1 Stimuli

The stimuli for this experiment consisted of a two white panels each containing a single large black shape – a circle and a triangle (see Figure 10).

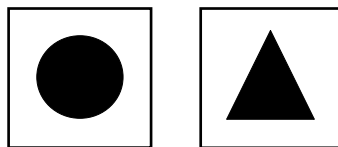


Figure 10: Stimulus panels for Experiment 2 – circle/triangle shape discrimination, S+ = circle

5.2.2.2 Procedure

As with Experiment 1, this experiment was conducted using correction trials (the subject was shown the same stimuli for each trial until a correct choice was made). Again, a correct response was recorded only if the first choice was correct. The subject was shown 10 pairs of stimuli during each daily session and the number of correct choices out of 10 was recorded. The correct choice for this experiment was the circle panel.

After an initial 10 sessions of trials the results did not differ significantly from chance, so a further 10 sessions were conducted for a total of twenty sessions.

5.2.3 Results

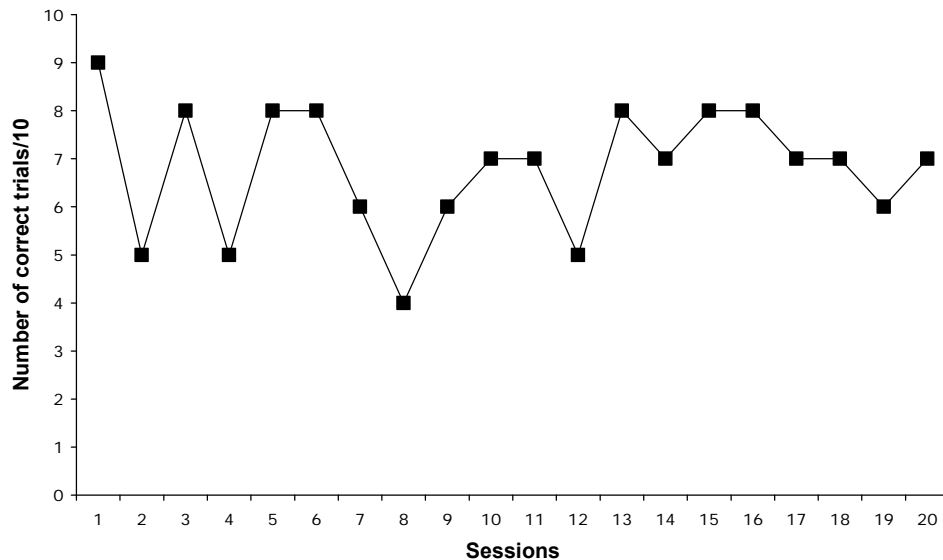


Figure 11: Number of correct responses to circle/triangle shape discrimination task, S+ = circle (correction trials)

The data were grouped into four blocks of five sessions and analysed using a two-tailed binomial test on the cumulative score of each block (number correct out of 50, chance = 25/50). While block one was significantly different from chance (correct responses = 35/50, $z = 2.83$ $p < .01$), block two was not significant (correct responses = 31/50, $z = 1.70$, $p > .05$). Blocks three and four were both significantly different from chance (correct responses = 35/50, $z = 2.83$, $p < .01$ for both blocks). The significant results from blocks three and four meet the criterion for learning the task.

While the pattern of results for individual sessions was fairly erratic, with no clear learning curve exhibited, evidence of learning was demonstrated across blocks, with the final five sessions showing the most consistent responses (see Figure 11).

The only individual session result that was significantly different from chance (90%, $p < .05$, two-tailed binomial) was on day 1. The subject did not achieve above 80% in an individual session for the remaining 19 sessions.

5.2.3.1 Side bias

The results were then examined to determine how many times per session the subject chose either the right-hand or left-hand side (see Figure 12).

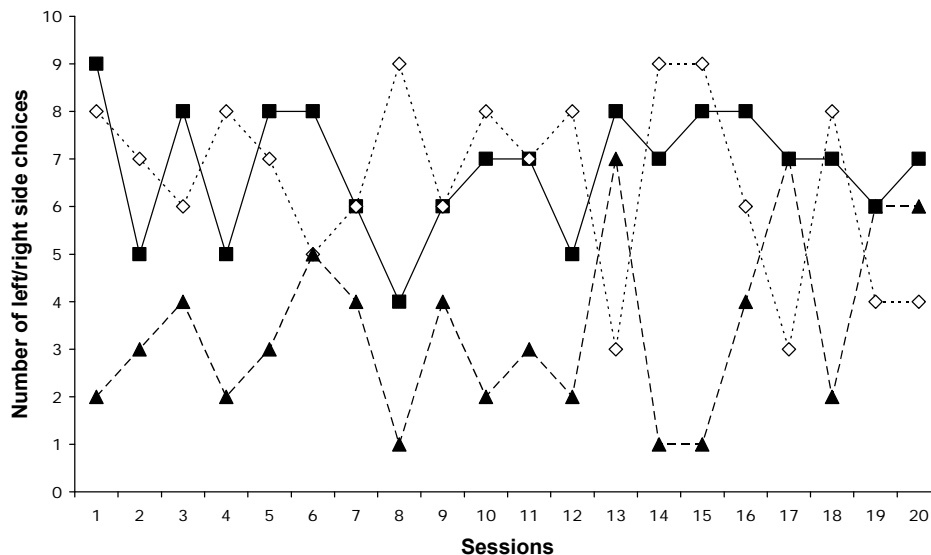


Figure 12: Number of left/right choices in circle/triangle shape discrimination task, S+ = circle (correction trials). ◇ = the number of left-hand choices, ▲ = the number of right-hand choices, ■ = the number of correct responses

Visual examination of the graph indicates the subject initially showed a bias for the left-hand side but by the second half of the experiment that bias diminished. The more consistent results during this period suggest that this is because she was selecting on the basis of the correct stimulus regardless of side.

5.2.4 Discussion

The results of this experiment show that an echidna is capable of learning a visual discrimination using shapes, supporting Gates' (1973) finding. In addition, both Pitpa and the subjects of Gates' (1973) study that met the experimental criteria took less time to learn the discrimination than rats on a similar task (Fields 1932).

However, the results also suggest the subject found this task more difficult to learn than the black/white discrimination used in Experiment 1 (see section 5.1). The shape discrimination took longer to learn than the black/white discrimination and, unlike

Experiment 1, the subject only achieved 90% in one individual session. While consistency improved in the later sessions, the early individual sessions were erratic, with a good result one day followed by a poor result the next and vice versa, a pattern also seen in Gates' (1973) experiment. This could suggest the subject was trying different methods to solve the problem or that the training experienced in Experiment 1 may have interfered with learning – for example, she may have been trying to select the stimulus that looked blackest. Alternatively, the inconsistent results could merely be the result of variation in daily performance due to external or internal factors. However, by the end of the shape experiment, the subject was achieving more consistent results suggesting one of the former scenarios is more likely.

Gates (1973) found echidnas were easily able to learn to discriminate between black and white stimuli as well as stimuli containing horizontal and vertical lines. However, as with this experiment, the subjects took longer to learn the shape discrimination, an occurrence Gates also attributed to the inherent greater difficulty of the task. This phenomenon has also been observed in pigeons. Conditional discrimination experiments conducted by Cumming and Berryman (1965) indicated that while pigeons can easily learn to match hues they have great difficulty learning to match geometric forms (Carter and Werner 1978). While further study would be needed to make direct comparisons, the idea of shape being more difficult to discriminate than hue makes intuitive sense. It seems self-evident that shape would be a more complex visual stimulus than black/white. It also seems logical that shape would be a more difficult discrimination than horizontal/vertical, as orientation is a basic visual feature while shapes are composed of different combinations of orientations. However, other species have demonstrated contradictory results. Sappington and Goldman (1994), for example, found the horses in their study took longest to learn the black/white discrimination and showed a general decrease in the time taken to learn successively more difficult shape discrimination problems (although this could also be the result of growing familiarity with the testing scenario).

It is worth noting that neither this study nor that of Gates (1973) conclusively shows that echidnas discriminate on the basis of the shape of the whole triangle or the whole circle – a point that could be made about most shape discrimination studies. They may utilise some feature of the stimulus (such as the base of the two shapes) to make the

discrimination, a phenomenon that has been observed in rats (Gates 1973). This idea receives some support from Gates' (1973) experiment testing the echidna's ability to learn a mirror-image discrimination. While the subjects were able to discriminate between a triangle and an inverted triangle fairly easily, they were unable to discriminate between left-right (horizontal) mirror-image triangles within the 500-trial limit set by the experimenter. While the subjects may have been successful given more time, or simply been unable to perform the discrimination, Gates (1973) also suggests another possibility. If the subjects were using only a part of each shape to make the discrimination based on its presence or absence in a particular area of the stimulus panel then, depending on the area chosen, the upright-inverted triangle problem might be easier to learn than the left-right (horizontal) triangle problem. For example, the difference between the bottom of a triangle versus the tip of a triangle (as seen in the inverted problem) might be easier to learn than the difference between the right and left corners of a triangle (as seen in the left-right horizontal problem). Further study would be needed to determine the validity of a feature-based theory and what, if any, features of the stimuli were being used.

However they accomplish the discrimination, the combined results of this and Gates' (1973) study suggest that echidnas can perform shape discrimination. In addition, it demonstrates that echidnas have the visual acuity to differentiate between solid geometric shapes in preparation for the experiments conducted later in this study.

5.2.4.1 Side bias

As in Experiment 1 (see sections 5.1.3.3 and 5.1.4.1), the subject seemed to learn the correct visual stimulus despite an initial left-side bias. However, the graph does not tell the whole story as it only shows the first choice on each trial. Interestingly, on a number of occasions when Pitpa incorrectly chose the right-hand side, she continued to incorrectly choose the right-hand side during the correction trials (during which the stimuli remained unchanged) multiple times, up to a maximum of 10 times during one particular trial. She did not exhibit the same behaviour towards the left-hand side on as many occasions and certainly not to the same extent. This right-hand perseverance was also seen several times in Experiment 1, however despite the behaviour she eventually learned to choose the correct visual stimulus in both experiments.

5.3 Experiment 3: Conditional shape discrimination

5.3.1 Introduction

This experiment was designed to train the subject in the conditional discrimination procedure. That is, using the same pair of stimuli, choose one stimulus under one condition and the other stimulus under another condition. The shapes that the subject had learned to discriminate in Experiment 2, circle and triangle, were used again here.

5.3.2 Method

5.3.2.1 Stimuli

For this experiment two pairs of stimulus panels were used. The first pair was the same as that used in Experiment 2 – white panels containing a black circle and a black triangle. The second pair of panels was identical to the first except the panels had a black background and white shapes (see Figure 13). This method of using stimuli that combine both the conditional and discriminative cues as the background and foreground of the stimulus respectively first came to widespread notice in an experiment by Lashley (1938b), who tested conditional discrimination in rats using a white upright and an inverted triangle as the discriminative cues and backgrounds that were either black or made up of horizontal stripes as the conditional cues (see sections 3.2.2.1.4 and 3.2.3). In this experiment, however, both the discriminative and conditional cues changed in each set of stimuli.



Figure 13: Stimulus panels for Experiment 3 – circle/triangle conditional discrimination, S+ = circle (black-on-white panels), triangle (white-on-black panels)

5.3.2.2 Procedure

In Experiment 1 the subject was reinforced for choosing the circle shape on the black-on-white panels and that condition was also reinforced here. However, when the second pair of panels was presented (white-on-black) the subject was rewarded for choosing the triangle. This then fulfilled the 'if ... then' requirements of a conditional discrimination – i.e. if the stimulus pair is black on white, then choose circle; if the stimulus pair is white-on-black, then choose triangle (see section 3.2.1).

Using the randomisation schedule selected for these experiments (see section 4.4.3), both the position of the correct response (left or right) and the choice of paired stimuli (black-on-white or white-on-black) were randomly determined.

The initial set of 10 sessions was conducted using correction trials in the same manner as Experiments 1 and 2. However, the final six sessions were non-correction trials (see Sutherland and Mackintosh 1971) with the stimulus pair and food position being changed for each trial whether a correct choice was made or not (see section 4.4.3). The session ended when 10 correct choices had been made.

5.3.3 Results

5.3.3.1 Correction trials

No real evidence of gradual improvement could be observed when the results for the correction trials were graphed (see Figure 14). The best two individual sessions, which were both significantly different from chance (90%, $p < .05$), were found in the middle two days.

When the results for these trials were grouped into two blocks of five days and analysed using a two-tailed binomial test, it was found performance in the first block was significantly different from chance (correct responses = 38/50, $z = 3.67$, $p < .001$). There was a slight deterioration in the second block, however it was still a highly significant result (correct responses = 37/50, $z = 3.39$, $p < .001$), meaning the subject fulfilled the task criterion.

5.3.3.2 Non-correction trials

In the non-correction condition the results were in the form $10/x$ (where x = the number of trials taken to reach 10 correct responses) instead of $y/10$ (where y = the number of correct responses from a total of 10 trials) as used in the correction trials. To provide a more consistent basis for comparison for this experiment, the non-correction trials were also graphed and analysed using the results from the first 10 trials to also give a $y/10$ format. (All subsequent experiments were conducted using only non-correction trials, however for comparative purposes both measures of performance were graphed and analysed.)

The results of the non-correction trials were fairly consistent throughout the six sessions (Figure 14) when analysed with a two-tailed binomial test using both measures of performance. Averaged across the six sessions the results were highly significantly different from chance when analysed both as $y/10$ (correct responses = 49/60, $z = 4.91$, $p < .001$) and $10/x$ (correct responses = 60/73, $z = 5.5$, $p < .001$) and improved on the correction trial results.

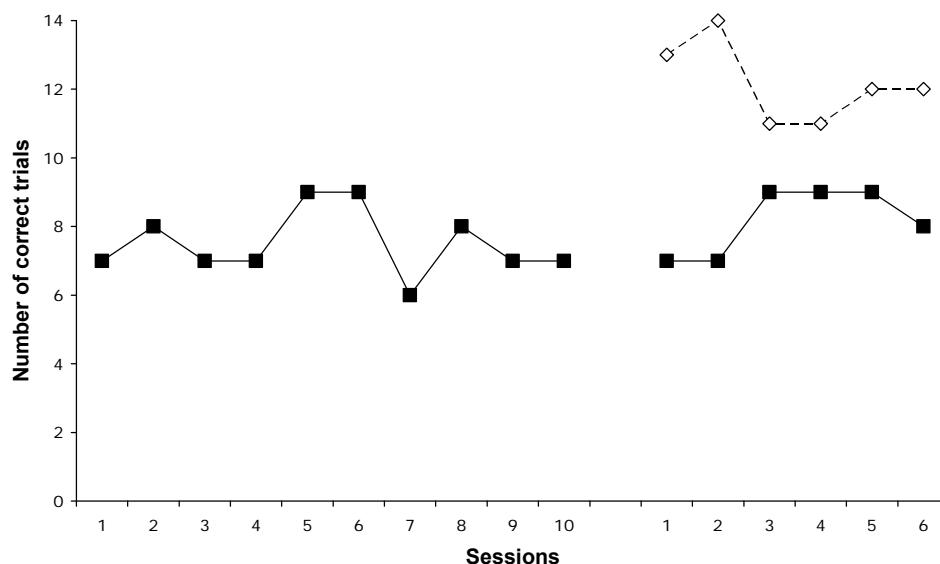


Figure 14: Number of correct responses to circle/triangle conditional discrimination task, S+ = circle (black-on-white panels), triangle (white-on-black panels). The first 10 sessions show the results of the correction trials, the subsequent six sessions show the results of the non-correction trials. ◇ = the number of trials until 10 correct responses were made, ■ = the number of correct responses in the first 10 trials

A further analysis was conducted to determine if the prior training in the black-on-white (S+ = circle) condition (see Experiment 2) had any effect on the results. The results for each condition (black-on-white, S+ = circle and white-on-black, S+ = triangle) were calculated separately using the y/10 data for both the correction and non-correction trials (black-on-white panels = 57/77 correct; white-on-black panels = 67/83 correct). A chi-squared test found no significant difference in performance between the two colour conditions ($\chi^2 = 1.03$, $p = 0.31$). The results were then converted into percentages in order to graphically compare the varying proportions of the colour conditions in each session caused by the randomisation procedure (see Figure 15).

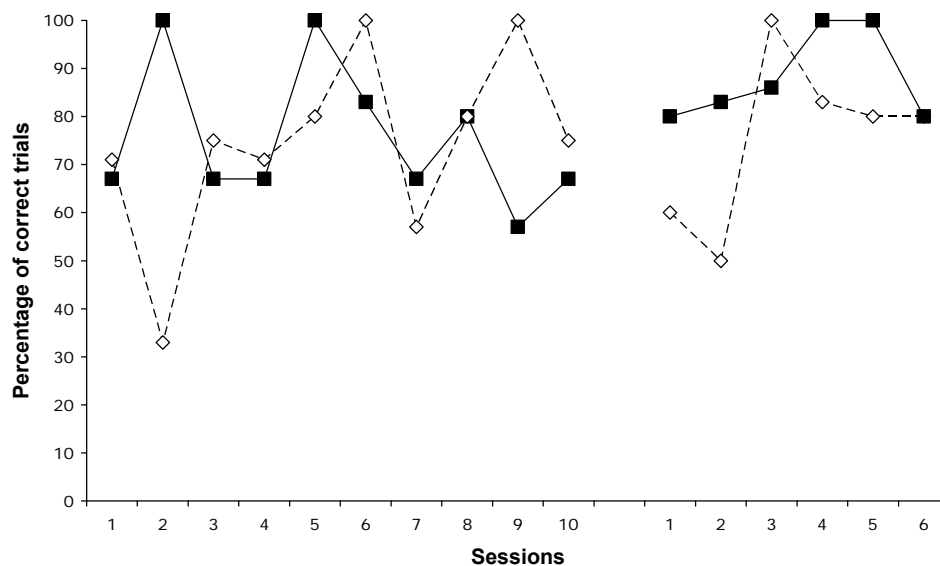


Figure 15: Percentage of correct responses to the circle/triangle conditional discrimination task for each colour condition (using y/10 data, y = the number of correct responses from a total of 10 trials). The final six sessions were non-correction trials. ■ = white-on-black panels (S+ = triangle) (novel stimuli), ◇ = black-on-white panels (S+ = circle) (previously trained)

5.3.4 Discussion

The results of this experiment show an echidna is able to perform a conditional discrimination using a similar combined stimulus method to that used by Lashley (1938b) to demonstrate conditional discrimination in rats. However, while the results of this experiment seem to demonstrate a more sophisticated discrimination than the first two experiments, the subject may have simply memorised each stimulus configuration instead of utilising a more generalised conditional discrimination rule, an explanation described by the configuration model (see section 3.2.4.1). The fact that the results

indicate a fairly shallow learning curve seems to support this conclusion. This would need to be tested using a larger number of training stimuli and transfer trials – which was done in Experiments 5 and 7. As the purpose of this experiment was mainly to familiarise the subject with the conditional discrimination procedure to be used in later experiments, transfer trials were not conducted.

Performance may also have been confounded by transfer from the Experiment 2 discrimination to the new ‘negative’ (white-on-black) stimuli. That is, she may have viewed both the black-on-white circle and the white-on-black circle as the same. However, this seems less likely following Gates (1973) finding that an echidna that had successfully learned the circle/triangle shape discrimination did not immediately transfer the discrimination when presented with ‘negatives’ of the stimuli. Despite being rewarded for choosing the same shape for both the ‘negative’ and ‘positive’ stimulus pairs, performance on day one of transfer testing fell to a statistically random 50%. Another possibility is that the overall results were based on the echidna doing very well on the previously trained black-on-white condition, but performing at chance for the new white-on-black condition. However, when the results of each colour condition were compared (see section 5.3.3.2 and Figure 15), it showed there was no significant difference in performance between the two conditions.

On a procedural level, performance did not appear to deteriorate when sessions were changed to the non-correction condition, indicating the subject did not require this extra ‘training’ to perform the task, and the rest of the experiments were conducted in the non-correction condition.

5.4 Experiment 4: Same/different categorisation, S+ = same

5.4.1 Introduction

The previous experiments proved that the subject was capable of performing discriminations based on colour and shape; however these stimuli are defined by simple physical characteristics. This experiment attempted to determine whether an echidna could discriminate between stimuli that have more abstract properties emerging out of

the relationship between stimuli rather than the stimuli themselves – an ability that has been described as a higher-level’ cognitive task (see sections 3.7.6.2.4, 3.8.3.3 and 6.2.2.1). To ensure the subjects were not merely memorising all the stimuli, transfer trials were conducted using novel stimuli.

5.4.2 Method

5.4.2.1 Stimuli

Training trials

For this experiment, the stimuli all had black backgrounds containing four white shapes each. There were six different *same* panels containing four identical shapes and six different *different* panels containing four non-identical shapes made up of combinations of the shapes used for the *same* panels. The six shapes were each used the same number of times in the six *different* panels and, as far as possible, in different positions (see Figure 16).

