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Abstract

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Visual recognition memory across contexts

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Abstract

In two experiments, we investigated the development of representational flexibility in visual recognition memory during infancy using the Visual Paired Comparison (VPC) task. In Experiment 1, 6- and 9-month-old infants exhibited recognition when familiarization and test occurred in the same room, but showed no evidence of recognition when familiarization and test occurred in different rooms. In contrast, 12- and 18-month-old infants exhibited recognition irrespective of testing room. Thus, flexibility across a change of room was observed at a younger age than flexibility across a change of background has previously been seen with the VPC procedure (Robinson & Pascalis, 2004). To determine if limitations in representational flexibility across a change of background could be overcome by experiences during encoding, in Experiment 2, 6-, 9-, 12- and 18-month-old infants were familiarized with a picture on multiple backgrounds. At all ages, infants showed recognition across a change in background at test. These findings indicate that dissociating an item from its context during encoding may be an important factor in understanding the representational flexibility of visual recognition memory in infancy. Developmental changes in representational flexibility are likely driven by changes in the functional maturity of the hippocampal formation, and experience.

Recognizing a person or an object when they are encountered in a different context is essential to developing social relationships and knowledge of the physical world, and thus the effects of a change of 'context' (broadly defined as any feature that is not part of the 'to-be-remembered' information, or features that are irrelevant or not pertinent in a particular event or setting) on memory retrieval in infancy have been widely studied . Young infants encode a wide range of contextual information into their memory representations, including the background upon which an object is presented (e.g., Haaf, Lundy & Coldren, 1996; Robinson & Pascalis, 2004), the people who are present (e.g., Learmonth, Lamberth & Rovee-Collier, 2005), the room in which learning occurs (e.g., Bushnell, McCutcheon, Sinclair & Tweedlie ,1984; Hayne, Boniface & Barr, 2000), and the details of particularly distinctive visual features of their immediate environment (Butler & Rovee-Collier, 1989; Borovosky & Rovee-Collier, 1990). For very young infants the continued presence of this contextual information is critical to the retrieval of encoded information (for review see Rovee-Collier, Hayne & Colombo, 2001; Hayne, 2004). The ability to retrieve memories across a change in the contextual features encoded in memory has been characterized as 'representational flexibility' (e.g., de Haan, Mishkin, Baldeweg & Vharga-Khadem, 2006; Eichenbaum, 1997; Richmond & Nelson, 2007) and develops during the infancy period (for review see Jones & Herbert, 2006). In the mature brain, representational flexibility is thought to be a critical feature of memory representations encoded and retrieved through the hippocampus and its connections in the medial temporal lobe (MTL) memory system (Eichenbaum, 1997; Sauvage et al., 2008). Characterizing the emergence of representational flexibility may shed light on the functional maturation of this network of brain areas and on the development of specific forms of memory that are reliant on this network (de Haan et al., 2006).

Many authors have proposed that there is a qualitative division between two types of association formation, 'relational' and 'binding', that occur during the encoding of memory representations (e.g., Eichenbaum, Otto & Cohen, 1994; Moses & Ryan, 2006; Ryan & Cohen, 2004; Yonelinas, Kroll, Dobbins & Soltani, 1999). Associations encoded in terms of the relationship between an item and contextual features are known as relational representations and are thought to form the underlying basis of representational flexibility. In contrast, binding refers to representations which contain contextual features that are tightly bound, or fused together, with an item. Whilst relational representations are thought to be exclusively mediated by the hippocampus, bound representations can be supported by surrounding regions such as the perirhinal cortices (for review see Eichenbaum, Yonelinas and Ranganath, 2007). Crucially, whilst memory for an item can be easily retrieved in the absence of information with which it is relationally associated, it is theoretically harder to retrieve memory for an item in the absence of information with which it has been bound (Cohen, Poldrack & Eichenbaum, 1997).