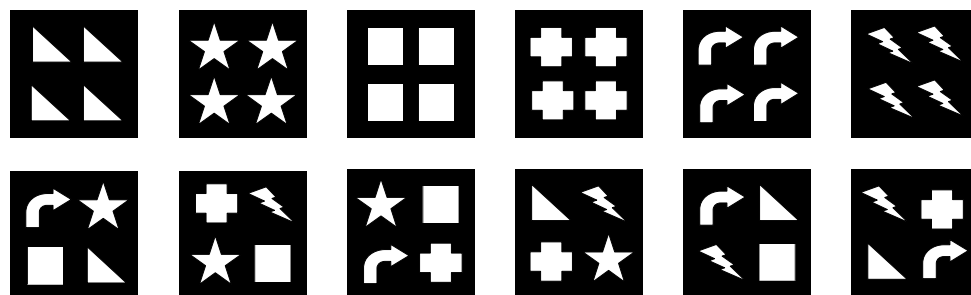


Figure 16: Stimulus panels for Experiment 4 – same/different discrimination, S+ = *same*

Transfer trials

For the transfer trial, six new *same* panels and six new *different* panels were introduced using six novel shapes (see Figure 17) arranged in the same fashion as the training stimulus panels (see Figure 16).

As the circle and triangle shapes had been used in previous experiments, these shapes were not used for any of the same/different trials.

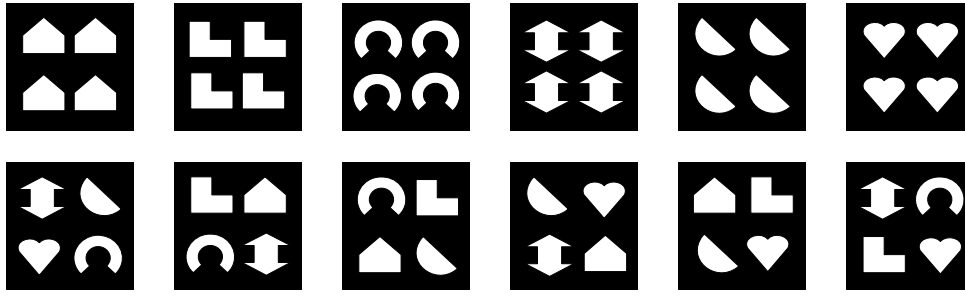


Figure 17: Novel stimulus panels for Experiment 4 – transfer of same/different discrimination, S+ = *same*

5.4.2.2 Procedure

As discussed in section 5.3.4, all experiments were now being conducted using non-correction trials in which incorrect responses were not repeated.

Training trials

Each pair of stimuli that were presented consisted of one *same* and one *different* panel. For this experiment, the *same* panel was rewarded. The randomisation schedule was used to determine whether the correct response was located on the left or right door and the *same* and *different* panels were shuffled between each trial to randomise the stimuli.

Transfer trials

During the transfer trials, novel pairs of stimuli were introduced randomly throughout each session using the randomisation schedule. The results were then analysed to determine if there was a drop in performance when the new stimuli were introduced.

5.4.3 Results

The learning phase results were grouped into two blocks of six sessions, with the transfer trials a separate block of six sessions, and the results analysed using a two-tailed binomial test. As mentioned earlier, to provide easy comparison with the previous experiments the results were graphed (see Figure 18) and analysed using two measures of performance – $y/10$ (y = the number of correct responses in the first 10 trials) and $10/x$ (x = the number of trials until 10 correct).

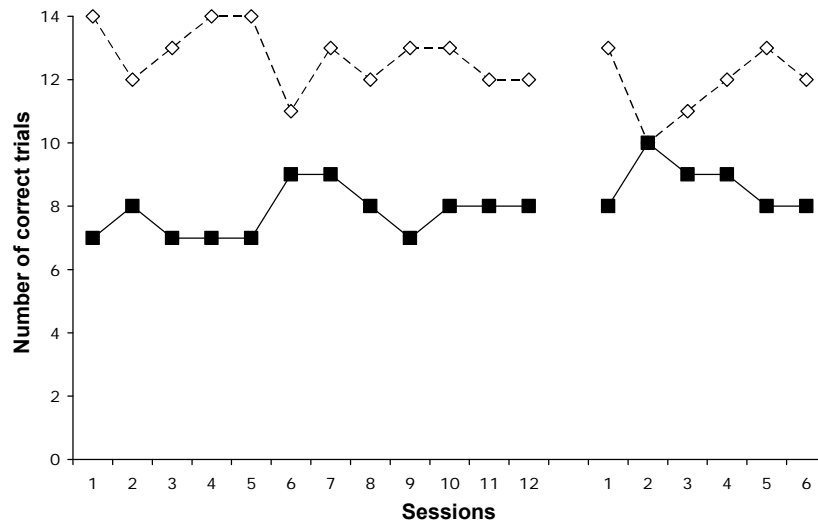


Figure 18: Number of correct responses to same/different task, S+ = same. The first 12 sessions show the learning phase, the subsequent six sessions show the transfer trials. \diamond = the number of trials until 10 correct responses were made, \blacksquare = the number of correct responses in the first 10 trials

Training trials

In the learning phase, performance was highly significantly different from chance in the first block (y/10: correct responses = 45/60, $z = 3.87$, $p < .001$; 10/x: correct responses = 60/78, $z = 4.76$, $p < .001$) and the second block (y/10: correct responses = 48/60, $z = 4.65$, $p < .001$; 10/x: correct responses = 60/75, $z = 5.20$, $p < .001$).

Transfer trials

Performance in the transfer phase was also highly significantly different from chance (y/10: correct responses = 52/60, $z = 5.68$, $p < .001$; 10/x: correct responses = 60/71, $z = 5.82$, $p < .001$) and was not significantly different from performance in the second block of the training phase using a chi-squared test on 10/x data ($\chi^2 = 0.51$, $p = 0.48$).

Using the 10/x data, the results were analysed to compare the subject's performance on the novel stimuli to that of the training stimuli used in the transfer trials (training stimuli = 28/33 correct, novel stimuli = 32/38 correct). A chi-squared test found no significant difference between performance on the training and the novel stimuli ($\chi^2 = 0.01$, $p = 0.94$). The results were then converted into percentages in order to graphically compare the varying proportions of each stimulus type in each session caused by the randomisation procedure (see Figure 19).

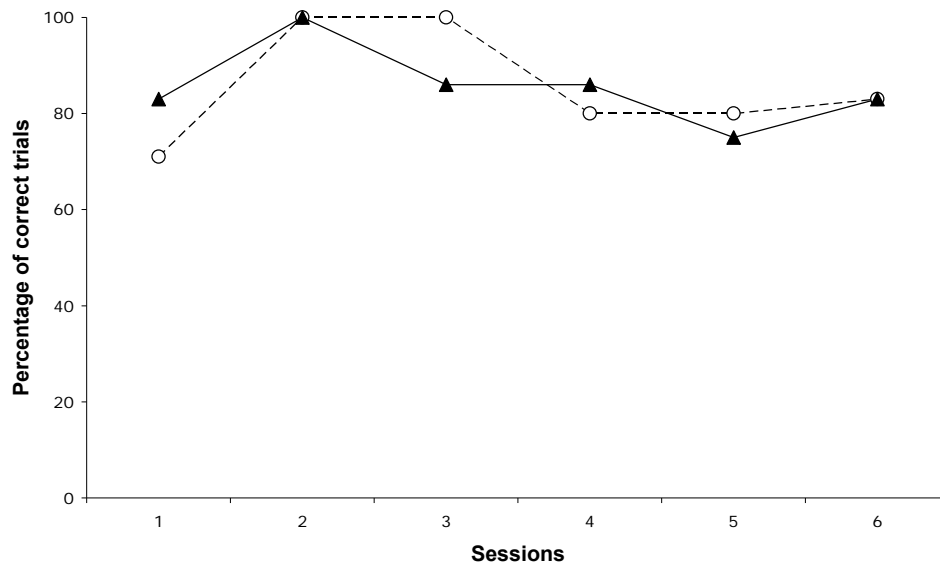


Figure 19: Percentage of correct responses to training and novel stimuli during same/different transfer trials, S+ = same (using 10/x data, x = the number of trials until 10 correct). ○ = percentage of correct responses to training stimuli, ▲ = percentage of correct responses to novel stimuli

It has been asserted by some authors (e.g. Chausseil 1991; Herman et al. 1994; Macphail 1982; Thomas 1996; Thomas and Noble 1988) that the demonstration of ‘conceptual’ behaviour must be based on first-trial transfer data otherwise the subject could be utilising ‘non-conceptual’ mechanisms such as specific stimulus configurations or a limited sample-specific recognition procedure (also see sections 3.2.4.5, 3.7.3.2 and 6.1.2). Pearce (1997) also requires first-trial, novel stimulus transfer to acknowledge a performance as relationally based (see section 3.7.6.2.4). However, Wright and Katz (2006) argue that simply reporting what happened on the first presentation of transfer stimuli would have “little if any statistical power” (p. 235). While this study takes the latter view, it is worth noting that on day one of the transfer trials performance on the novel stimuli was both substantially better than chance and even slightly better than that for the repeated training stimuli – 83% correct (novel stimuli) versus 71% correct (training stimuli).

5.4.4 Discussion

This experiment shows that the subject was able to categorise stimuli on the basis of the same/different concept, the first time this ability (or any form of categorisation) has been demonstrated in the short-beaked echidna or any monotreme. The fact that the

results in the transfer trial were not significantly different from those of the second block of the learning phase and that there was no significant difference in performance between the training and novel stimuli in the transfer trials indicates she was not merely memorising the stimuli but had learned to apply a generalised same/different criterion. The parity of Pitpa's performance between the training and test stimuli in the transfer trials is in contrast to that found in a perceptual categorisation task with pigeons using a similar testing procedure with interspersed novel and repeating stimuli (Bhatt et al. 1988). While the pigeons in that study were able to categorise the novel stimuli at levels far exceeding chance, they performed better on the repeated stimuli suggesting that, unlike Pitpa, memorisation may have facilitated their performance to some degree.

This ability to transfer performance to novel stimuli is the generally accepted criterion for same/different discrimination (Thompson 1995; Wright and Delius 2005; see section 3.7.2.1.1 and 3.8.3.3). As mentioned in section 3.8.3.3, in their well-known study of same/different learning in pigeons Wasserman et al. (1995) asserted that "accurate choice responding in the presence of [novel stimuli] constituted the prime evidence of same-different conceptualisation" (p. 249). However, some authors have created more rigorous criteria. Wright and Katz (2006) asserted that: "In our opinion, a subject that has learned an S/D concept ought to be able to perform as accurately with novel stimuli as with training stimuli (p. 235). According to the authors, if transfer is merely at a level between chance and the baseline training results, the performance can only be said to be "partial" concept learning that suggests multiple cues are controlling behaviour. To claim "full" concept learning Wright and Katz (2006) have the more stringent requirement that transfer be equivalent to baseline and both performances are above 80% to ensure that the subject is utilising relational information in both the transfer and training trials (e.g. Katz et al. 2002; Wright 1991; Wright et al. 2003; Wright et al. 1983). Pitpa was also able to satisfy this requirement, with an average of 80% correct in the final block of the training trials and an average of 87% percent in the transfer block.

While comparing species performance based on different, or even the same, experimental procedures is problematic (see section 1.3.1), Pitpa appeared to solve the task relatively quickly compared to some other species (see section 3.7.3). According to Castro et al.'s (2010, p. 36) analysis of their pigeons' performance: "... fast learning

and relearning suggests that pigeons had mastered a same-different concept rather than having learned specific responses to specific configurations of stimuli.”

Simultaneous presentation of stimuli

Same/different categorisation is considered a ‘higher-level’ task only if it is based on relational learning, so the testing procedures were chosen to maximise the possibility of the subject utilising relational rather than more prosaic methods to perform this task. One decision was how the stimuli would be presented. Same/different categorisation experiments can be conducted using simultaneous or successive presentation of stimuli; however it was decided to use simultaneous presentation for a number of reasons. Successive presentation of stimuli allows for the possibility that same/different categorisations are performed using factors other than the relationship between stimuli and there is some debate about whether successive procedures like delayed matching-to-sample require particularly sophisticated cognitive abilities. As discussed in section 3.7.6.1, a number of authors contend that the matching/non-matching paradigm can be solved using less difficult means than identity, such as conditional discrimination (“if red sample, pick red”). Even if an animal is able to demonstrate a generalised matching (or non-matching) ability and is not just memorising conditional rules, it can be argued that they are just responding on the basis of relative familiarity (“what did I just respond to”) or are subject to other mediating factors (Shettleworth 1998).

On the other hand, a number of authors have concluded that simultaneous procedures are more likely to provide evidence for relational learning (Castro et al. 2010; Mazur 2002; Premack 1983a; Shettleworth 1998; see section 3.7.2.1.5). Premack (1983a, 1983b) has argued that the procedural differences between successive matching-to-sample and simultaneous same/different tasks lead to important conceptual differences in what is learned and that the only true test of same/different categorisation is when the stimuli are presented simultaneously. In addition, Premack (1983b, p. 127) claims: “There is not only a clear procedural difference between the two procedures, but also a striking difference in difficulty. The successive task is far easier than the simultaneous task.” (See also Pearce 1997 and Shettleworth 1998 for fuller discussion).

The fact that Pitpa was able to solve the same/different task using a simultaneous procedure gives added credence to claims of relational and even conceptual discrimination (see sections 3.7.2.1.5 and 3.7.6.2.4). According to Castro et al. (2010, p. 36): "... it is likely that simultaneous presentation not only promotes comparison of the Same and Different arrays, but that it also encourages learning of the relational same-different concept."

Number of stimulus elements

This study utilised a multi-element stimulus array similar to that introduced by Wasserman et al. (1995) and others (see sections 3.7.3.3 and 4.3.2), albeit containing fewer elements than most of these studies. One reason for using fewer (and simpler) shapes per panel than the Wasserman et al. (1995) model was to help compensate for the echidna's poorer visual acuity. However, it also served the purpose of reducing the potential for the subject to use perceptual cues contained in multi-element stimuli that have cast doubt on the results of these types of studies (see section 3.7.6.2.3).

One of these perceptual cues is uniformity, in which the *same* arrays appear to have a greater linear orderliness of rows and columns than the *different* arrays. As discussed in section 3.7.6.2.2, Young and Wasserman (1997) pointed out that the pigeons in the similarly designed Wasserman et al. (1995) experiment may have solved the discrimination on basis of uniformity instead of using relational information. Young and Wasserman (1997) argued against this proposition on the basis of the performance decrement between the training and testing arrays and perhaps more convincingly by demonstrating that pigeons could perform the discrimination with nonlinear, disorderly arrays. It is important to note that just because pigeons can perform same/different categorisation without reference to perceived orderliness does not mean that another species like the echidna can do likewise. However, this explanation seems much less likely in this experiment due to differences in the design of the multi-element arrays. As discussed previously (section 4.3.2), the use of only four items per stimulus panel, as well as the selection of shapes of different size, regularity and orientation, reduced the possibility of this effect confounding the results.

It has also been suggested that entropy (a numerical calculation of variability) may be behind the success of non-human subjects using multi-element displays in same/different categorisation experiments. Basically, the higher the number of items in the multi-element array, the greater the entropy of the *different* displays and the greater the difference between them and the (zero entropy) *same* displays. According to some authors, non-human subjects might be using this entropy difference, rather than relational information, to solve same/different discriminations (Young and Wasserman 1997; see section 3.7.6.2.3 for full discussion).

Experiments demonstrating that non-human subjects can perform same/different discriminations using very low-entropy, two-item stimuli (e.g. Blaisdell and Cook 2005; Katz and Wright 2006; see section 3.7.3.3) or even language-based procedures where entropy is not a factor, such as that used with Alex the African Grey parrot (Pepperberg 1987; see section 3.7.3.4) are considered evidence that at least some non-human subjects under certain conditions are capable of performing same/different discriminations without relying on entropy (see full discussion in section 3.7.6.2.3). Some authors have even suggested that the only way to ensure that relational information is used to solve same/different discriminations is to use two items (e.g. Blaisdell and Cook 2005; Premack 1983b).

This study used four items – a lower number than that used in most multi-element displays, but still higher than the two-item ‘gold standard’. However, it could be argued that the entropy difference between a two- and four-item display is still fairly negligible. While the 16-item *different* multi-element array used by Wasserman and colleagues (e.g. Wasserman et al. 1995; Young and Wasserman 1997) has an entropy value of 4.00, the entropy value of a four-item *different* display is 2.00, much closer to that of a two-item display with an entropy value of 1.00.

In addition, experiments with a number of species have indicated that the point at which entropy differences become manifest is around eight-items (or a *different* stimulus entropy value of 3.00). Rhesus monkeys tested using a similar procedure to that used here required training with eight-item displays (in addition to conditional cues similar to those used in Experiments 5 to 7) before being able to perform the task using lower entropy stimuli (Flemming et al. 2007). When baboons were tested with displays

containing two to 24 elements, the baboon responded indiscriminately when presented with displays of either two or four elements, leading the authors to determine the baboons were utilising entropy differences to solve the discrimination with the higher-item displays (Wasserman, Young and Fagot 2001). Similarly, when Young, Wasserman and Garner (1997) assessed the performance of pigeons using stimulus arrays containing a decreasing number of items (16, 14, 12, 8, 4 and 2) they found that while reducing the number of items to 12 or 14 icons did not affect performance, reducing the number of items in the displays to 8 icons led to a significant decrease in choice accuracy. Castro et al. (2010) found a similar effect in a conditional same/different task (see section 3.7.4 and Experiments 5 and 7 below), with a high percentage of correct responses using 24-, 20-, 16-, 12- and 8-icon arrays, but much lower accuracy with 4- and 2-icon arrays.

There is no reason to suppose that echidnas are any more sensitive to detecting low-level entropy variations than other animals, so the fact that Pitpa was able to succeed with comparatively low-entropy, four-item arrays goes some way towards supporting the possibility that she was responding to the stimuli on the basis of relational information.

Training set size and stimulus type

Another interesting aspect of this experiment is the fact that Pitpa was able to correctly transfer to novel stimuli after training with a relatively small training set of just six *same* and six *different* stimulus panels. It has been suggested that training set size may represent a quantitative difference in performance in same/different categorisation, with smaller set sizes being associated with more ‘advanced’ species such as humans and apes (Wright et al. 2003). As discussed earlier (section 3.7.3.1), monkeys and chimpanzees are able to match novel stimuli in a match-to-sample task using a stimulus set as small as two items, although the monkeys did not show complete transfer (D’Amato, Salmon and Colombo 1985; Oden et al. 1988). On the other hand, pigeons in previous matching studies using single-element stimuli have required training with a large number of stimuli (e.g. Wright et al. 1988). A similar trend has been demonstrated with pigeons in simultaneous same/different studies using single-element stimuli, with the most convincing demonstrations found using large training sets (e.g. Blaisdell and

Cook 2005; Wright and Katz 2006) and studies demonstrating gradual improvement in performance as training set size was increased for pigeons, capuchin monkeys and rhesus monkeys (Wright 2010) (see section 3.7.3.3).

There is little consensus about the ramifications of training-set size. For example, Wasserman and Bhatt (1992) suggested repetition of a finite number of training stimuli can weaken ‘concept’ learning and Wright and Katz (2006) claimed too few training stimuli led to item-specific rather than relational learning. However, Mackintosh (2000) has claimed that when a large number of training stimuli are used then “... it becomes difficult to rule out the possibility that transfer will be based on the physical similarity between supposedly novel test stimuli and some of the stimuli used in training” (p. 132).

It is possible that the small learning set required to achieve criterion performance in this study may be a reflection of the nature of multi-element stimuli. The pigeon same/different study of Wasserman et al. (1995) also utilised multi-element stimulus arrays and, unlike previous pigeon relationally based studies, required only a small learning set (8 *same* arrays and 8 *different* arrays in Part 1) for the subjects to learn the task. It is possible that multi-element stimulus arrays may prove easier to learn than the more commonly used single-element stimuli. It is worth noting that performance in the Wasserman et al. (1995) study improved in Part 2 when 16 *same* arrays and 16 *different* arrays were used. As discussed in section 4.4.4, it is possible that that result was confounded by the prior learning in Part 1 and the use of both previously trained (Part 1) and previously seen (Part 2) icons in the testing stimuli. However, other research on perceptual and abstract categorisation has also shown that larger training sets lead to stronger generalisation performance in testing (see Wasserman 1993b for a review).

It is also possible that another factor in reducing learning set size may be the use of stimuli of a relatively basic perceptual nature. Both this experiment and that of Blaisdell and Cook (2005) used relatively simple geometric shapes as stimulus elements, in contrast to more intricate clipart images and photographs used in other studies (see section 3.7). Flemming (2011) suggested that the success of Blaisdell and Cook’s (2005) experiment might be attributed to the simple stimuli encouraging a focus on the relational information present, rather than a focus on specific stimulus features (see

section 3.7.6.2.3). Other experiments that have demonstrated that pigeons and monkeys require much larger learning sets (e.g. Katz et al. 2002; Wright and Katz 2006; Wright et al. 2003) have used the more complex types of stimuli. Lombardi et al. (1984) point out that colour photographs, for example, are exceptionally salient and memorable for pigeons (Nelson and Wasserman 1981) and they can generalise extensively between them (Wright and Cumming 1971). If, as some believe, large learning sets discourage the use of simple solutions such as item-specific learning and encourage the use of a more economical generalised principle (Lombardi et al. 1984; Wasserman and Bhatt 1992; Wright and Katz 2006), it follows that pigeons, with their prodigious memory for pictorial stimuli (see section 3.4.4.2.1), would require extremely large learning sets to acquire a generalised same/different ability when these types of stimuli are used.

Number of training trials

In addition to a small learning set, Pitpa was able to successfully transfer performance to novel stimuli after just 153 training trials (including both correct and incorrect responses). While this is relatively high compared to some primate studies (for example, those showing primates can match novel stimuli after learning just one matching problem – D’Amato, Salmon and Colombo 1985; Oden et al. 1988; see section 3.7.3.1), it is impressive compared to pigeons. Wasserman et al. (1995), for example, trained pigeons in their multi-element same/different task for 8000 trials in Part 1 and 4480 trials in Part 2 of their experiment before moving to the testing phases (see section 3.7.3.3). As discussed above, multi-element stimuli similar to that used in this experiment appears to enable pigeons to successfully learn same/different categorisations using a much smaller learning set than that required for other experimental procedures. However, they still seem to require a relatively large number of training trials to achieve criterion. The fact that Pitpa was able to transfer the performance to novel stimuli using a relatively small number of training trials makes it less likely that she made use of stimulus generalisation (see section 3.1.4.1.1) as the basis of transfer, which is a danger with using large numbers of training stimuli (Wright and Katz 2007).

This disparity between the number of training trials required for this study compared to that of Wasserman et al. (1995) may be a reflection of species differences. Pigeons are

notorious for requiring a very large number of trials to perform match-to-sample tasks compared to many other species that have been studied, requiring training for thousands of trials before they are able to acquire a generalised matching ability (e.g. Wright et al. 1988; see section 3.7.3.1). It has been suggested that this is due to the pigeon's large capacity and propensity for rote learning, which would inhibit the use of a generalised identity rule (Delius 1994; see section 3.7.3.1). In addition, pigeons have displayed a propensity for attempting to perform perceptual categorisations using small, fine details (as illustrated by Cerella's 1980, 1982, 1986 cartoon experiments discussed in section 3.4.4.4.1). It is possible this tendency is also operating in same/different experiments. This may lead them to attempt multiple rules to solve the task that work some of the time, thus requiring many trials to learn a generalised rule.

Stimulus contact

One aspect of this experiment that may have assisted Pitpa's performance is the use of a viewing period and direct stimulus contact. A number of studies have found the introduction of stimulus contact (and the accompanying improvement in attentiveness) has facilitated various types of cognitive studies, including same/different discrimination (e.g. Cook et al. 1995; Gibson et al. 2006; Wright et al. 2003; see section 3.7.3.3).

5.5 Experiment 5: Same/different conditional categorisation (1)

5.5.1 Introduction

In Experiment 4 the subject successfully learned to discriminate on the basis of the same/different concept and in Experiment 3 was able to perform a conditional discrimination based on shape. This experiment attempted to combine these two abilities and determine if the subject could perform a conditional discrimination based on the same/different concept.

5.5.2 Method

5.5.2.1 Stimuli

For this experiment there were two sets of stimuli. The first set was the transfer stimulus panels used in Experiment 4 (Figure 17) in which each panel contained four white shapes on a black background. There were six different *same* panels containing four of the same shapes and six different *different* panels containing four different shapes made up of combinations of the shapes used for the *same* panels. The six shapes were each used the same number of times in the six *different* panels and, as far as possible, in different positions. The other set of stimuli were identical to the first, except they contained black shapes on a white background (see Figure 20, see also Figure 5).

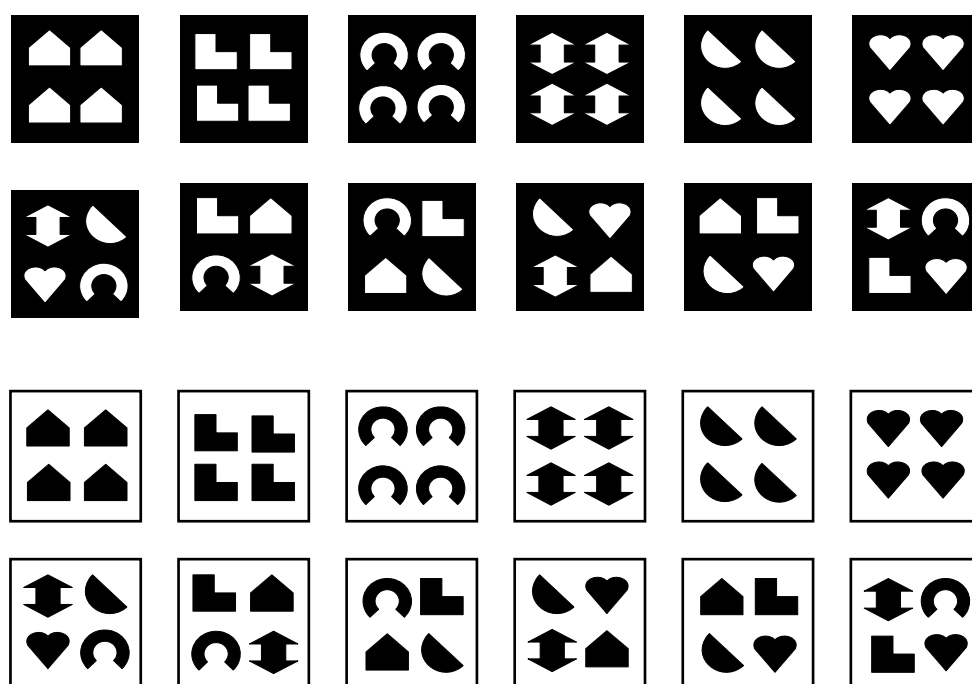


Figure 20: Stimulus panels for Experiment 5 – conditional discrimination, S+ = *same* (white-on-black panels), *different* (black-on-white panels). The *same* panels are the transfer panels used in Experiment 4 (Figure 17)

5.5.2.2 Procedure

The subject was shown a pair of stimuli from either the white-on-black or the black-on-white set which contained a *same* and a *different* panel. She had previously been rewarded for choosing *same* when using the white-on-black panels in Experiment 4 and

that condition was also reinforced here. However, in this experiment, when the subject was presented with a pair of black-on-white panels she was reinforced for selecting *different*. A similar procedure using a pair of multi-element stimuli, one containing all identical stimuli, the other containing all non-identical stimuli, with background colour indicating S+ for each trial was also used by Flemming et al. (2007) with rhesus monkeys.

As with previous experiments, the randomisation schedule was used to determine whether the correct stimulus was placed on the left or the right door. The schedule was also used to determine whether a stimulus pair from the white-on-black or the black-on-white set was used in each trial. The stimulus panels were shuffled between each trial to randomise the selection of individual panels.

5.5.3 Results

The trials were grouped into in four blocks of five sessions. The results were then graphed (see Figure 21) and analysed with a two-tailed binomial test using two measures of performance – $y/10$ (y = the number of correct responses in the first 10 trials) and $10/x$ (x = the number of trials until 10 correct).

Performance in block 1 was significantly different from chance ($y/10$: correct responses = 33/50, $z = 2.26$, $p < .05$; $10/x$: correct responses = 50/73, $z = 3.16$, $p < .01$), block two was not significant ($y/10$: correct responses = 31/50, $z = 1.70$, $p > .05$; $10/x$: correct responses = 50/84, $z = 1.75$, $p > .05$). In block three the results were significant ($y/10$: correct responses = 33/50, $z = 2.26$, $p < .05$; $10/x$: correct responses = 50/79, $z = 2.36$, $p < .05$). However, in block four the results were mixed. In the $y/10$ format the results were just barely significant (correct responses = 32/50, $z = 1.98$, $p < .05$), while in the $10/x$ format the results were significant (correct responses = 50/76, $z = 2.75$, $p < .01$).

Visual examination of Figure 21 suggests more consistent performance in the last two blocks.

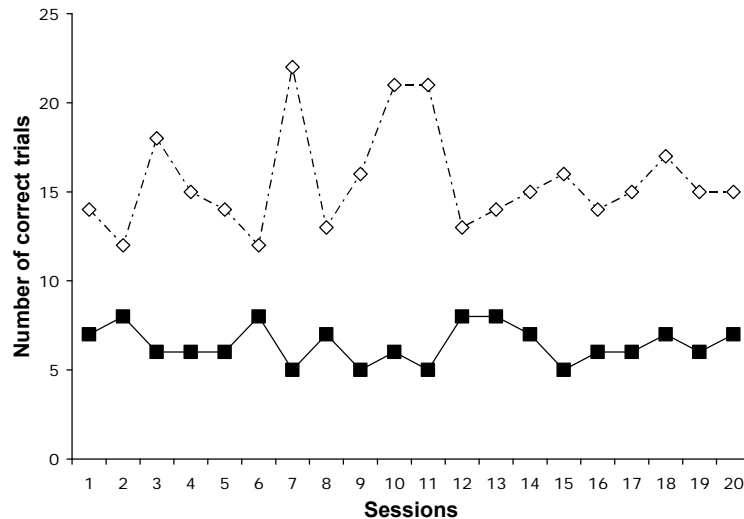


Figure 21: Number of correct responses to same/different conditional discrimination task, S+ = *same* (white-on-black panels), *different* (black-on-white panels). \diamond = the number of trials until 10 correct responses were made, \blacksquare = the number of correct responses in the first 10 trials

A further analysis was conducted to examine whether the comparatively poor results in this experiment were due to the subject selecting *same*, the correct response in the previous experiment, regardless of the colour condition.

The results for each condition (white-on-black and black-on-white) were calculated separately (using the 10/x data) (white-on-black = 95/152, black-on-white = 105/160). A chi-squared test found no significant difference between performance on the *same* versus the *different* trials ($\chi^2 = 0.33$, $p = 0.57$). The results were then converted into percentages in order to graphically compare the varying proportions of each stimulus type in each session caused by the randomisation procedure (see Figure 22).

The graph indicates some improvement in *different* results and deterioration of *same* results towards the end of the experiment.

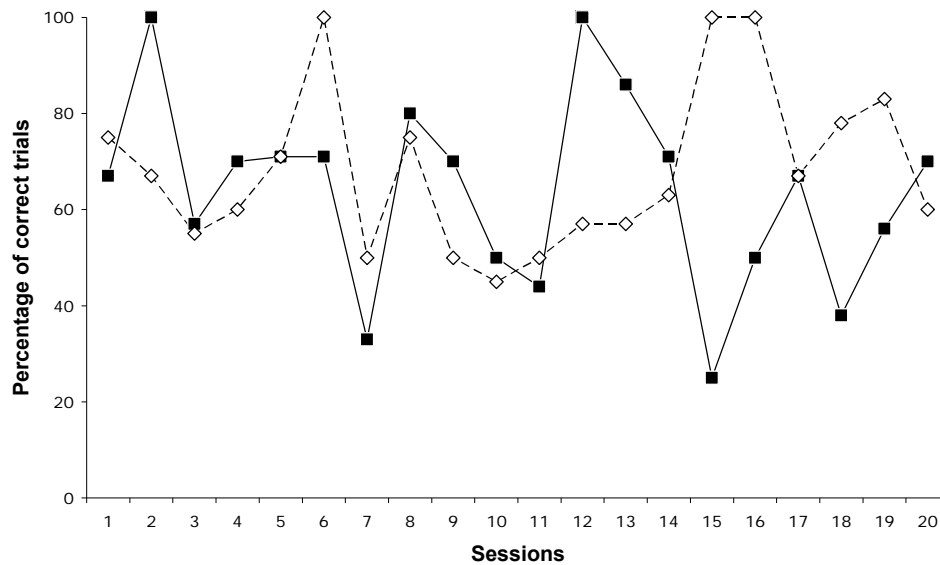


Figure 22: Percentage of correct responses to the same/different conditional discrimination task for each colour condition (using 10/x data, x = the number of trials until 10 correct). ■ = white-on-black panels (S+ = *same*) (previously trained), ◇ = black-on-white panels (S+ = *different*) (novel stimuli)

5.5.4 Discussion

Despite the fact that the subject seemed to be showing some improvement in the final block of sessions, she seemed to find this task much more difficult than the previous experiments. While she technically reached the training criterion (two consecutive blocks significantly above chance), it was by such a small margin, particularly the y/10 figure for Block 4, that it was decided the result was insufficiently robust to claim she had mastered this task.

A chi-squared test and visual examination of the graph (Figure 22) comparing the number of correct responses to the *same* stimuli, on which she was trained to a high standard in Experiment 4, to correct responses to the *different* stimuli, which she had not previously encountered, revealed no evidence the poor results were due to the subject favouring *same*. Indeed there is some indication the subject started to perform better on the *different* panels at the expense of the *same* panels towards the end of the experiment, perhaps indicating she was learning the *different* condition. However, in general the results suggest the introduction of the conditional discrimination led to confusion and an overall deterioration in performance.

While the test situation appeared adequate for the echidna to successfully learn the previous tasks, this ‘combination’ discrimination is considered more difficult than more basic ‘either/or’ discriminations. According to Gates (1973), difficult discriminations are more liable to break down when the behavioural paradigm and test situation are unsuitable. Given the echidna’s success on the previous discrimination experiments in this study, it seems unlikely that factors such as modality, apparatus, motor issues or motivation were the cause of the echidna’s seeming inability to master this problem.

However, due to the increased difficulty of this task, it was possible that the subject required more training to learn the task. As has been discussed a number of times in this study, the fact that an animal cannot learn a task under one set of circumstances does not necessarily mean that they are incapable of learning the task (see sections 1.3.1 and 3.7.3). Considering the subject did show some signs of learning and to ensure the subject had every chance to perform successfully in this experiment, it was decided to train the *different* condition separately, then retest the conditional same/different experiment and see if previous training in both conditions would facilitate learning.

5.6 Experiment 6: Same/different categorisation, S+ = *different*

5.6.1 Introduction

Following the lack of success with the same/different conditional discrimination tests conducted in Experiment 5, this experiment aimed to enable the subject to learn the *different* condition separately in the same manner as the *same* condition was learned in Experiment 4.

In addition, blind trials were also conducted at the end of the experiment to demonstrate there was no unintentional cueing from the handler during these experiments.

5.6.2 Method

5.6.2.1 Stimuli

The stimuli used for this experiment (see Figure 23) were the black-on-white *different* panels used in Experiment 5 (see Figure 20), with the same stimuli being used for the blind trials.

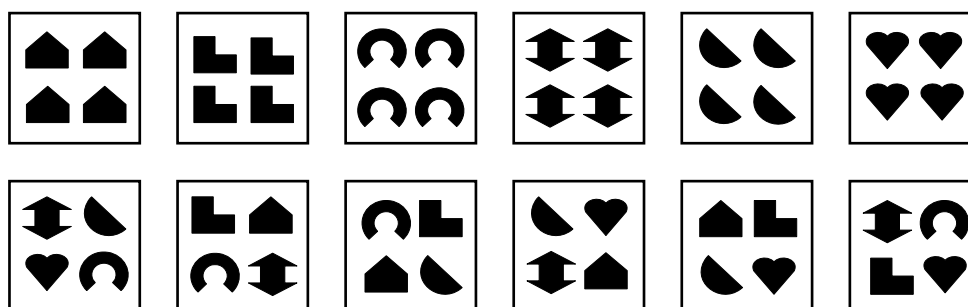


Figure 23: Stimulus panels for Experiment 6 – same/different discrimination, S+ = *different*. The panels are the *different* panels used in Experiment 5 (Figure 20)

5.6.2.2 Procedure

Training trials

One pair of stimuli was presented per trial with each pair consisting of one *same* and one *different* panel. For this experiment, the *different* panel was reinforced. A randomisation schedule was used to determine whether the correct response was located on the left or right door and the *same* and *different* panels were shuffled between each trial to randomise the stimuli. Due to the fact that the same/different discrimination had been successfully tested in Experiment 4, and that this experiment was designed primarily to train the *different* condition before repeating the conditional same/different experiment, it was not considered necessary to perform transfer trials.

Blind trials

The blind trials were conducted in the same manner, however a 42cm x 103cm plywood board was placed on top of the start box directly above the swing doors (see Figures 24 and 25).

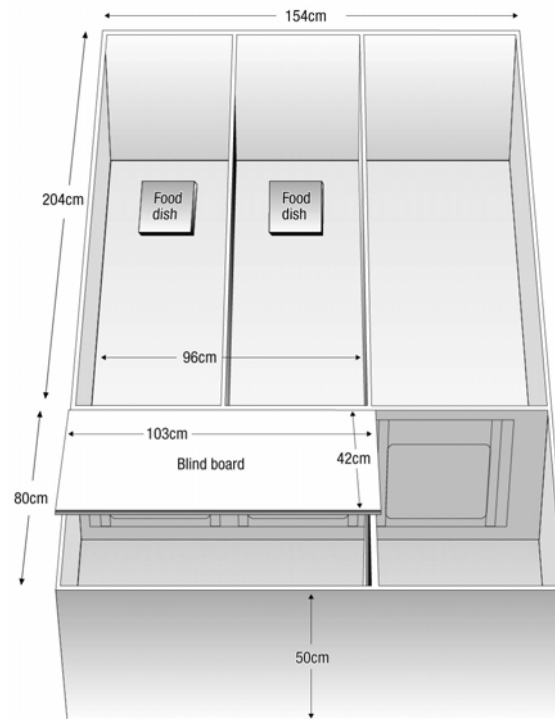


Figure 24: Three-dimensional diagram of the apparatus with the blind board



Figure 25: Photo of the apparatus with the blind board

The board blocked the view of the stimulus panels on the doors, preventing the handler from knowing on which side the correct stimulus was located. Another person was enlisted to change the stimulus panels and the food dishes between trials while the handler stood at a distance and facing away from the apparatus.

At the beginning of each trial the handler lowered the subject underneath the blind board to view the stimuli and make her selection.

5.6.3 Results

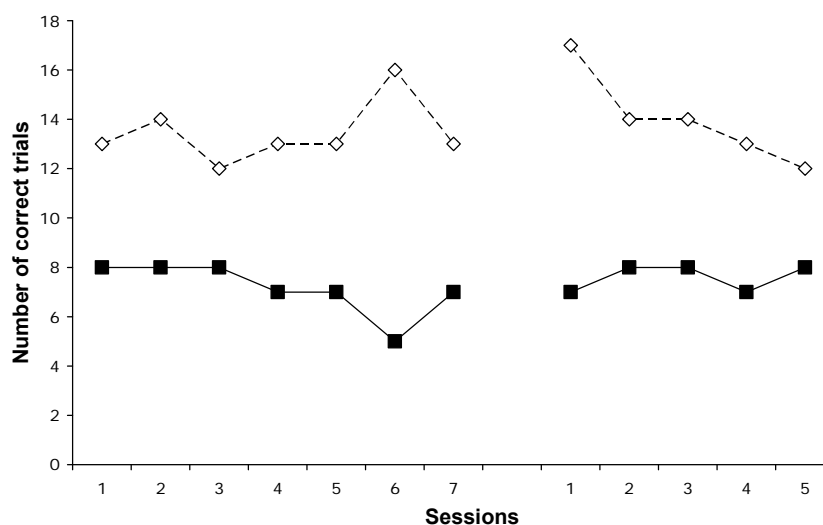


Figure 26: Number of correct responses to same/different task, S+ = different. The final five sessions show the blind trials.
 ◇ = the number of trials until 10 correct responses were made, ■ = the number of correct responses in the first 10 trials

The results were analysed using a two-tailed binomial test in two blocks – the seven initial training sessions and the five blind trial sessions. The results were graphed (see Figure 26) and analysed using two measures of performance – $y/10$ (y = the number of correct responses in the first 10 trials) and $10/x$ (x = the number of trials until 10 correct).

Training trials

Performance in the block of training sessions was highly significantly different from chance ($y/10$: correct responses = 50/70, $z = 3.59$, $p < .001$; $10/x$: correct responses = 70/94, $z = 4.74$, $p < .001$).

Blind trials

Performance in the block of blind sessions was also highly significantly different from chance ($y/10$: correct responses: 38/50, $z = 3.68$, $p < .001$; $10/x$: correct responses = 50/70, $z = 3.59$, $p < .001$).

A chi-squared test using the 10/x data showed there was no significant difference between the training and blind trial results ($\chi^2 = 0.19$, $p = 0.66$).

5.6.4 Discussion

Despite the lack of transfer trials, the results of this experiment training the *different* condition provide some confirmation of the Experiment 4 results showing the subject is able to learn an abstract discrimination on the basis of the same/different concept. The results of this experiment are comparable to those of the *same* discrimination in Experiment 4, with both showing results significantly different from chance. The results are also much improved on those in Experiment 5, indicating the subject's poor performance in that experiment was most likely due to the test itself and not some other factor.

Blind trials

The results for the training trials and the blind trials were both highly significantly different from chance, and a chi-squared test confirmed that there was no significant difference between them, indicating the introduction of the blind board did not lead to deterioration in performance. This suggests that inadvertent handler cueing did not contribute to the subject's performance in these experiments.

Support for this view can also be found in the fact that Pitpa performed poorly in the previous experiment. As discussed in section 5.5.4, the inability of a subject to perform a particular task while succeeding on others trained in the same manner suggests that the subject is unlikely to be making use of inadvertent experimental cues or more basic associative processes relating to stimulus reinforcement (see Huber 2001).

5.7 Experiment 7: Same/different conditional categorisation (2)

5.7.1 Introduction

In previous experiments, the subject was successfully trained on both the *same* and the *different* discrimination concepts. Having been trained in both concepts, this experiment repeats the conditional concept discrimination tested in Experiment 5 to determine whether the additional training on the *different* concept would improve her performance on this task.

One possible reason for an improved performance could be that the subject had merely now memorised all the stimuli. To determine this, transfer trials with new stimuli were conducted at the end of the experiment.

5.7.2 Method

5.7.2.1 Stimuli

Training trials

The stimuli for the first part of the experiment (see Figure 27) were the same as those used in Experiment 5 (see Figure 20).

Transfer trials

The stimuli for the transfer trials were created using six novel shapes arranged in the same fashion into six *same* and six *different* black-on-white panels and six *same* and six *different* white-on-black panels (see Figure 28).

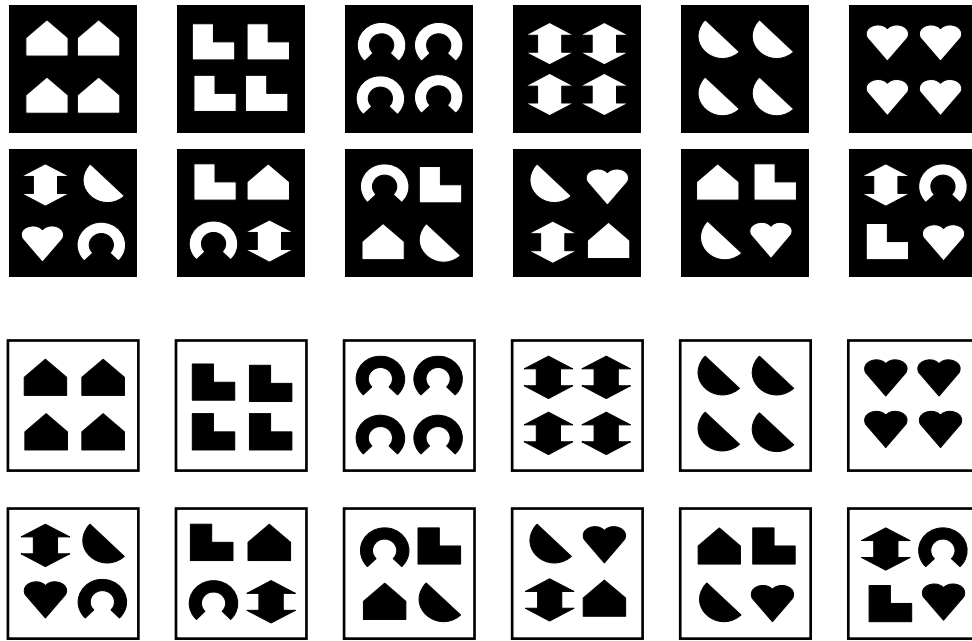


Figure 27: Stimulus panels for Experiment 7 – conditional discrimination,
 S+ = *same* (white-on-black panels), *different* (black-on-white panels).
 These panels are the same as those used in Experiment 5 (Figure 20)

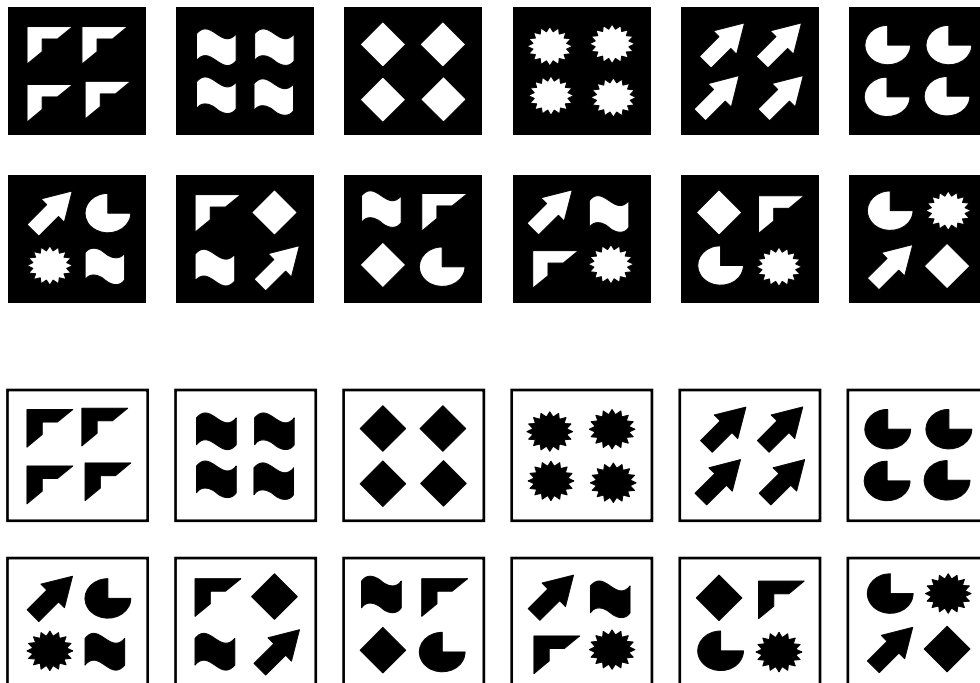


Figure 28: Novel stimulus panels for Experiment 7 – transfer of
 same/different conditional discrimination, S+ = *same*
 (white-on-black panels), *different* (black-on-white panels)

5.7.2.2 Procedure

Training trials

The sessions were conducted in the same manner as Experiment 5.

Transfer trials

During the transfer trials both novel and existing pairs of stimuli were randomly presented using the randomisation schedule. To ensure that transfer in this experiment was truly above chance, it was decided to conduct an additional block of five sessions after transfer criterion had been reached.

5.7.3 Results

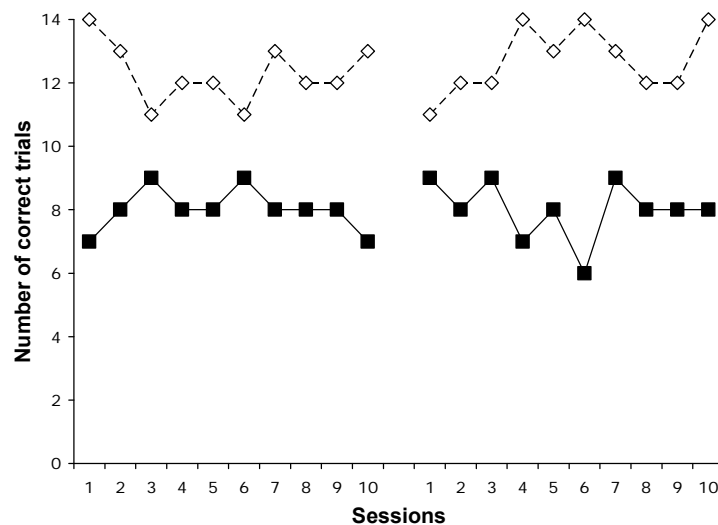


Figure 29: Number of correct responses to same/different conditional discrimination task, S+ = same (white-on-black panels), different (black-on-white panels). The first 10 sessions show the learning phase, the second 10 sessions show the transfer trials. \diamond = the number of trials until 10 correct responses were made, \blacksquare = the number of correct responses in the first 10 trials

The learning phase trials were grouped into two blocks of five sessions and the transfer trials were grouped into two blocks of five sessions and the results analysed using a two-tailed binomial test. The results were graphed (see Figure 29) and analysed using two measures of performance – $y/10$ (y = the number of correct responses in the first 10 trials) and $10/x$ (x = the number of trials until 10 correct).

Training trials

Performance in block one of the training phase was highly significantly different from chance (y/10: correct responses = 40/50, $z = 4.24$, $p < .001$; 10/x: correct responses = 50/62, $z = 4.83$, $p < .001$) as was performance in block two (y/10: correct responses = 40/50, $z = 4.24$, $p < .001$; 10/x: correct responses = 50/61, $z = 4.99$, $p < .001$), meeting the training criterion.

Transfer trials

Performance in block one of the transfer phase was also highly significantly different from chance (y/10: correct responses = 41/50, $z = 4.53$, $p < .001$; 10/x: correct responses = 50/62, $z = 4.83$, $p < .001$) as was performance in block two (y/10: correct responses = 39/50, $z = 3.96$, $p < .001$; 10/x: correct responses = 50/65, $z = 4.34$, $p < .001$). The subject met the transfer criterion as performance in the first block of the transfer trials was not significantly different from performance in the second block of the learning phase using a chi-squared test ($\chi^2 = 0.04$, $p = 0.85$).

Using the 10/x data, the results were then analysed to compare the subject's performance on the novel stimuli to that of the training stimuli (block one: novel stimuli = 31/40 correct, training stimuli = 19/22 correct; block two: novel stimuli = 33/41 correct, training stimuli = 17/24 correct). A chi-squared test found no significant difference between performance on the training and the novel stimuli in either block one ($\chi^2 = 0.71$, $p = 0.40$) or block two ($\chi^2 = 0.79$, $p = 0.37$) of the transfer trials. The results were then converted into percentages in order to graphically compare the varying proportions of each stimulus type in each session caused by the randomisation procedure (see Figure 30).

The results also show that Pitpa's performance on the novel stimuli on day one of the transfer trials was 100% correct and even better than that for the repeated training stimuli presented during the same session (75% correct).

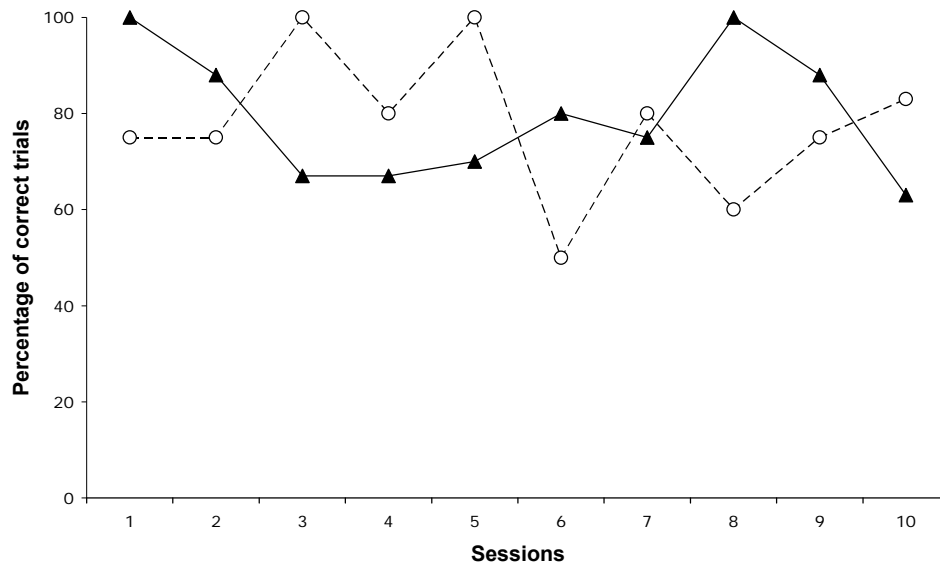


Figure 30: Percentage of correct responses to training and novel stimuli during same/different conditional discrimination transfer trials, S+ = *same* (white-on-black panels), *different* (black-on-white panels) (using 10/x data, x = the number of trials until 10 correct). ○ = percentage of correct responses to training stimuli, ▲ = percentage of correct responses to novel stimuli

5.7.4 Discussion

The fact that the results in the first block of the transfer trials were not significantly different from those of the second block of the learning phase and that there was no significant difference in performance between the training and novel stimuli in the transfer trials indicates that transfer did take place. This result is further strengthened by the fact that the highly significant transfer performance was repeated in a second block of transfer trials. The transfer results suggest the subject was not merely memorising the stimulus combination in each condition as suggested by the configuration model (see section 3.2.4.1) or learning stimulus specific relations using the multiple-rule model (see section 3.2.4.4). Rather, that the subject was able to use a single generalised rule (see section 3.2.4.5) to perform a conditional discrimination based on simultaneously presented same/different relations – a rarely tested task that has been previously demonstrated in monkeys (Burdyn and Thomas 1984; Flemming 2011; Flemming et al. 2007) and pigeons (Castro et al. 2010) (see section 3.7.4).

To ensure that the monkeys in their experiment had not learned equivalence classes based on the identity of the stimuli rather than relying on the ‘concepts’ of *same* and *different*, Flemming et al. (2007) conducted transfer tests with novel stimuli almost a

year after the original study. The success of those tests led the authors to conclude that item-specific learning was not responsible for the monkeys' behaviour and was seen as "evidence that the concepts of *same* and *different* were learned" (p. 58). This argument also holds true for Pitpa's transfer performance. Flemming et al. (2007) did utilise trial-unique novel stimuli in their transfer tests while the transfer stimuli in this experiment were randomly repeated, however the fact that Pitpa's performance showed no significant deterioration when the novel stimuli were introduced suggests there was no equivalence class-based learning phase with the new stimuli and that she continued to respond on the basis of conditional cues and relational information.

Furthermore, as with Experiment 4 (see section 5.4.3), the condition required by some authors of successful performance on the first appearance of novel stimuli was fulfilled as Pitpa scored 100% on the first presentation of the novel stimuli on day 1 of the transfer trials. Indeed, Thomas and Kerr (1976) claim successful performance on first-trial transfer tests "precludes the possibility that specific stimulus patterns had been learned and thus permits the conceptual interpretation" (p. 336).

One issue that must be addressed is the differing results of Experiments 5 and 7. The fact that the subject was now able to succeed in the same task that she had struggled with in Experiment 5 may be the result of the subject receiving training in both sets of conditions (*same* and *different*) before this experiment instead of just *same*. In their experiment combining conditional discrimination and oddity problems, Thomas and Kerr (1976) claimed that "prior mastery of the oddity concept was essential to the conditional discrimination task" (p. 336).

This theory gains some support from the fact that the study demonstrating conditional same/different discrimination in rhesus monkeys utilising a similar paired discrimination procedure to that employed here (Flemming et al. 2007) also separately trained its subjects to criterion in each conditional rewarded relation (*same* and *different*) before changing to randomly alternating the conditional rewarded relation on a trial by trial basis. Following separate training in each conditional relation, the rhesus monkeys in Flemming et al.'s (2007) experiment "rapidly learned to select the correct relation" (p. 58) in randomly alternating trials just as Pitpa did. Similarly, Burdyn and Thomas (1984) pre-trained their squirrel monkeys in a regular same/different task (as

was done here) and separate *same* and *different* conditional tasks before testing with the alternating conditional procedure.

While not dealing with the addition of a conditional component, Edwards et al. (1983) point out that in the successful simultaneous same/different procedure used by Premack (1976), the chimpanzee was given explicit training in both the *same* and *different* categorisations. However in matching-to-sample and oddity-from-sample experiments, in which pigeons appear to learn very little about the alternative to which they have been trained (see Carter and Eckerman 1975; Cumming and Berryman 1965; Zentall et al. 1981), their ability to utilise a generalised rule when novel stimuli are presented is reduced (Zentall and Hogan 1978). Although the additional pre-training provides a plausible explanation for Pitpa's eventual success, another possibility is that performance was facilitated merely by the subject having had more training with the testing paradigm.

The fact that the subject took much longer and required more training to learn this task compared to the standard same/different categorisations in Experiments 4 and 6 suggests that she found the conditional task more difficult. This finding supports Thomas' (1980, 1986, 1996) hierarchical model that places same/different conditional categorisation ("relational concepts I") as a "level 7" task above the standard same/different categorisation (relative class concept) on "level 6".

It seems logical that a task that requires the subject to make a selection based on two separate discriminations, in this case both 'black or white' and 'same or different', would prove more difficult than tasks in which they only have to decide on the basis of one discriminative rule. In fact, as discussed in section 3.2.1, numerous studies have indicated that a single discrimination is learned more quickly than a conditional discrimination using the same stimuli (Mackintosh 1974). Indeed, Pitpa learned each of those single discrimination tasks relatively quickly in Experiments 1 and 4. A similar phenomenon has also been found in pigeons. Matching-to-sample studies have shown that pigeons have greater difficulty matching accurately using compound samples in which they have to attend to more than one rule compared to single-rule samples (Carter and Werner 1978).

However, in Flemming et al.'s (2007) study with rhesus monkeys, the addition of discriminative cues actually seemed to facilitate learning of same/different discrimination reversals in which the monkeys had previously shown perseverative errors. Similarly, Castro et al. (2010) found pigeons learned the conditional same/different task (both the training and transfer sections) faster than the same/different task in other experiments (e.g. Young and Wasserman 1997). However, there were a number of experimental differences other than the conditional rule between the two experiments that may have accounted for the improved performance, including type of icons, observing response requirement, the size of the icon pool, simultaneous presentation of stimuli and direct responding to the stimuli (see section 3.7.3.3). It is also worth noting that the performance of Castro et al.'s (2010) pigeons dropped when the multi-element stimuli were reduced to 4 and 2 items, suggesting entropy played a role in their performance (see section 3.7.3.3).

Further experiments would be needed to determine exactly how Pitpa solved this task. For example, as Thomas et al. (1990) have pointed out (see section 3.2.1 and 3.2.3), there is no way of knowing whether the putative hierarchical design of this type of experiment – in this case background colour as the superordinate (conditional) cue modulating the selection of the subordinate (discriminative) cue of same/different shapes – was the way in which Pitpa actually solved the discrimination. In fact, some experiments have suggested that rather than an “if-then” hierarchical strategy, simultaneous presentation of stimuli leads animals to learn “what goes with what” (e.g. Thomas and Schmidt 1989). In the case of this experiment, it can only be said with any certainty that one cue modulated responding to the cue with which it was paired.

Thompson and Oden (2000) have suggested a non-relational method of solving the conditional same/different task in which the subject only has to perform a single physical matching operation. In this scenario, in the presence of the *same* cue the subject should choose the set in which one item matches the other (A is A). In the presence of the *different* cue, the subject merely has to choose the other set without any reference to relationship between the *different* items. Flemming et al. (2007, p. 59) endorsed Thompson and Oden's (2000) belief that, “an organism that understands conceptual relations must also be able to abstractly recode those relations so that they

can be applied in different experimental paradigms.” That is, that the subjects should be able to label relations in some way.

Flemming et al. (2007) tested whether the rhesus monkeys in their conditional same/different experiment were using the conditional cues in the manner suggested by Thompson and Oden (2000) by applying Thompson and Oden’s (2000) criteria and seeing whether the colour cues could operate in a bi-directional manner as labels for the relations of *same* and *different*. They found two of the five monkeys were able to choose the correct colour in the presence of the S+ relation (*same* or *different*) – essentially labelling those relations, according to the authors, and suggesting the monkeys were using relational information to solve the task. This test was not conducted in this study. However, unlike Flemming et al.’s (2007) monkeys, Pitpa had already demonstrated the ability to solve the same/different task without the use of conditional cues in previous experiments (see Experiments 4 and 6), suggesting she was both capable of and practised at performing discriminations using relational information without needing to resort to Thompson and Oden’s (2000) single-matching procedure.

CHAPTER 6

GENERAL DISCUSSION

6.1 Cognitive abilities of echidnas

This study set out to determine whether an evolutionarily ‘primitive’ animal could perform a ‘high-level’ cognitive task. As discussed in sections 5.1 and 5.2, this study firstly confirmed the results of two echidna studies demonstrating black/white discrimination (Gates 1973; Buchmann and Rhodes 1978) and one study showing circle/triangle shape discrimination (Gates 1973). It also demonstrated an echidna is able to perform what are considered to be relatively difficult and rarely demonstrated tasks in non-humans – same/different categorisation and conditional same/different categorisation (see sections 5.4 and 5.7). However, what is less certain is what mental abilities were being utilised by the subject to master the more complex tasks – whether she used relatively prosaic perceptual mechanisms or relied on the relationship between the stimuli or even an identity ‘concept’ to solve the discrimination.

6.1.1 Relational categorisation

As discussed in section 3.7.6, there are a number of theories about how animals are able to successfully perform same/different categorisations. One of the first considerations in any type of categorisation experiment is to ensure that the subject did not use basic perceptual mechanisms rather than relational cues to master the task. In this case, the fact that the subject was able to transfer the same/different discrimination to novel stimuli in Experiment 4 (S+ = ‘same’) and Experiment 7 (conditional same/different) suggests she was doing more than merely memorising stimuli. Katz and Wright (2006), for example, claimed the impressive transfer performance of their pigeons in a same/different experiment indicated the birds were basing their judgments on the “relationship between the items ... and not some other cue” (p. 84).

The transfer results also met the more stringent requirements of some authors of transfer performance equivalent to baseline and above 80% and the utilisation of only first-trial transfer data (see sections 5.4.3 and 5.4.4). Even an elemental theorist like Pearce (1997) allowed that correct selection on the first trial of transfer tests in matching experiments indicated that at least some species could solve discriminations using “relational information” (p. 125-126). (See also section 3.7.6.2.4).

For many authors, successful transfer performance is considered sufficient evidence of relational categorisation (see section 3.7.2.1.1 and 3.8.3.3). However, others have suggested that some or all animals may utilise more prosaic associative mechanisms to solve same/different tasks (see section 3.7.6). According to Jerison (1985, p. 30): “Operant conditioning procedures have been remarkably successful in training animals to act as if their performance was based on ‘higher mental processes’, even when it was demonstrably based on associative learning.”

It is important to remain open to more prosaic explanations for Pitpa’s success in this experiment. It has been shown in a number of studies that animals can respond to stimulus features other than those intended by the experimenters (Lashley 1938a; Thomas 1994; see also section 3.4.4.4.1). According to Hanggi (1999): “At best, researchers can attempt to control for such cues by designing stimuli that are equal in brightness and lacking other cues to which an animal may respond” (p. 251). In this experiment, the stimuli were designed to prevent inadvertent cueing from factors such as brightness, perceptual grouping, entropy, uniformity, colour and individual shapes (see section 4.3). In addition, a number of other methodological decisions were made to help ensure Pitpa used relational information rather than some other means to perform this experiment. These included apparatus design and operation to prevent inadvertent cueing from extraneous visual, olfactory and auditory cues (see sections 4.2 and 4.4.3) and the introduction of blind trials to rule out experimenter cueing (see section 5.6). (Some of these are also discussed in Thomas’ (1996) list of requirements for conceptual learning in section 6.1.2).

In terms of the experimental procedure, a simultaneous same/different method was used instead of the delayed matching/non-matching to sample procedure because matching tasks can potentially be solved using non-relational means such as conditional discrimination and relative novelty (see section 3.7.6.1), whereas simultaneous procedures are more like to be solved using relational means (see sections 3.7.2.1.5, 3.7.6.2.4 and 5.4.4).

While it is not possible to categorically state that Pitpa did not make use of some undetermined mechanism or cue, the measures taken in the design of this experiment to prevent inadvertent cueing, and the fact that performance was not uniform, dropping

with the introduction of a more complex ‘conditional’ experimental paradigm (see sections 5.5 and 5.6.4), provide a reasonable degree of confidence that the results were relationally based.

6.1.2 Concept learning

While it seems likely that Pitpa used some form of relational information to solve the same/different discrimination in this experiment, did she in fact demonstrate concept learning? While there has lately been more circumspection around claiming conceptualisation for non-human categorisation performance, there are still many authors willing to label the type of performance demonstrated in this study as “conceptualisation” (e.g. Wasserman et al. 1995), “concept learning” (e.g. Blaisdell and Cook 2005; Flemming et al. 2007; Wright and Katz 2006; Wright et al. 1984) and “abstract-concept learning” (e.g. Wright et al. 2003) (see section 3.8.3.3).

However, as discussed in section 3.8.1, there is no general consensus on a definition of concept learning. Lea (1984b) has argued that the term can be interpreted on two levels – what was being categorised and how the subject achieved the categorisation. According to the first, most parsimonious definition – categorisation of stimuli grouped according to human-defined concepts, in this case *sameness* and *difference* – Pitpa was capable of conceptualisation. However, most recent studies that claim conceptual performance tend to require evidence that the subject demonstrated the ability to make the discrimination based on something other than low-level perceptual cues (e.g. Young and Wasserman 1997). In fact, there are cautionary tales about scientists overestimating an animal’s discriminative abilities.

As noted in section 3.4.4, a number of perceptual categorisation studies that set out to train animals to discriminate on the basis of a perceptual ‘concept’ have found the subjects actually mastered the task using less complex means (e.g. Greene 1983; Honig and Stewart 1988; Huber et al. 1999). D’Amato and Salmon (1984) point out that there is a “natural, and quite understandable, tendency of investigators to stress the cognitive accomplishments of the animal subjects with which they are most intimately connected” and warn that care must be taken that reported complex cognitive processes are not “in

the eye of the beholder” (p. 164). With this warning in mind, Pitpa’s performance has been examined using a number of widely accepted criteria for concept learning.

The most commonly cited criterion for conceptualisation is that a categorisation performance can be generalised to novel stimuli. Wasserman et al. (1995, p. 249) described successful transfer of performance to novel stimuli as “the critical test for conceptualisation” (see also sections 3.8.3.1.1 and 3.8.3.3 for discussions of transfer tests as evidence of concept learning). As discussed in relational categorisation above (section 6.1.1), Pitpa was able to transfer the task to novel stimuli, including the more stringent requirements for overall and first-trial performance levels.

While transfer of a categorisation performance to novel stimuli has traditionally been considered sufficient evidence of concept learning by many authors, a number of other criteria have been proposed. Firstly, there are arguments that only some types of experiments can be considered as tests for conceptualisation. While some authors claim that conceptualisation can be applied to perceptually based tasks (see section 3.8.3.1), others argue that concept learning can be more definitively demonstrated when it is based on abstract thinking (Vonk 2003, see section 3.8.3.3) – that is, rather than relying directly on perceptual cues (so-called perceptual concepts such as ‘tree’ and ‘human’, see section 3.4) they are solved by judging the relationship between stimuli. Wright et al. (2003), for example, state that: “Abstract concepts are rules about relationships (e.g. identity) among stimuli” (p. 184). The fact that the successful performance of the same/different task by Pitpa appears to be based on the utilisation of relational rather than perceptual information gives some weight to conceptual claims.

It has been further argued that ‘true’ same/different concept learning requires not only transfer to novel stimuli, but also the use of simultaneous (rather than successive) presentation of stimuli. Premack (1983a), for example, claimed that the successive matching-to-sample (or oddity-from-sample) task can be solved using more prosaic methods such as familiarity, while simultaneous presentation is more likely to involve conceptual learning (see section 3.7.2.1.5). This experiment fulfilled the simultaneous procedure criterion.

In addition to simultaneous procedures, some authors have suggested that subjects should utilise only two items to demonstrate *same* or *different* (Blaisdell and Cook 2005; Premack 1983b). After the two-item same/different task is learned, “the degree to which this behaviour transfers to novel situations having *same* and *different* relations is taken as evidence of concept formation” (Blaisdell and Cook 2005, p. 67). The main objection to multi-element stimuli being used to represent *same* or *different* in these types of experiments is that they have sometimes been found to be controlled by perceptual mechanisms such as symmetry or entropy rather than the relationship between elements (e.g. Young and Wasserman 1997; Young, Wasserman and Garner 1997; see sections 3.7.6.2.2 and 3.7.6.2.3).

This experiment uses four rather than two items to indicate *same* or *different*, however the stimuli were designed to reduce the potential for low-level perceptual mechanisms such as symmetry or brightness (see section 4.3.2) and there is experimental evidence to suggest that entropy only starts to influence performance in displays containing eight items or higher (see section 5.4.4), making it unlikely that these cues would have supplanted relational or conceptual behaviour in this case.

In addition to the more general criteria discussed above, Allen (1999), Thomas (1996) and Katz et al. (2007) have created more formal sets of criteria for concept learning against which Pitpa’s performance can be judged. Allen (1999) proposes a three-clause schema by which an organism might “reasonably be attributed a concept” (p. 37).

- i) **The subject systematically discriminates some Xs from some non-Xs.** Allen (1999) specifically states that same/different categorisation and transfer to novel stimuli fulfil the requirements of condition (i).
- ii) **The subject is capable of detecting some of its own discrimination errors between Xs and non-Xs.** Allen (1999) cites as an example of the fulfilment of this requirement the behaviour of pigs in a study conducted by himself and others (Keddy-Hector et al. unpubl.). After the pigs were performing at an overall rate of about 90%, they would still occasionally make wrong choices. Before any feedback was provided, some pigs would attempt to back away from their incorrect choice. As mentioned in section 4.4.3, Pitpa also

occasionally headed towards an incorrect choice, then changed direction and selected the correct one.

- iii) **The subject is capable of learning to better discriminate Xs from non-Xs as a consequence of its capacity (ii).** According to Allen (1999), this clause is harder to articulate and defend, however he believes evidence of this type of integrated processing mechanism linking perceptual categorisation and recognition of perceptual error suggests the operation of an independent representation of what the perception is supposed to represent, i.e. a concept, and provides a stronger case for the attribution of a concept. Allen (1999) offers no examples of this clause being statistically proven and it cannot be demonstrated here, however Pitpa's demonstration of endogenous error detection (clause ii) suggests that fulfilment of clause (iii) might be possible.

Thomas (1996) has created an even more elaborate set of rules that the author argues must be met in order to show that an animal has responded conceptually.

- i) **The subject must be able to respond correctly to new exemplars.** Pitpa's performance did not deteriorate with the introduction of novel stimuli so she fulfilled this requirement. However, Thomas also required transfer tests to conform to optimal criteria, which were either the use of trial-unique stimuli (i.e. using each stimulus only once) or using only the results of the first trial with new exemplars as evidence of 'concept' use. There is some support for requiring trial-unique stimuli for transfer trials to eliminate the possibility that learning could contaminate transfer performance (e.g. Katz and Wright 2006; Katz et al. 2002; Wright 1997; Wright et al. 1988; Wright et al. 2003). While this experiment did not use trial-unique stimuli, the issue of transfer performance contamination was addressed using Thomas' other optimal criterion – using only the results of the first trial with new exemplars. In both the same/different experiment (Experiment 4) and the conditional same/different experiment (Experiment 7), performance with the novel stimuli on day one of the transfer trials (the first appearance of the novel stimuli) was 83% and 100% respectively and showed no deterioration relative to the repeated training stimuli.

- ii) **Inadvertent experimenter cueing of animals must be avoided.** This was certainly a danger in this experiment as the experimenter was working in direct physical contact with the subject. However, experimenter-naïve blind trials were undertaken to address this issue. Handler cueing also seems less likely due to the variable nature of the results for different experiments. If the subject's performance was due to handler cueing it seems likely the results would be fairly uniform. In fact, the results suggest the subject found some tasks, such as the initial presentation of the same/different conditional discrimination in Experiment 5, more difficult than others.
- iii) **The results must be replicated by other experimenters using other animal subjects.** Hopefully this will be undertaken in the future (see section 6.5).
- iv) **The odour of food reinforcers must not be uniquely linked to the correct stimuli.** This was particularly important in this experiment as the subject has a very good sense of smell (see section 2.1.4.2). As discussed in section 4.2, both distance and wooden lids on the food dishes (which had been successfully tested in several previous experiments) were used. These measures seemed effective as the subject visually checked on each trial whether the dish contained food or not.
- v) **Irrelevant stimulus cues, such as brightness, must be avoided.** The different shapes used on the stimulus boards were of varying surface areas so both the same and different boards would be of varying degrees of brightness and no brightness level would be associated with either condition (see section 4.3.2).
- vi) **The possibility of memorising specific patterns or properties of objects must be precluded.** The possibility of the subject memorising patterns is unlikely as both the same and different boards were arranged in the same pattern. In terms of the properties of the stimuli, the same set of shapes was used in both the same and different boards and they contained both symmetrical (e.g. square) and asymmetrical (e.g. lightning bolt) shapes (see section 4.3.2).
- vii) **Responding based on stimulus generalisation must be precluded.** The visually basic nature of the stimuli makes it unlikely the subject would fail to discriminate a new item from one she had seen previously.

More recently, Katz et al. (2007) put forward the three criteria that they believed were important to establish abstract-concept learning, all three of which were fulfilled in this experiment (see chapter 5).

- i) **Transfer stimuli must be novel.**
- ii) **Transfer stimuli should not be repeated.** Alternatively, trial 1 performance should be used.
- iii) **Full abstract-concept learning in which baseline performance is equal to transfer performance should be achieved.**

Based on all of the above criteria, it seems valid to claim that Pitpa demonstrated a same/different ‘concept’ in terms of Lea’s (1984b) first level (she was able to categorise on the basis of human-defined categories) and appeared to be utilising relational, rather than simply perceptual, information to do so. Like Wasserman et al.’s (1995) pigeons, she came to respond “in accord with the abstract concept that collections of numerous complex visual stimuli are all the same or that they are all different” (p. 249). As to Lea’s (1984b) second level of conceptualisation – how it is performed – this study, in common with other animal behaviour experiments, cannot definitively determine whether the performance was based on processes equivalent to those utilised by humans. In addition, as Watanabe et al. (1993) point out, even if animals are using concepts, they might not be the same ones as the experimenter.

However, it is also possible that it might not be an either/or proposition between conceptually based performance in humans and more basic perceptual mechanisms in animals. As discussed in section 3.8.2.1, some authors argue that even in humans conceptual behaviour incorporates perceptual mechanisms. According to Goldstone and Barsalou (1998), the distinction between perceptual and conceptual is artificial and particular tasks lie along a perceptual-conceptual continuum. Wasserman et al. (2002, p. 356) agree, stating: “The degree to which a process is conceptual thus depends on the degree to which it is independent of the perceptual details.” There were obviously some perceptual aspects to this discrimination performance common to all such studies, as Pitpa had to identify and compare the items to make an appropriate response. However, as discussed in chapter 4, in addition to transfer trials numerous steps were taken to help ensure this study was not affected by perceptual cues that would override relational

information. According to Wasserman et al. (2002), these types of precautions lend credence to the idea that the performance was closer to the conceptual than to the perceptual end of the continuum.

Whatever the mechanism used to discriminate relational concepts in categorisation experiments, one question that has been asked is whether those concepts are pre-existing or are taught as part of the experimental procedure (see section 3.4.4.1). A number of authors have claimed the former for their subjects. Herrnstein and Loveland (1964, p. 551), for example, claimed for their perceptual categorisation study that: “The speed with which their performances improved, coupled with the complexity and variety of even the first slides used, strongly suggests that they entered the experiment with the concept already formed” and Lombardi et al. (1984, p.6) stated: “... we think they already had [the oddity concept] before the experiment began”. Some support for this view was provided by Irle and Markowitsch’s (1987) study showing squirrel monkeys can perform a non-match-to-sample task without specific training. Similarly, Wasserman et al. (2002) found pigeons attended to the same/different relations among items in visual displays despite their not being rewarded for doing so.

However, other authors believe it may be impossible to determine whether subjects are demonstrating the acquisition of a new concept or the use of an existing concept due to the confounding influence of the subject’s acquisition of the reinforcement contingencies (Bailey and Thomas 1998; Thomas and Ingram 1979). Hayes and Nissen (1971, p. 79) even went so far as to say: “We cannot imagine any set of operations, applied to any subject, that could detect a concept without at the same time operating to induce its formation.” Thomas and Ingram (1979, p. 42) added: “In other words, the acquisition of new concepts and the detection of existing concepts are hopelessly confounded with the subject’s acquisition of the reinforcement contingencies, thus, the distinction between newly learned and existing conceptual behaviours is scientifically meaningless.”

If Herrnstein and Loveland’s (1964) theory is correct, the speed with which Pitpa learned the same/different task would suggest she already possessed a same/different ‘concept’, however, in light of the concerns expressed above, it is also possible her rapid acquisition of the task was instead indicative of a relatively proficient learning

ability. The question of what this study might indicate about the echidna's cognitive abilities will be dealt with in the next section.

Finally, even if it could be definitively demonstrated that an animal could perform a same/different task using the same conceptual mechanisms as a human, that does not mean that the animal would possess the full range of a human's ability to conceptualise. "Because of the proximity of the term 'concept' to 'abstract thinking', we must be careful not to conclude too swiftly that fulfilling basic prerequisites of concept formation is indicative of the full range of cognitive phenomena that come with conceptual thinking in humans" (Chittka and Jensen 2011, p. R118).

6.2 Echidna intelligence

Having demonstrated same/different categorisation, conditional same/different categorisation and (according to many authors) relationally based concept learning, can any generalised claims be made about the cognitive abilities of the echidna? As discussed in the introduction (chapter 1), researchers have come up with numerous definitions for 'cognition' and 'intelligence'. Cognition seems to be a less loaded term than intelligence. While the former is associated with more general mental processes, the latter has strong associations with high-level 'academic' abilities in humans.

6.2.1 Cognition

To start with the less contentious term – did the subject of this experiment exhibit behaviour that could be described as cognitive? According to a popular textbook by Shettleworth (1998, p. 5), cognition is merely the "mechanisms by which animals acquire, process, store, and act on information from the environment", while McLean (2001, p. 243) states: "... the terms 'cognitive' and 'cognition' both encompass a range of mental abilities from simply perceiving and sensing through understanding and conceiving a notion." Under these types of catch-all definitions, every behaviour from the simplest stimulus reflex to a scientist studying quantum physics could be called cognition.

On the other hand, there are those who attempt to deny cognitive processes in animals altogether (see discussion in Tomasello and Call 1997) or reserve some cognitive processes for primates (Premack 1983a). According to Premack (1983a, p. 360): “Cognition (as a kind of computation) presupposes abstract representation, and I know of no evidence for representation of this kind in the nonprimate.” Premack (1983a) claims evidence for “abstract representation” in the realm of relational categorisation is found only at the level of second-order same/different categorisation (see section 3.7.5) and he considers it “improbable” that the task will ever be performed by non-primates.

However, a number of authors have taken a middle road. Cheney and Seyfarth (1990) suggested a definition of cognition as “the ability to relate different unconnected pieces of information in new ways and to apply the results in an adaptive manner” (p. 9). According to the authors, this definition is useful when applied to animal studies because it examines cognition in terms of what animals do without specifying any underlying mental mechanisms.

Tomasello and Call (1997) put forward an approach in which “all behavioural adaptations involving some degree of flexibility and complexity are seen as cognitive” (p. 431). So, when attempting to achieve a goal, a cognitive adaptation presupposes both a flexible way of perceiving and understanding a situation and a flexible choice of behavioural means. They contrasted this type of behaviour with innate, inflexible behaviours created by evolutionary processes that are not open to modification by the individual organism (for example, ants remove anything that smells of oleic acid from their nests, whether it is a dead ant or an obviously live ant coated with oleic acid by experimenters, Wilson 1971). The authors further stated that just because a behaviour has been elicited with instrumental conditioning does not mean that cognitive processes are not being used – the options for the subject may have been limited by the experimenter, however the subject must still utilise flexible perceptual and behavioural strategies to varying levels of complexity to solve the problem.

Zentall (1999) agrees with the ‘flexible’ view of cognition – that it firstly involves behaviours that cannot be explained by basic associative mechanisms (see section 1.2.1.2) and secondly implies that there is some form of active processing of stimuli that occurs between stimulus input and response output. Zentall (1999) claims that one of

the behaviours that satisfies these conditions is the active structuring of stimuli according to abstract relationships such as identity, or ‘sameness’.

So, while not universally accepted, based on the above definitions, it is not unreasonable to claim that Pitpa’s performance in this experiment was cognitive.

6.2.2 Intelligence

There are numerous problems with using artificial tests to determine intelligence in animals. The performance of a species is a combination of its abilities and the particulars of the task presented (Bitterman 1960, 1965). Thus, the failure of a species (or individual) to perform a particular task does not necessarily mean that they are incapable of doing so. Rather, it may be that the experimental situation was in some way unsuitable – “some contextual variable, such motivational level or response requirement, may have been inappropriate” (Kamil 1994, p. 17). (See section 3.7.3 for examples).

Some authors have even questioned the overall applicability of intelligence testing in animals. Hodos (1986) points out that intelligence tests are biased in design towards humans and their closest primate relatives. For example, they are primarily visual, which favours primates over animals which rely more on other sensory modalities. “... one should judge animal intelligence not from the perspective of human behaviour, but from the perspective of how well the animal is adapted to the demands of its own environment. I see little value in asking how well a crow performs as a human being” (Hodos 1986, p. 85). Similarly, Zentall (2000b, p. 198) cautions “... we humans are the ones deciding what is intelligent behaviour. We make up the rules and the testing procedures, and those tests may be biased in favour of our particular sensory, motor and motivational systems. We should avoid letting such non-intellectual differences affect our assessment of intellectual capacity.”

In addition to these issues, there is the broader problem of definition. Intelligence is a problematic term even when applied to humans and any claims of what constitutes ‘intelligent’ behaviour depend entirely on the definition being used. As discussed in the introduction (chapter 1), researchers have come up with numerous definitions for

intelligence. Some authors use the term to label what are generally considered fairly basic mental processes. For example, Jolly (1966) equated intelligence with learning and the solving of discrimination learning problems and Thomas' (1996) hierarchy encompasses tasks from habituation (level 1) to biconditional concepts (level 7) as relating to various levels of relative intelligence (see section 1.3.2.1). On the other hand, others like Macphail (1982, 1985, 1987) believe that animal behaviour is governed by only basic forms of learning (habituation and associative learning) and does not contain anything resembling human intelligence (see section 1.2).

Many authors believe animals are more than the automatons that Macphail suggests, and that animal intelligence can be found in those behaviours that are not governed by basic associative mechanisms. Tomasello and Call (1997) suggested that an organism may be said to have solved a problem “intelligently” when it does not use overt trial-and-error, but rather relies on information from a source other than direct perception – that is, that it utilises some form of mental representation such as memory, inference, categorisation or insight.

Cheney and Seyfarth (1990) also distinguish between animal intelligence that involves “knowing how” (the ability to perform a specific task based on recognition of a particular stimulus) and “knowing that” (the ability to use knowledge more generally and flexibly that can be divorced from a particular response) (see also Dickinson 1980; Whiten and Byrne 1988). Cheney and Seyfarth (1990) suggest that while abilities such as the dance ‘language’ of honeybees and the navigational skills of homing pigeons are impressive, the animals cannot apply their knowledge to problems in another context. Because of this, “we rarely think of animals like homing pigeons or bees as intelligent in the human sense, primarily because their sophisticated performance seems limited to specific, highly circumscribed spheres” (p. 17).

Finally, Hodos (1986) makes the useful distinction between “intelligence” as an abstract concept (based on the judgement of the observer) and “intelligent behaviour” which is observable and measurable. “The hallmark of intelligent behaviour, in the sense in which the term is used to describe human behaviour, should be how the individual animal reacts in the face of a new challenge to its survival” (Hodos 1986, p. 85).

Using these definitions for this experiment; because Pitpa's performance seemed to involve more than basic associative mechanisms, consisted of a task widely considered to be relatively complex and demonstrated the flexibility of performing an unfamiliar task in a novel context, it is not unreasonable to say she behaved intelligently. According to Fagot et al. (2001, p. 317): "It is a highly advanced intellectual feat for animals like pigeons and baboons to detect the sameness or differentness of a collection of visual stimuli and to make two distinctively different responses in order to report those same-different relations ..."

The next step is to examine the implications of this potentially 'intelligent' behaviour. The fact that a 'primitive' species was capable of performing a relatively complex task can be interpreted in a number of ways. Firstly, that that species has a relatively high level of intelligence compared to other species; secondly, that it is a specific cognitive module that bears no relation to performance on other tasks or thirdly, that it implies that the task is not, in fact, a relatively rare 'high-level' ability and is in fact quite widespread among numerous species.

6.2.2.1 High level of general intelligence

According to some authors, the echidna's ability to perform a 'high-level' task is suggestive of a relatively high level of general intelligence. As discussed previously (section 3.8.3.4), many authors consider same/different categorisation to be such a task. Wasserman, Young and Fagot (2001, p. 163) point out that: "The categorisation of two or more items as the same as or different from one another requires a level of abstract conceptualisation that was previously thought to be unique to human beings" while Edwards et al. (1983, p. 349) describe same/different concept learning as "clearly indicative of a cognitive capacity not typically attributed to non-humans". According to Wright and Katz (2006, p. 234), "The ability to judge relationships that transcend stimulus features is ... considered higher-order learning" while Huber (2001, Chapter 2, online) believes that "the ability to learn relational or abstract concepts is more likely to provide evidence of intelligence".

The addition of the conditional component to the same/different procedure is considered to make the task even more difficult. In their 1995 study, Hanggi and Schusterman suggest that conditional discrimination learning is a "complex problem" requiring

“higher-order cognitive skills” (p. 543), while Thompson and Oden (1996) describe conditional same/different categorisation as an “even more complex variation of a same/different discrimination” (p. 151).

Because of the perceived difficulty of the same/different task, a number of authors have used the concept learning abilities of different species as a “measure of intelligence or general cognitive ability” (Wright and Katz 2006, p. 235). These include D’Amato, Salmon and Colombo (1985), Herman et al. (1989), Herrnstein (1990), Premack (1978, 1983a, 1983b), Thomas (1980, 1996), Thompson (1995) and Thompson and Oden (2000). According to this criterion, it could be argued that the results of this experiment indicate that echidnas (or at least this one) are relatively intelligent. Similarly, Pitpa’s ability to quickly adapt to the unfamiliar setting and procedures of the experimental process is also suggestive. According to Macphail (1982, p. 4), “intelligence ... is held to manifest itself in all those situations in which subjects are required to adapt to novel circumstances”.

As discussed earlier (sections 1.3.2.1 and 1.3.2.2), Thomas (1996) is more systematic and claims that a species’ ranking on his hierarchy of cognitive abilities equates to its relative intelligence. Thomas’ (1996) own criteria for demonstrating conceptual learning were used to assess the results of this experiment (see section 6.1.2). It can be argued that, pending independent replication, this experiment meets those criteria. If that is the case, using Thomas’ intelligence hierarchy model (1996), an echidna has demonstrated level 3 learning ability (black/white discrimination), level 6 learning ability (the same/different class concept) and level 7 learning ability (a class concept (same/different) in a conditional relationship (if white-on-black then ‘same’, if black-on-white then ‘different’)). Thomas’ system also assumes that an animal that can perform successfully at one level can perform successfully at each of the preceding levels (Thomas 1996).

If Thomas’ claims are accepted, it would suggest the echidna, far from being cognitively ‘primitive’, ranks fairly highly in terms of overall intelligence. In fact other authors have used Thomas’ hierarchy to assess the learning ability or ‘intelligence’ of their subjects (e.g. Sappington and Goldman 1994 with horses; Burdyn and Thomas 1984 with squirrel monkeys).

However, as discussed in sections 1.3.1 and 1.3.2.2, making generalisations about either general or comparative intelligence based on the ability to perform a single task is fraught with pitfalls. As Hodos (1986, p. 84) points out: "... intelligence is not a biological property, like height or brain size; it is an abstraction based on value judgements about an organism's behaviour made by an intelligence tester. If the persons or animals do not do well on the test, they are judged to have low intelligence. If they possess ample quantities of the behavioural characteristics that the observer values, they are said to be rather intelligent."

Similarly, the creation of some kind of species intelligence hierarchy based on experimental results has been heavily criticised by many authors, in part due to the multitude of species differences and experimental variables that can influence performance (see sections 1.3.1 and 1.3.2.2). According to Tomasello and Call (1997, p. 430): "It is simply not meaningful or useful to discuss ... which animal species is 'more intelligent' or more 'cognitively advanced' than another" and we should "expunge this way of talking from our scientific discourse".

Despite these objections, it does not follow that there is no value in examining the performance of different species on tasks of varying complexity (see section 1.3.2). For example, Pepperberg (1983) explained her view of the value of task hierarchies in examining the accomplishments of Alex the African Grey parrot (see section 3.7.3.4): "Acquisition of categorical concepts, rather than categorical instances, is viewed by many researchers to imply advanced cognitive abilities (Premack 1978; Thomas 1980). While we are not attempting to find where our subject may fit on any relative 'intelligence' scale, we do believe that consideration of the hierarchies by which researchers attempt to assess intelligent behaviours enables the accomplishments of our subject to be better understood" (p. 184).

So, while making grandiose claims about the comparative intelligence of echidnas based on this study is ill-advised, it is not unreasonable to assert that the reverse idea of echidnas as cognitively 'primitive' due to their evolutionary history (see chapter 2) must be challenged as they have demonstrated the ability to perform what are generally considered to be cognitively demanding tasks previously thought to be the exclusive domain of more evolutionarily 'advanced' animals.

6.2.2.2 Isolated cognitive module

The arguments of the authors in the preceding section (6.2.2.1) seem to suggest that the echidna's successful performance of a conditional relational categorisation task in this experiment is evidence of more generalised cognitive ability. However, while this study has stressed the importance of not underestimating the mental abilities of the echidna based purely on its position in the evolutionary timeline, it is equally important not to overestimate its abilities based on the results of a few artificial tests. It does not necessarily follow that competence in one area generalises to abilities in other fields.

Psychology traditionally ordered animals according to a phylogenetic scale from 'primitive' single-celled organisms at the bottom to 'advanced' man at the top, with the rest of the animals arranged in a linear fashion in between (Hodos and Campbell 1969) – a theory which has been rejected by many scientists (see section 1.3.1). While it cannot be denied that there is a general trend towards increasing complexity in both cerebral development and behaviour throughout the evolutionary timeline, it is by no means a constant progression from 'simple' to 'complex'. As Oakley and Plotkin (1979) point out, complexity or competence in one area does not guarantee those attributes in all areas – for example, man is inferior in the water to a fish – and the demands of an animal's ecological niche can lead to the development of particular skills more sophisticated than its general problem solving abilities.

As discussed in section 1.4, modular-based cognitive theory suggests that animals can develop a relatively sophisticated cognitive skill in one particular area in response to ecological demand, while continuing to utilise more basic cognitive mechanisms in other areas. Essentially, animals can display what may be labelled 'intelligent' behaviour in one area, but not another. As Cheney and Seyfarth (1990, p. 17) point out, "animals often seem to have a kind of 'laser beam' intelligence – extraordinarily powerful when focused in a single domain but much less well developed outside that narrow sphere". For example, honeybees dance to communicate only about food and the spatial location of objects and not other information, probably due to the fact that it is a "specialised adaptation that cannot be extended to other contexts" (Cheney and Seyfarth 1990, p. 259).

This type of specialisation occurs throughout evolution, with some areas becoming more sophisticated while others remain unchanged. According to Salas et al. (2003), “the brains of extant vertebrates are likely a mosaic of both primitive and derived characteristics” (p. 73). An example of uneven development can be found in human physical evolution. In a number of aspects of skeletal morphology (dentition, persistence of the clavicle, number of digits on hands and feet) we are more like ancestral generalised mammals than are rats, cats, sheep or horses. While our brains are progressive, we are primitive in many other ways (Jerison 1973).

According to theories put forward by authors such as Huber (1995), Jerison (1976) and McLean (2001) (see section 1.4); cognitive abilities are the result of selective ecological pressures on species in areas such as food acquisition, home range size and environmental variation. The results of this experiment in demonstrating ‘higher’ mental abilities in the area of categorisation are congruent with the echidna’s ecology and behaviour (see section 6.3). However, it does not necessarily follow that the echidna would be equally competent in tests of other ‘higher’ abilities. Cheney and Seyfarth (1990), for example, posit that non-human primates possess an intelligence that is highly domain-specific, with little transfer across domains. Their theory is based on the fact that vervet monkeys can display a relatively high level of ‘intelligence’ in one domain (e.g. vocal communication), but not in other domains that seem to require no more complex computational procedures (e.g. inferring the location of predators from tracks and other signs).

To apply this idea to the echidna, tool use is considered by some authors to be a fairly sophisticated cognitive ability involving an understanding of causal relationships and an ability to decide between relevant and irrelevant aspects of various problems (Hauser 1997; Limongelli, Boysen and Visalberghi 1995; Mulcahy, Call and Dunbar 2005). However, tool use would appear to be superfluous to the echidna, as it already possesses very effective digging (large front and rear claws) and probing (snout and long tongue) apparatus for its foraging needs (Griffiths 1989), as well as lacking the physical capability to easily handle objects. As such, it would not be expected to have developed sophisticated abilities in the area of tool use.

Wright and Katz (2006), who have extensively studied same/different learning in birds and primates, offer some support for a modular view of relational categorisation. “Abstract-concept learning and abstract thinking may be dependent upon specially evolved cognitive (brain) structures or cognitive ‘modules’ to perform these higher-order cognitive tasks (e.g. Cosmides and Tooby 1994; Geary and Huffman 2002; Gigerenzer 1995, 1997; Hermer and Spelke 1996; Wagner and Wagner 2003)” (p. 235).

So, even if Pitpa’s performance in this particular task were generally considered to be ‘intelligent’, there is currently no evidence to suggest that it reflects a more generalised intelligence. Further study of other ‘higher’ abilities in the echidna would help to shed further light on this issue.

6.2.2.3 Common cognitive ability

The view of relationally based same/different learning as a ‘higher-order’ cognitive task that reflects favourably on species that can successfully perform it (either in terms of general intelligence or as a specific cognitive module) receives considerable support from the literature (see sections 6.2.2.1 and 6.2.2.2). However, there is another possibility. That is, that same/different categorisation is a common cognitive ability that has not been widely demonstrated due to inappropriate experimental techniques and a lack of cross-species testing.

The idea that similarity, or *sameness*, plays a fundamental role in human cognition has a long history (Wasserman and Young 2010). James (1950/1890, p. 459) claimed: “This sense of sameness is the very keel and backbone of our thinking” and that it was “the most important of all the features of our mental structure” (p. 460). Some authors, both then and now, consider the ability to recognise abstract concepts such as *sameness* as not only important to, but also exclusive to, humans (see section 3.8.2.1). Others have used the results of studies conducted with a small number of species to suggest that at least some animals can recognise relational *sameness* (see section 3.7.3). However, a number of authors have gone further and suggested that because of, rather than in spite of, the fundamental importance of *sameness* in human cognition, that the ability is evolutionarily ancient and widespread.

Behavioural ecology assumes that “most patterns of behaviour, like most morphological structures, have evolved and serve some adaptive function” (Cheney and Seyfarth 1990, p. 10). According to some authors, one of the most basic adaptations is the ability to recognise change. “Most basic to the function of perception, and necessary in the context of adaptation to changing environments, is the ability to detect invariances that reflect the generic characteristics of objects and events” (Hanggi 1999, p. 244).

Delius (1994, p. 25) claims that:

The question whether animals are able to command the abstract twin concept of identity and oddity is among the earliest to be experimentally investigated by comparative psychologists interested in exploring the phylogenetic origins of cognition. That is not surprising, as the capacity of detecting equality or inequality relations among events of variegated nature must be considered an essential prerequisite for several forms of reasoning.

Delius (1994) further argues that the ability to classify objects on the basis of either sameness or oddity in both birds and mammals (including humans) “may be derived from a very basal, phylogenetically primitive stimulus-specific habituation mechanism controlling the orienting response and alternative specific responses” (p. 25). James (1950/1890) suggested that even “creatures extremely low in the intellectual scale [like polyps] may have conception. All that is required is that they should recognise the same experience again” (p. 463). As discussed in section 3.8.2.1, there is experimental support for the idea that at least some of the processes involved in human conceptualisation are in fact fairly common perceptual mechanisms.

As discussed in the introduction (section 1.2), there are those who believe not only that a particular ability, such as same/different categorisation, is phylogenetically widespread, but that the intellectual abilities of animals are all the same and utilise only basic associative mechanisms – the so-called general process learning theory. Macphail’s (1985) “null hypothesis” is based on the idea that there is no difference in the intellectual capabilities of non-human vertebrate animals, so if one animal can perform a task, they all could, provided suitable testing procedures could be devised. According to Macphail (1982), based on his theory there is no reason to suppose any mammal with adequate vision could not develop visual concepts. The problem with this idea is Macphail’s assumption that if an ability has been demonstrated in two distantly

related species, it can be found in all species, despite the lack of empirical evidence. According to Kamil (1994), Macphail is guilty of “an extreme willingness to believe in the untested intellectual capacities of animals” (p. 20).

Macphail goes further and claims that unless it is proved that experimental variables are not responsible for species differences, his hypothesis that there is no differences in intelligence among vertebrates must hold (Kamil 1994). However, it can never be conclusively proved that a species lacks a particular learning ability; it can always be argued that adequate testing methods have not yet been utilised. As Kamil (1994) states: “Proving that there is no set of circumstances in which an animal can learn a particular task (e.g. that frogs cannot acquire language-like behaviour) is impossible” (p. 20).

One way to mount a case against Macphail’s contention that experimental variables are responsible for any demonstrated species differences is to find external criteria (e.g. natural history or ecology) that correctly predict differences in performance among a number of species. For example, Rumbaugh and Pate (1984) used an encephalisation index to successfully predict species differences among 11 non-human primate species when tested on a complex learning task. It is highly unlikely that experimental variables could have produced this correlation by chance, casting doubt on the universality of Macphail’s contention (Kamil 1994). (See also section 1.2.2).

Despite these criticisms, one of the underlying assumptions of Macphail’s hypothesis is demonstrably true – changes to experimental variables can both improve performance and enable previously unsuccessful species to perform specific cognitive tasks. The fact that a species fails to master a particular task in an experiment does not ‘prove’ that they don’t have that cognitive ability. The failure may be caused by any number of variables, such as unsuitable experimental procedures or motivational issues – an idea that is supported by the fact that some species that initially failed in same/different tasks succeeded when different procedures were tried (see section 3.7.3).

Wright et al. (2003) support the view that experimental variables may account for species differences in same/different categorisation. They claim that both task-based hierarchical (section 1.3.2) and modular (section 1.4) views tend to underpin these experiments, making them an all-or-nothing test – the subjects either have the ability or

not. Because of this, experiments testing this type of cognitive ability often tend to be one-shot demonstrational experiments rather than parametric manipulations, however the outcome is often not as clear as the authors' suggest. For example, some experiments that have purported to demonstrate 'abstract-concept' learning in pigeons and monkeys have been based on test performances considerably weaker than the training performances. Conversely, experimental variables have also been shown to negatively skew the outcomes (see Wright et al. 2003; section 3.7.3 for examples). According to the authors, "there are many ways for abstract-concept learning to fail and many fewer ways for it to succeed. It is, however, only the latter result that is significant" (Wright et al. 2003, p. 195).

These factors led Wright et al. (2003) to favour a general process account of same/different categorisation over one based on the idea of selective cognitive modularity (see section 1.2.3). Specifically, that same/different learning is likely to be "a general property of virtually all vertebrates, independent of whether such ability arose through homology (shared ancestry) or homoplasy (shared ecological pressures)" (p. 195). However, unlike Macphail, the authors acknowledged that there are "different degrees of generality" (p. 195) and there may be quantitative differences between species. They also stressed that further exploration of the mechanisms of same/different categorisation was the key to ultimately determining whether differences in performance reflect a fundamental, qualitative difference in cognitive capability, supporting a modular account, or merely a quantitative difference affecting task acquisition, supporting a general process account.

Even if one accepts the view that same/different categorisation is a universal cognitive ability, it does not necessarily follow that all species do it in the same way. William James (1950/1890) pronounced over a century ago that "it is the bane of psychology to suppose that where the results are similar, processes must be the same" (p. 528). It is possible that while same/different categorisation may be relatively common, different species may have evolved different methods to perform the same task. Smith et al.'s (2008) comparison of humans and monkeys in a same/different task led them to state that: "... different species may not always construe or perform even identical tasks in the same way" (p. 361). Some species may indeed use 'higher-level' relational analysis or even human-like concepts, while others may use more prosaic mechanisms. It is

worth noting that while many species have demonstrated same/different learning using delayed matching to sample procedures, which can potentially be solved using relatively basic cognitive processes (see section 3.7.6.1), only a few species have so far been shown to successfully perform the task using the supposedly more difficult simultaneous procedure, which is more likely to be solved using relational information (see section 3.7.2.1.5).

For example, Giurfa et al. (2001) found that even honeybees were able to learn a delayed matching and non-matching to sample task and transfer the performance to new stimuli and even to different stimulus modalities (olfactory to visual). The experiment was also repeatable in different laboratories using different experimental set-ups, procedures and subjects. According to the authors: “Our results question the view that vertebrates, and in particular primates, may be the only animals able to form ‘sameness’ or ‘oddity’ concepts. They also show that higher cognitive functions are not a privilege of vertebrates” (p. 932). However, it is worth noting that this study was conducted using a successive matching/non-matching procedure, which has been criticised by authors such as Premack (1983a, 1983b) as having “little to do with same/different” (Premack 1983b, p. 127) (see sections 3.7.2.1.5 and 3.7.6.1).

According to Wynne (2001), further research with a wider range of species is necessary to form an opinion about the distribution of same/different categorisation. “Studies of concepts such as same-different ... have only been carried out on a very narrow range of species ... – far too few to be able to draw any conclusions about the distribution of these kinds of ability” (Wynne 2001, p. 189). However, according to Shettleworth (1998, p. 18), “Studying a few very diverse species, it could be argued, is the best way to reveal processes general to all species” and McLean (2001, p. 242) claims “... it is the diversity of those species which appear to exhibit higher mental abilities ... which provides reasonable grounds on which to speculate about the ubiquity of such abilities within animals in general”.

In light of these conflicting viewpoints, it is prudent to be cautious about the broader implications of this experiment (see also Kamil’s, 1994, criticism of Macphail above). However, the fact that a monotreme has been added to the list of species that have demonstrated simultaneous same/different categorisation gives additional credence to

the idea that the ability to classify objects as *same* or *different* may be a more basic and widespread skill than authors such as Herrnstein (1990), Thomas (1980, 1996), Thompson (1995) and Pearce (1997) have suggested. For example, Mercado et al. (2000) claimed that similarities between the same/different categorisation performance of dolphins and primates was surprising considering their very different evolutionary history, ecology and neurology. “Such parallels suggest that mammalian brains analyse environmental features using ‘basic’ processes that are evolutionarily old and, therefore, likely common across a wide range of mammalian species” (p. 92).

In Delius’ (1994) review of same/different learning in pigeons, the author sought to demonstrate the ubiquity of same/different abilities among mammalian species by going “one further evolutionary stage back” (p. 26) from primates to birds. This study can be viewed in a similar light by establishing same/different learning in one of the oldest mammalian species (see section 2.1.2). The fact that such an evolutionarily and, in many respects, physiologically ‘primitive’ animal as the echidna is capable of successfully performing this task could be used to support either a general process account (same/different as a universal cognitive process) or a modular account (same/different as a more commonly distributed cognitive module).

6.3 Reasons for ‘high-level’ performance

While some authors believe that same/different categorisation is a fairly basic, widespread cognitive ability (see section 6.2.2.3), there is plenty of support for the idea that successfully performing the task (particularly with the added conditional configuration) is indicative of either a high level of general intelligence (section 6.2.2.1) or the possession of a sophisticated cognitive module (section 6.2.2.2). While there is currently little evidence to support the idea of the echidna as a species of relatively high intelligence, it is certainly true that the results of this experiment demonstrate an unexpected cognitive faculty in a species once viewed as an “animated pin-cushion” (Buchmann and Rhodes 1978, p. 144). Because of this, it is worth examining why what are considered by many authors to be relatively advanced cognitive abilities may have developed in an animal of the “lowliest status in the mammalian series” (Smith 1902 cited in Griffiths 1968, p. 101).

As discussed earlier (sections 1.4), evolutionary theory suggests that cognitive abilities do not develop without some ecological impetus (e.g. Dawkins 1986; Humphrey 1976), so it is unlikely that a cognitive ability demonstrated in laboratory experiments does not have some correlation in a species' natural behaviour. For example, Cheney and Seyfarth (1990) argue that the ability of squirrel monkeys and chimpanzees to solve transitive inference problems (see section 3.2.2.1) in captivity is based on their understanding of dominance hierarchies in the wild rather than simply being an artefact of human training.

A number of possible catalysts for the evolution of cognitive abilities in humans and other animals have been proposed, some of which are examined below for their potential applicability to the echidna. While these factors are dealt with separately here, they are not necessarily mutually exclusive. As Falk (1990) points out, it is notoriously difficult to establish one factor as a “prime mover” (p. 334) of brain evolution and cognitive development, while Tomasello and Call (1997) find implausible “the view that there should be a ‘single cause’ of the evolution of intelligence in recent evolutionary history” (p. 354). It is perhaps more likely, and closer to biological reality, that a combination of factors accounts for the evolution of cognitive abilities (Eckhardt 1987; Foley 1990). With this in mind, it is still worth exploring some possible triggers for cognitive development in the echidna.

6.3.1 Neurophysiology

A physiologically based explanation as to why an echidna might be able to perform a purportedly difficult cognitive task is found in the relative complexity of some aspects of its neurophysiology. According to a number of popular indices, the brain of the echidna is considered ‘advanced’ – relatively large brain size compared to body weight and spinal cord mass, fairly large and highly gyrified cerebral neocortex, extremely large frontal cortex and relatively complex sensory processing mechanisms (see section 2.2.1). These features are considered by many authors to be correlates of a high degree of ‘intelligence’ (e.g. Byrne 1993; Falk 1990; Jerison 1973, 1985; Pearce 1997; see section 2.2.1).

Many authors believe that species with larger brains show greater behavioural flexibility and more of the general ability to respond appropriately to novel events (see section 2.2.1.1). It could be argued this was demonstrated by Pitpa's rapid acclimatisation to the experimental process and acquisition of the tasks (see chapter 5 and section 6.2.2.1), although the effect of her being a relatively 'tame' animal must also be considered (see section 6.4.5). More specifically, the relatively large prefrontal cortex of the echidna might relate directly to relational categorisation. According to Ashby and Waldron (2000, p. 10), in humans there is "abundant evidence that the prefrontal cortex is critically important" for category learning. It has also been suggested that the prefrontal cortex (or an analogue to the mammalian prefrontal cortex in the case of animals such as pigeons) plays a critical role in abstract-concept learning such as same/different categorisation (Freedman and Miller 2008; Wright 2010; see section 3.9).

However, while a relatively complex neurophysiology suggests the mechanism by which echidnas might perform complex cognitive tasks, it does not address the causative selective pressure for an increase in both brain structure and cognitive development. The energetic cost of neural tissue suggests that there must be some fitness advantage to the large size of the echidna's frontal cortex (see section 2.2.1.1). So why does a seemingly simple animal like the echidna have such highly developed brain structures, particularly when the other Australian monotreme, the platypus, does not? As discussed earlier (section 2.2.1.1), factors such as the echidna's low body temperature and metabolic rate may help explain how echidnas are able to physiologically support a larger brain, but not why their seemingly superfluous cerebral apparatus developed.

The comparative approach to brain size in humans and other animals has yielded a variety of theories to account for brain expansion. According to Eckhardt (1987, p. 207): "Expansion in brain size ... was in all likelihood a response shaped by many influences and one which produced benefits broadly related to enhanced cognitive powers." Large relative brain size and neural complexity (and the presumed corresponding increase in cognitive abilities, see section 2.2.1) has been linked to a number of life history, ecological and social parameters (Foley 1990), some of which are examined below in relation to the echidna.

6.3.2 Life history

A number of aspects of life history have been shown to significantly correlate with relative brain size in primates and other mammals. However, many of these such as gestation length, neonate weight and weaning age (Harvey, Martin and Clutton-Brock 1987) are difficult to compare to the echidna due to its unusual (for a mammal) reproductive techniques. A lack of data makes comparisons on the basis of factors such as age of first reproduction and interbirth intervals (Harvey et al. 1987) also problematic.

One factor that can be compared is that of extended life span, which has been linked to large relative brain size (Allman, McLaughlin and Hakeem 1993; Harvey et al. 1987). Echidnas are long-lived animals that have been recorded living for up to 49 years in captivity (Griffiths 1978; see section 2.1.5), although exactly what part this may have to play in brain encephalisation has not yet been fully explained. According to Smith (1990), “larger brains would be of little use to short-lived mammals” (p. 365). One theory, known as the “cognitive buffer hypothesis”, suggests that large brains allow species to better survive environmental challenges through flexible behaviours, leading to increased survival rates and a longer reproductive life (Sol 2009; see section 2.2.1.1). Some evidence for this theory has been found in studies on primates (Allman et al. 1993) and birds (Sol, Szekely, Liker and Lefebvre 2007).

6.3.3 Tool use and language

Tool use has also been suggested as a prime catalyst for enlarged brain size and the subsequent purported increase in ‘intelligence’; however this theory has been subject to contradictory evidence and criticisms of an androcentric interpretation of prehistory (Conkey and Spector 1984; Jarvenpa 1993). In addition, it is difficult to determine whether increased brain size is a cause or a consequence of tool use. Irrespective of its validity, it is extremely unlikely to apply to the echidna, which has never been observed using tools and appears to have no need to do so as it is physically well equipped to deal with its everyday foraging activities (see sections 2.1.7 and 6.2.2.2).

Similarly, while the use of language has been touted as a possible catalyst for brain expansion in humans (Cheney, Seyfarth and Smuts 1986), this obviously is not a valid theory for the mostly non-vocal echidna (Rismiller 1999).

6.3.4 Social demands

Many authors believe a complex social environment has led to the development of sophisticated cognitive abilities in animals such as dolphins (Herman 1980) and primates, including humans (Bovet and Washburn 2003; Byrne and Whiten 1988; Cheney and Seyfarth 1985; Humphrey 1976; Jolly 1966; Whiten and Byrne 1997). Barton (1996), for example, found a consistent correlation in primates between neocortex size and social group size and Dunbar (1992) and Sawaguchi and Kudo (1990) found correlations between sociality and relative brain size in several primate species. Herman (2002) even suggests that: “Social living and social pressures may be major selection forces driving the evolution of intellect” (p. 275).

As the echidna is a mainly solitary animal (see section 2.1.6) there has been little selective pressure for the development of social abilities and any subsequent increase in ‘intelligence’. A number of authors claim that the neurological seat of this socially mediated ‘intelligence’ is found in the neocortex – that is, relative neocortical volume is a function of group size and the larger the group, the larger the neocortex (Dunbar 1993). This view led Hassiotis et al. (2003) to ask “why an animal like the echidna, which leads a solitary existence and has no known complex social life, has such a highly gyrified cortex” (p. 828).

However, the link between social complexity and intelligence is by no means established, with authors such as Kamil (1994) considering such an argument premature. According to Penn and Povinelli (2012), “the relationship between encephalisation and social complexity is spotty at best” and “there is little support for the hypothesis that sociality was the causal agent for increased encephalisation in mammals” (p. 531). The authors claim their argument is supported by the fact that there are a number of examples where there appears to be no relationship between sociality and encephalisation, such as across extant Carnivora (e.g. cats, dogs, bears, weasels)

(Finarelli and Flynn 2009). Similarly, social complexity does not appear to be linked to brain size in birds (references in Healy and Rowe 2007).

Other scientists argue there is nothing specific about the neocortex that indicates it controls social behaviour, and indeed, some species of insect (which have no neocortex) have very complex social organisation (Jerison 1993). These authors claim neocortex size (and by inference ‘intelligence’) may be due to selection from factors other than or in addition to social ones (Janson 1993). These could include the development and enlargement of sensory-perceptual and motor systems (Jerison (1993) – factors that would be driven by ecological, rather than social, demands.

6.3.5 *Environmental demands*

According to proponents of mosaic evolution (see section 1.4), cognitive abilities evolve in response to ecological demands. In line with this idea, a number of authors have suggested that an examination of the ecology and natural behaviour of subjects can provide some basis for speculation about their experimental performance. For example, in analysing the exceptional learning set performance of the marsupial fat-tailed dunnart (Bonney 2001) (see section 1.3.1), Wynne (2001) suggests that the most likely explanation is found in their habitat – which involves catching fast-moving insects and invertebrates in an arid and predator-filled environment. In a comparative study of configural learning in quokkas and fat-tailed dunnarts, Bonney and Wynne (2003) found only the dunnarts were able to fully complete the experimental tasks. According to the authors, the dunnarts’ challenging ecological niche leads them to be highly responsive to stimuli predicting reinforcement while the quokkas’ less demanding niche (grazing for vegetation in protected communities) may not require the same level of processing of multiple or conflicting stimuli.

So what ecological challenges have echidnas faced that have led them to evolve the ability to perform complex same/different categorisations? At first glance, echidnas don’t seem to have particularly demanding problems in their environment. They have no real predators (except man) and have virtually no social structure (see sections 2.1.5 and 2.1.6) – factors often associated with ‘higher-level’ learning abilities (see section 6.3.4). However, in her study of same/different learning in coatis, Chausseil (1991)

concluded that the coatis comprehension of the same/different principle was not crucial to the coatis in their natural environment in a specific sense, rather that “it is related to a more general ability, namely the versatile utilisation of visual cues in their environment” (p. 35).

This versatility in dealing with environment cues becomes even more important when a species needs to adapt to extremely variable environments, a factor that has also been linked to the development of certain cognitive abilities. Tomasello and Call (1997) surmise that when rapid ecological changes during individual lifetimes are the rule, evolution would favour the development of flexible learning and assessment capabilities over rigidly programmed behavioural systems. “... it is presumably the case that cognitive adaptations have evolved most frequently in situations in which environmental conditions change with some rapidity during the lifetime of the individual” (Tomasello and Call 1997, p. 12). More specifically, Huber (1995) claims animals that have adapted to a wide variety of environments require a greater filtering mechanism to identify disparate stimuli, leading to the development of perceptual categorisation skills. Similarly, Shettleworth (1998) suggests the ability to acquire new discriminations improves with experience and that the processes involved “are likely to be important in variable environments in nature” (p. 215).

This theory fits in with what is known about the echidna’s distribution (see section 2.1.1). Together with the house mouse, the echidna has the most widely divergent habitats of all mammalian species and is found in every major terrestrial ecosystem from desert to alpine (Augee et al. 2006; Griffiths 1968, 1978). Examples of the echidna’s behavioural flexibility in response to divergent environmental conditions are found in its hibernation and reproductive behaviours (see sections 2.1.8 and 2.1.9). It is also congruent with the echidna’s neuroanatomy. Quantitative neuroanatomical studies have demonstrated that the enlargement (or decrease) of certain parts of the brain is consistent with species’ special adaptations to different environments (Kruska 1988). Jerison (1976) suggested that a large forebrain (and the echidna’s is proportionately larger than man’s, see section 2.2.1.3) is the result of adapting to the demands of diverse ecological niches. When a species has to deal with diverse environments, one hypothesis is that large brains have evolved to allow the behavioural flexibility to cope with novel or altered conditions (see section 2.2.1.1). To test this theory, global

databases of introductions to novel environments of more than 600 bird introduction events (Sol et al. 2005) and 400 mammal introduction events (Sol et al. 2008) were examined and the results suggest larger brains do help birds and mammals respond to novel conditions. This led the authors to conclude that “enlarged brains function, and hence may have evolved, to deal with changes in the environment” (p. 5460).

6.3.6 Foraging demands

Another ecological factor that might contribute to cognitive development is the demands of foraging. McLean (2001) suggests that the manner in which an animal locates and captures food exerts significant selection pressure for the evolution of cognitive abilities. He argues that natural selection dictates that animals should evolve appropriate mental abilities to deal with the requirements of their particular ecological niches. “Locating and capturing food should correlate closely with, and be significantly indicative of, mental ability in animals” (McLean 2001, p. 246). Other authors have suggested the predator-prey “arms race” also leads to increasing intelligence: “... as prey species grew cleverer, their predators and competitors survived only by also becoming cleverer, and vice versa” (Jolly 1966, pp. 153-154).

Ostensibly, the foraging demands of the echidna do not seem to be particularly cognitively demanding and certainly therian anteaters do not show the degree of encephalisation seen in the echidna (Hassiotis et al. 2003; see section 2.2.1.2). However, according to McLean (2001), foraging for food that has a patchy distribution presents unique challenges requiring the evolution of “higher mental abilities” (p. 241) (see also Krakauer and Rodriguez-Girones 1995). The energy savings of remembering the location of food patches would be highly adaptive in terms of saving wasted foraging trips. Because of this, it would be expected that species that forage from food patches would show cognitive abilities not found (or at least not to the same degree) in species whose food is distributed relatively homogeneously, such as folivores. Echidnas forage mainly on termite mounds and ant’s nests – which represent food “patches”. McLean’s theory suggests that echidnas should have faced a greater evolutionary imperative to develop more sophisticated mental abilities than species whose food is more evenly distributed or in closer proximity. McLean’s theory is supported by the

findings of Foley (1990) and Clutton-Brock and Harvey (1980), who linked patchy resource distribution with greater encephalisation in primates.

In addition to patchy resource distribution, another foraging factor that may lead to increased cognitive development is optimal foraging. It has been argued that the kinds of learning studied in conditioning experiments such as this one have evolved under selective pressure to forage optimally (Lea 1981). Like many animals, the echidna has demonstrated the ability to employ optimal foraging strategies and adjust its foraging efforts in response to prey abundance, quality and defence (see section 2.2.2.1). According to Augee et al. (2006), such “farming of prey” (p. 49) would require a detailed mental map of prey species, location, depth, density and nutritional value, as well as the ability to take into account the influence of time of year and temperature on prey behaviour. The authors argue the echidna uses its “massive frontal cortex” to process this information and think about alternative actions, a safer option than trying them first in the real world. “Sophisticated processing in the frontal cortex of this wealth of data could be essential for forward planning ... These functions in the echidna might represent what we would call conscious awareness ...” (Augee et al. 2006, p. 49).

The ability to undertake this type of detailed forward planning and decision-making may contribute to the echidna’s ability to perform in categorisation training tasks. According to Hanggi (1999, p. 250): “Individuals may also use categorisation abilities to more easily locate forage, avoid predators, and travel over large areas of terrain” while Giurfa et al. (2001) suggested in their same/different experiment with honeybees that: “Such concepts might contribute to improve foraging activities” (p. 932).

6.3.7 Home range size

Some authors (e.g. Clutton-Brock and Harvey 1980) have theorised that the size of an animal’s home range, and the concomitant need for greater spatial memory, may contribute to larger brains and greater learning abilities. Milton (1981) described a possible correlation between brain size and the size of animal’s home range. He suggested the larger brain of the spider monkey, *Ateles geoffroyi*, compared to the howler monkey, *Alouatta palliate*, was due to the far larger home range of the spider monkey and the consequent extra brain space required for a larger mental map.

However, this purported increase in overall brain volume does not seem to relate to neocortex size, at least in primates. When Barton (1993) analysed volumetric brain structure data collated by Stephan, Frahm and Baron (1981) in light of a number of variables, he found that only breeding group size, not home range size, accounted for increased neocortical size. Furthermore, while Hassiotis et al. (2003) speculated that the echidna's enlarged frontal cortex might be related to the enhanced spatial and/or olfactory memory required by its home range, there are comparably sized eutherian mammals with bigger home ranges (Nicol et al. 2011; see section 2.1.6) that don't exhibit the same cortical enlargement.

6.4 Methodological issues

6.4.1 Generalisation of artificial experiments

Like other psychologically based studies of this type, this experiment is limited in its general applicability to categorisation behaviour in the wild. Herrnstein (1985, p. 144) points out that "... what an animal does in a particular setting is not likely to be the proper measure of what it is capable of doing generally" and Cheney and Seyfarth (1990, p. 6) claim that one of the problems with laboratory experiments is that "their relevance to the animals' natural social behaviour is often unclear".

Authors such as Huber (1995) and Kamil (1994) have argued that an assessment of an animal's knowledge is typically underestimated by its performance in a classical learning situation. For example, Cheney and Seyfarth (1990) claim that the use of arbitrary stimuli like lights, shapes and tones that an animal would never encounter in its natural habitat increases the chances that an animal may not understand the problem or lack motivation in what it perceives as an unfamiliar or even hostile environment. According to Cheney and Seyfarth (1990, p. 6), the use of artificial stimuli "increases the likelihood that results will underestimate or fail to reveal a subject's true ability".

One example of this phenomenon is found in the contrast between the relatively poor performance of marmosets in more traditional experimental settings (e.g. Miles and Meyer 1956) with the more successful results of Menzel and Juno (1982, 1985) using group-living marmosets in a more naturalistic environment (Kamil 1994). Similarly,

Roberts and Mazmanian (1988) used the inability of squirrel monkeys to categorise on the basis of pictures of birds vs. other animals in an artificial categorisation task to claim monkeys were unable to make this type of abstract categorisation. However, other authors have demonstrated that young vervet monkeys can distinguish between birds and other animals in the wild (Huber 2000).

Alternatively, it is also possible that the results of laboratory experiments might overestimate the cognitive abilities of wild animals. For example, research with captive apes has demonstrated cognitive abilities not yet found in the same species in their natural habitat – a disparity explained by some authors as resulting from training animals in skills they would not naturally need nor possess (see review in Cheney and Seyfarth 1990). However, as Cheney and Seyfarth (1990) point out, the natural existence of such abilities cannot be discounted while systematic reviews of laboratory-induced skills have yet to be conducted in the wild.

Kamil and Yoerg (1982) have argued that more natural environments better preserve “ecological validity” and, as Tomasello and Call (1997, p. 117) noted, “Perhaps exemplars of real birds that fly and sing, for example, would make a difference in how subjects categorise animals”. However, while this may be the case, such naturalistic stimuli does not allow for the specifics of the controlling features of stimuli to be isolated and identified in the same manner as artificially constructed stimuli. As Huber (2000) points out, observations in the wild are not sufficiently reliable to discount laboratory experiments and processes based on perceptual and associative theories. According to Cheney and Seyfarth (1990, p. 5), laboratory experiments are valuable because: “Their precision and control ... are unlikely to be matched by any study conducted in the field. Different experiments can focus precisely on different cognitive skills and allow one to state explicitly what would constitute evidence that an individual possesses a particular ability.”

Vaughan and Herrnstein (1987) claim that although many researchers question the applicability of artificial laboratory experiments, this reasoning suggests that animals use different behavioural principles in artificial situations than they use in nature. The authors suggest it is more likely that the same basic behavioural principles are used in both settings and that they can best be initially discovered in a simplified and contrived

situation. Lefebvre et al. (2004, p. 234) echo Macphail's (1982) view that: "Contrary to passive observation of animals in the wild, the response to the unnatural demands of captive experiments can reveal the full range of an animal's capabilities ... and these responses are assumed to reflect the way individuals deal with changes in their natural environment." Vaughan and Herrnstein (1987) suggest a combination of the two approaches could be productive – using the more simplified and controlled experimental procedures to establish basic processes, then building on that knowledge to explore more complex situations, including those that more closely resemble the natural environment.

As discussed previously (see section 1.5), the question being addressed by the type of experiments conducted in this study is not do the subjects *do* this behaviour in the wild, but *can* they do it at all, and artificial stimuli and controlled experimental conditions are necessary to identify the specifics of these kinds of behaviours. So, while the general applicability of these results to the natural behaviour of echidnas must be treated with caution, artificial experiments such as this one at the very least demonstrate that echidnas are capable of conditionally mediated relational categorisation under these experimental conditions. Evolutionary theory suggests that cognitive abilities do not evolve unless they serve some adaptive function (see section 6.3); however it is uncertain whether these results reflect a specific ability utilised in the wild or are indicative of a relatively robust, generalised learning ability. Further study using experimental techniques more closely resembling 'natural' settings could be helpful in illuminating how (or even if) these specific abilities manifest themselves in the echidna's 'normal life' (see section 6.5).

6.4.2 Procedural issues

One of the less satisfactory aspects of this experiment was the fact that the experimenter was in direct physical contact with the subject, leaving open the possibility of inadvertent cueing. Unfortunately, housing restrictions imposed by the zoo made it impossible to conduct the experiments within an automated apparatus. While the issue of cueing was addressed with the use of experimenter-naïve blind trials (see section 5.6), it would be preferable if future experiments made use of a fully automated apparatus which does not require experimenter handling.

Another procedural issue related to the environment within which the experiment was conducted. Zoo policy meant that the subject had to remain within the confines of its enclosure and could not be relocated to an indoor laboratory setting for the experiments (although they did take place in an off-exhibit area). The outdoor setting meant that there were distractions from a number of sources (e.g. birds, falling leaves, people walking near the enclosure, loud noises from zoo construction work etc.), although some attempt to ameliorate changes in environmental conditions was made by conducting the experiments at approximately the same time of day. On the other hand, it could also be argued that the more familiar naturalistic environment was less stressful and perhaps contributed to the echidna's ability to perform to the best of her ability (see section 6.4.1). In fact, some experiments have shown that animals perform better when they are tested in their home environments compared to remote testing chambers (see Crofts et al. 1999).

6.4.3 Modality

Despite the subject succeeding in the task, it could be argued that the modality was not optimal for an echidna. Thomas (1996) claims that the focus of a cognitive study should be on the processes involved rather than on specific tasks or apparatuses. Task variables, such as the stimuli, rewards, responses, environmental conditions etc. should be optimal for the species being studied so it is able to perform to the best of its ability. In this study, visual stimuli were used for reasons of practicality and species comparison. However, while many birds and mammals are considered visually dominant animals (Cook 2000), vision has historically been considered to be of little importance to the echidna (Elliot Smith 1902; Griffiths 1968; Walls 1942) and indeed evidence seems to indicate that it relies heavily on olfactory, auditory and tactile sensory information (Gates 1973) (see section 2.1.4). However, as discussed in section 2.1.4.1 and demonstrated in this experiment, anatomical and behavioural studies have shown that the echidna is capable of a reasonable level of visual acuity and discrimination. As the echidna appears to primarily use its other senses to forage, it raises the question of what use the echidna makes of its visual abilities or, in other words, why they have evolved.

One possibility suggested by Gates (1973) is that vision is used as a valuable supplement to the other senses in performing certain activities, as has also been suggested for the bat (Suthers, Chase and Braford 1969). In echidnas, vision might be used for activities such as predator detection, general orientation or locating food sources – particularly when those activities are conducted at greater distances than the range of its other senses. Vision might also be used when the echidna's other senses are being used for other tasks, such as using its vision for predator detection when its olfactory, tactile and auditory systems are involved in foraging and feeding (Gates 1973).

The idea of echidna vision being used for predator detection is supported by the anatomical structure of its eye. Its flat corneas, protruding eyes and lack of physical obstruction near its eyes would give the echidna a fairly panoramic view ideal for detecting predators (Gates 1973). As Gates (1973) pointed out in his study, echidnas are very sensitive to even slight movements in their vicinity and immediately assume a defensive posture.

If the echidna does in fact use its visual sense to supplement its other senses, it may help explain its ability to perform visual same/different categorisations. The sorts of visual activities proposed by Gates (1973) for the echidna – such as predator detection, orientation and location of distant food sources – would be greatly enhanced by the ability to efficiently categorise on the basis of *same* and *different*. There is also the possibility that the echidna utilises same/different categorisation in its dominant sensory modalities and that there is some level of cross-modal transfer of the ability to its subordinate visual sense.

This study adds further support to the argument that cognitive tasks, or at least same/different categorisation, is not limited to a species' dominant sense (Herman et al. 1989; see section 3.7.3.4). However, given that the echidna appears to rely more on its olfactory, auditory and tactile senses than its vision (Gates 1973, section 2.1.4), it might be beneficial to base a future study on one of its more dominant senses (see section 6.5).

6.4.4 Number of subjects

This study was originally designed to be conducted using four subjects instead of one. However, as discussed previously (see section 4.1.2.1), one subject became ill and two others were not used to being handled and became stressed both by handling and being in the apparatus. More extensive attempts to habituate them would have been prohibitively time consuming, as well as ethically questionable in a zoo setting, and the decision was made to continue with one subject. The single subject, Pitpa, was used to continual handling in her role as a demonstration animal for educating zoo visitors and did not appear stressed in the apparatus. Unfortunately, the zoo could not spare any more of their ‘tame’ echidnas for this experiment, as they were required for zoo activities.

While more than one subject would have been preferable, as discussed in section 1.5, these experiments were testing for the ability of a species to perform a particular task, a question that can be answered with a single subject (see section 4.1.2.2). Because of this it was decided to continue with one subject in a similar manner to other cognitive studies of this type (e.g. Pepperberg 1983, 1987, 1988; Roitblat et al. 1990; Schusterman and Kastak 1993, 1998; see section 4.1.2.2).

One issue with using only a single subject is the possibility of inter-individual differences with respect to task strategy (Chittka and Jensen 2011). For example, Elmore et al. (2009) found different methods being employed by pigeons in the same simultaneous same/different task, with evidence of item-specific learning by one pigeon and relational learning by two others. Similarly, while single-subject experiments can demonstrate a species’ capability, they do not provide any indication of how common an ability might be within that species. In this instance, it is impossible to determine where Pitpa falls in the normal spectrum of echidna capability. This study may not have mapped the full of range of an echidna’s ability, as other individuals may have been able to perform at a higher level. On the other hand, the use of a captive echidna, particularly one that has been raised in captivity, may mean Pitpa’s performance was exceptional (see section 6.4.5).

6.4.5 Use of captive subject

While the use of a ‘tame’ echidna facilitated the undertaking of this experiment, it also raises some questions about the generality of the results to wild echidnas. Pitpa is one of only a few echidnas born and raised in captivity (the vast majority of captive echidnas live some portion of their lives as wild animals, Augee et al. 2006) and has spent years being trained and interacting with humans in her role as a zoo demonstration animal.

According to Hyland (1993), thirty years of animal research on animals placed in novel and challenging (so-called ‘enriched’) environments has demonstrated a number of neural changes – increased cortical thickness and brain weight; altered cortical histology, neurophysiology and neurochemistry, and increased dendritic branching (reviews in Diamond 1988; Renner and Rosenzweig 1987; Rosenzweig and Bennett 1996; see also Hahn, Jensen and Dudek 1979). Rosenzweig (1971), for example, found experience-related effects increased the cortical volume of rats in the order of 5 to 10 per cent. Enriched animals have also been found to outperform their non-enriched counterparts on a variety of behavioural measures (Hyland 1993).

These results raise the question of whether Pitpa’s conditioning and the zoo environment in general constitute an ‘enriched’ environment which may have led to neurological ‘enhancements’ that contributed to her successful performance in these experiments. This is a difficult question to answer, particularly as some scientists take the opposite view. McGrew (1992) suggests that animals raised in captivity may have an impoverished existence compared to those in the wild, which may lead to more stereotypical, less complex behaviour and cognition. Indeed, it could be argued that a wild echidna would experience greater enrichment than a captive one, as it lives in a much bigger, more varied environment and deals with issues not experienced by captive animals, such as finding food and avoiding predators. In one of the few experiments directly comparing captive and wild animals in cognitive testing, Brodigan and Peterson (1976) found that wild-caught pigeons performed significantly better on a conditional discrimination task than domestic pigeons. The authors speculated the difference could be due to genetic or environmental factors, but stressed the need for further study.

Whether or not captivity constitutes an enriched environment, one advantage that Pitpa shares with other long-term experimental subjects as well as domestic animals is that she was very accustomed to training and handling (see section 4.1). According to Nicol (1996, p. 375): "... domestic animals often perform better on learning tasks than wild animals because they are less fearful." This may help explain Pitpa's faster task acquisition compared to that found in Gates' (1973, 1978) wild-caught echidnas which he struggled to habituate to handling, a problem also encountered in this experiment with captive, but non-handled, echidnas (see sections 4.1.2.1, 2.2.2.4 and 5.2.1).

Another issue is whether Pitpa, or indeed other seemingly high-performing individuals such as Alex the African Grey parrot (see section 3.7.3.4), are just particularly 'bright' or 'trainable' animals and not necessarily representative of the majority of their species. Differences in performance between individuals of the same species are often seen in cognitive studies. According to Keddy-Hector et al. (unpub.), "there is a tremendous amount of variation in the learning abilities of individuals" (p. 4). Sappington and Goldman (1994), for example, found a great degree of variation between the six horses used in their discrimination and concept learning experiments – from rapid and accurate responding up to the level of complex pattern categorisation to little learning beyond an initial black/white discrimination. Similarly, individual goldfish in Goldman and Shapiro's (1979) matching/oddity experiment showed variable results ranging from 57% to 88%. Individual variation in cognitive experiments has also been demonstrated in other species including pigeons, rats, sea lions, pigs, monkeys and chimpanzees (Keddy-Hector et al. unpub.) (see also D'Amato, Salmon and Colombo 1985; Elmore et al. 2009; Kastak and Schusterman 1994; Martin-Malivel and Fagot 2001).

One factor that could affect a particular individual's performance is age. Nissani, Hoefler-Nissani, Lay and Htun (2005) also found what they described as "remarkable variability" (p. 27) among the Asian elephants in their visual discrimination study – some elephants acquired the black/white discrimination in the first session after comparatively few trials, others took several sessions and hundreds of trials, while still others failed to learn the task by the end of the experiment. The variable performance correlated with the age of the subjects, with the older (but not elderly) elephants faring worse. The authors proposed the "age effect" may have been due to differing learning abilities between young and mature elephants or possibly due to a decline in the visual

acuity of captive adult elephants. In any case, Pitpa was still a relatively young animal when she participated in these experiments (see sections 2.1.5 and 4.1.1).

While these issues are relevant, they also apply to the numerous other cognitive studies undertaken with trained, captive animals (e.g. Gillan et al. 1981; Hanggi and Schusterman 1995; Herman et al. 1989; Pepperberg 1983, 1987). As discussed previously (section 4.1.2.2 and 6.4.4), the performance of this subject demonstrates that an echidna is capable of this cognitive performance. Whether that is reflected in the general wild population is a matter for further study (see section 6.5).

6.5 Further study

There are a number of avenues for further study resulting from this experiment. Firstly, independent replication is vital to ensure that some artefact of this experimental procedure, despite the precautions taken (see section 6.1.1), did not result in inadvertent cueing. In addition, further experimentation could help address some of the limitations of this study (see section 6.4). Testing this task with a variety of subjects; for example, multiple subjects, wild echidnas, echidnas of different ages and sex, would also help determine whether the ability is widespread among echidnas (see sections 6.4.4. and 6.4.5).

In terms of how the experiment is conducted, there is value to be had both in making the procedure more ‘artificial’ as well as more ‘natural’. A more controlled, laboratory setting would help reduce environmental cues and enable the elimination of experimenter handling (see section 6.4.2). It would also facilitate the investigation of the mechanisms underlying same/different categorisation in echidnas. Thompson summarised the state of research on relational categorisation in animals:

There is increasing evidence ... that animals categorise their world and do so on the basis of perceptual, if not abstract, relational similarity. On the one hand, investigators have developed standard procedures that permit them to map the nature and range of these concepts. On the other hand, they are sadly lacking in theory. Our understanding of the actual information controlling conceptual behaviour in animals lags far behind our ability to document categorical classes.

(Thompson 1995, p. 213)

Since Thompson's somewhat negative assessment, some progress has been made in experimentally examining the mechanisms by which pigeons and primates in particular perform same/different categorisations (see section 3.7.6). However, previously demonstrated examples of extra- and even intra-species variability in how such tasks are accomplished (see sections 3.7.3 and 3.7.6) suggest it would be fruitless to speculate whether such mechanisms might also apply to echidnas. Further research into the factors controlling the echidna's same/different discrimination would prove a valuable addition to this area of study (see below).

At the other end of the spectrum, conducting experiments designed to mimic naturalistic environments could also prove valuable (see section 6.4.1). Delius (1992) claims that increasing the ecological validity of traditional experimental procedures can lead to optimal learning, while Vaughan and Herrnstein (1987) suggest the use of experimental techniques that more closely resemble natural conditions could help illuminate how a task is applicable to an animal's wild behaviour. Some of these techniques could include the use of three-dimensional objects as stimuli (e.g. Burdyn and Thomas 1984; Spaet and Harlow 1943), the use of open-ended, polymorphous stimulus classes (e.g. Herrnstein and Loveland 1964), pitting qualitatively different reinforcers against each other (e.g. Hursh 1978) and allowing the subject to regulate the reserves of varying qualities of reinforcers (e.g. Collier and Rovee-Collier 1981; Lea 1982; Snyderman 1983a, 1983b) (see Vaughan and Herrnstein 1987). More challenging, but potentially equally valuable, would be to try and conduct experiments within an actual natural setting using natural stimuli.

As mentioned above, this study was conducted using visual stimuli despite it not being the echidna's dominant sense (see section 6.4.3). Another possible variation on this experiment would be to repeat the test using one or more of the echidna's more dominant senses – olfactory, auditory or tactile, or even its unusual electroreceptive abilities (see section 2.1.4.5). It would seem logical that the echidna would be more effective using one of these sensory modalities rather than its subordinate visual sense, although the results of experiments with other species (see section 6.4.3) suggest this may not necessarily be the case. Further investigation would be needed to test this theory. While there have been no cognitive experiments conducted on the echidna using olfactory or auditory stimuli, the fact that the echidna has demonstrated impressive

instrumental learning using visual/tactile stimuli is promising (Buchmann and Rhodes 1978; see section 2.2.2.4). Demonstrating same/different discrimination in a different modality would suggest that the task in echidnas is a generalised competence that is not modality specific and raises the possibility that this capacity is due to a single, higher-order abstraction mechanism (Cook and Brooks 2009). A related area of study would be to examine the echidna's ability to perform cross-modal same/different categorisation (see section 3.7.3.1). Echidnas have already displayed some level of cross-modal integration in the Buchmann and Rhodes (1978) experiment in which visual and tactile cues were used concurrently (see section 2.2.2.4).

Another possibility for further testing would be to perform the same/different task using more complex visual stimuli varying in colour, form and size (Thomas 1996). For example, while in this study the stimuli varied in form only, a more difficult scenario could be constructed by also varying colour and/or size across both the *same* and *different* stimuli in non-informative ways. The subject must then determine the relevant cue as well as performing the same/different task. These types of 'easy' and 'difficult' same/different problems have been tested in monkeys (Thomas and Frost 1983) and humans (Steirn and Thomas 1990). Of course, whether the colour variable could be used would depend on the extent to which the echidna possesses colour vision (see section 2.1.4.1). Until that issue is settled, perhaps variations in brightness levels could be used.

Despite the echidna's successful performance utilising the parameters of this experiment, it would be instructive to investigate how changing those parameters might affect the results. For example, there is evidence that methodological factors such as larger training sets, more icons per array and a greater number of training trials have led to a stronger performance in paired same/different tasks in other species (see sections 5.4.4 and 3.7.3). It would be interesting to see how any or all of these factors affected performance in the echidna. For example, reducing the number of stimulus elements from the four used in this study to the even lower-entropy two used in some other experiments (see sections 3.7.3.3 and 3.7.6.2.3) would be informative. If Pitpa (or another echidna) found the two-item task more difficult it would suggest that in this experiment Pitpa may have made use of entropy to perform the same/different task, a factor that has been demonstrated in other species such as pigeons, baboons and

monkeys (see section 3.7.6.2.3). If echidnas do use entropy, testing them with mixed, proportionally based *same* arrays would also provide information about whether they use a qualitative, rule-based approach (shown by selecting only very low entropy stimuli as *same* and everything else as *different*) or a quantitative, similarity-based method (shown by distinguishing small-disparity stimuli as *same* and large disparity stimuli as *different* (see sections 3.7.6.2.3 and 3.8.2.1).

Experiments could also be conducted to see if an echidna's same/difference performance was affected by changes to the physical characteristics of the stimulus arrays – if these changes had a detrimental effect on performance it would suggest the echidna's learning is strongly tied to the particulars of the training stimuli rather than using a more general same/different 'concept'. For example, varying the location of the items within the stimulus arrays (Castro and Wasserman 2010; Wasserman, Fagot and Young 2001; Young and Wasserman 1997) or rotating the stimulus items (Hollard and Delius 1982; Young and Wasserman 2001a) would help indicate whether some visual aspect of the stimulus arrangement was contributing to successful performance. Another possibility would be to vary the stimulus icons along a single dimension (Castro and Wasserman 2010). For example, would Pitpa still recognise a group of stimuli as *same* if they were the same in every respect except they differed in size? This would also help indicate how rigid the *same* classification is in echidnas. It could be argued that some level of flexibility would be adaptive because objects in the environment must be recognised under different conditions – e.g. lighting, angles and distances. (See Castro and Wasserman 2010; sections 3.7.4 and 3.7.6.2.2).

Wasserman et al. (1995) have also raised questions about the effect of permitting (e.g. Wasserman et al. 1995; Castro et al. 2010; this study) or prohibiting (e.g. Santiago and Wright 1984) training icons from appearing in both the *same* and *different* stimulus arrays. While including the same icons in both arrays reduces the possibility of item-specific cueing from individual shapes (see section 4.3.2), testing with non-repeating icons would negate the influence of item-specific memorisation on the learning process – which might either retard learning by removing that assistance or improve it by forcing the subject to rely only on relational cues. Studying the effects of any of the above types of experimental variables would be a productive avenue for further research in determining the processes behind the echidna's performance.

In addition, it would be interesting to study how an echidna performs in other variations of the same/different task (see section 3.7.3). For example, using a delayed matching-to-sample task (which would also allow for an examination of the echidna's working memory, e.g. Tavares and Tomaz 2002) or an oddity problem. An echidna could also be tested on conditional same/different using a conceptual conditional cue in the same manner as Burdyn and Thomas (1984) (see section 3.7.4). Another possibility would be to see if the echidna could master same/different categorisation using some variation of response keys or a go/no-go procedure to indicate whether items are the same or different (e.g. Edwards et al. 1983; Keddy-Hector et al. unpub.; Santiago and Wright 1984; Wright et al. 1984; Wright et al. 1983).

Finally, a valuable topic for future study would be to repeat these experiments with another monotreme, the platypus. Despite being members of the same taxonomic group, the platypus is thought to have evolved separately from the echidna for between 17 and 80 million years (see section 2.1.2), has a very different physiology and (semi-aquatic) ecology and does not possess the highly gyrified cerebral cortex or large frontal cortex of the echidna. It would be instructive in evolutionary terms to see whether the platypus could replicate the echidna's performance.

6.6 Conclusion

This study has contributed to the existing literature in a number of ways. Firstly, it has added to the very limited amount of information on the echidna's cognitive abilities, demonstrating for the first time that an echidna can perform a same/different categorisation using both unconditional and conditional discrimination procedures. This is of particular interest due to the echidna's unusual neurophysiology and unique evolutionary history, providing a valuable comparison case in animal cognition studies.

Secondly, it has added to the literature on same/different relational learning by expanding the number of species in which this ability has been found, as well as demonstrating for the first time that it has also evolved in monotremes. As Wasserman (1993b) points out: "Beyond rats, pigeons, monkeys, and apes, researchers know rather little about cognition in nonhuman animals. The field welcomes the systematic study of underrepresented species" (p. 222).

Thirdly, it adds to the general debate about animal ‘intelligence’. According to a hierarchical phylogenetic intelligence ranking, the echidna’s evolutionary history would place it squarely in the ‘primitive’ category. However this study shows it is capable of performing learning tasks more usually associated with more ‘highly evolved’ animals. This may be related to the relatively advanced nature of some aspects of the echidna’s neurophysiology – lending support to the argument that large, gyrified brains are associated with a greater degree of cognitive complexity and hence ‘intelligence’. Adding the echidna to the list of species that have demonstrated supposedly ‘advanced’ mental abilities has provided support for the argument that such abilities are more widespread than previously thought – either as generalised abilities or cognitive modules.

Finally, this study makes a contribution towards increasing the general understanding of the extent and variety of the mental capacity of animals. While this is important from a purely scientific standpoint, studies such as this also have far-reaching practical applications. It is important for the management and welfare of both domestic and captive wild animals to neither under- nor overestimate the mental abilities of animals, both in terms of providing appropriate and sufficient behavioural enrichment and in facilitating the implementation of effective training techniques. Both these factors would result in more successful husbandry and a reduced incidence of stress and unwanted behaviours. In terms of conservation, increased knowledge of the mental abilities of animals should assist in understanding the evolutionary niches required for the preservation of species.

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Appendix

SHORT-BEAKED ECHIDNA FOOD MIX

Low Fat Diet - December to June

Mincemeat (Beef)	4 kg
Wheatbran	500g
Eggs	19
Glucodin (Glucose supplement)	1716g
Olive Oil	336ml
Vitamin E Powder (Equine E)	47g
Calcium Carbonate	47g

Note: Soluvet is added on a daily basis when making up the above previously prepared mix. Currently is 4gr Soluvet to 495ml water and 540g of meat mix.