The mechanism by which a contextual feature is linked in memory to a central item (binding or relational association) may determine the means through which that feature influences recognition memory. In dual-process models of recognition memory, recognition consists of familiarity and recollection (see Yonelinas, 2002 for review; see Squire, Wixted & Clark, 2007 for an alternative view). A feeling of 'familiarity' for an item indicates knowing that the item has been previously encountered, but does not necessarily include details of where, when or in what context. Recollection, in contrast, involves 'remembering' a range of details about the previous occasion upon which the item was encountered (Gardiner, 1988; Jacoby, 1991; Mandler 1980; Tulving, 1985). Whilst recollection is thought to act upon hippocampally-based representations that support flexible retrieval, familiarity is thought to act on extra-

hippocampal representations (see reviews by Aggleton & Brown, 1999; Diana, Yonelinas & Ranganath, 2007; Eichenbaum et al., 2007). In the mature brain, retrieval across a change in encoded contextual features thus appears to occur through recollective-based recognition memory, which acts on relational associations formed by the hippocampus and connected regions.

What is known about the development of this system? Whilst a large body of research has failed to support the traditional view that hippocampally-based memory systems do not become operational until late infancy or early childhood (for review see Rovee-Collier et al., 2001), it is clear that there are profound developmental changes in the operation and expression of the MTL memory system across the first years of life (for review see Richmond & Nelson, 2007). Reviewing these changes, Nelson (1995; see also Nelson, 2000) proposes that very young infants possess a ‘pre-declarative’ memory system that relies on the hippocampus and supports rudimentary novelty detection. Over the first year of life, this is proposed to mature into a more adult-like “declarative” memory system that involves both the hippocampus and its connections with areas in the frontal lobe, and that supports both episodic and semantic retrieval. Increases in representational flexibility may be a critical component of this developmental shift.

In order to examine developmental changes in representational flexibility in recognition memory, Robinson and Pascalis (2004) used a Visual Paired Comparison (VPC) task to explore the effect of a change of context on recognition memory for a central item with 6-, 12-, 18- and 24-month-old infants, where the contextual feature manipulated was the colored background upon which the item was presented. Infants were first familiarized with an item on a colored background, before being presented with the now-familiar item, and a novel item. When the familiarization and test sessions were conducted with the items presented on the same

background, all age groups showed evidence of recognition memory (demonstrated by a preference for looking at the novel item). However, when the items were presented on a background of a different color than that present during familiarization, only the 18- and 24-month-old infants showed evidence of recognition. A subsequent study by Pascalis, Hunkin, Bachevalier and Mayes (2009), who used this paradigm with an adult human amnesic patient (YR) with a discrete lesion of the hippocampus and a group of monkeys with neonatal hippocampal lesions, revealed that the hippocampus plays a central role in successful recognition across a change of background in this task. These results concur with the observation that familiarity-based recognition can be strongly influenced by a change of background (Ecker et al., 2007a,b), and with the theoretical perspective that information that is “bound” together with a target item will have a strong influence on retrieval (Cohen et al., 1997).

One interpretation of the failure of 6- and 12-month-old infants to exhibit recognition across a context change (Robinson & Pascalis, 2004) is that the hippocampus might be unable to support recognition in the VPC procedure in the first year of life, perhaps because of insufficient functional maturity. As in monkeys or adult humans with hippocampal lesions (Pascalis et al., 2009), the absence of representational flexibility could then be attributed to a reliance on familiarity-based memory representations only, which are easily disrupted by a context change. This proposition is, however, inconsistent with three key findings. First, the monkey literature indicates that the hippocampus is critical to novelty preferences after a delay of 1 minute or longer (Nemanic, Alvarado & Bachevalier, 2004), but infants show novelty preferences in a VPC paradigm after delays of 1 to 5 minutes in the first year of life (Jacobs, 2000; Fagan, 1977). Second, representational flexibility is observed in other paradigms in infants 12-months and younger. For example, in research with operant conditioning and deferred imitation paradigms,

infants exhibit representational flexibility across substantial contextual changes at 9- and 12-months of age (e.g., Hartshorn et al., 1998; Hayne et al., 2000; Klein & Meltzoff, 1999).

Although little is known about the neural basis of performance in the mobile task, there is evidence that memory retrieval in the deferred imitation task requires a degree of hippocampal involvement (Adlam, Vargha-Khardem, Mishkin, & de Haan, 2005; McDonough, Mandler, McKee & Squire, 1995). Third, Richmond and Nelson (2009) recently showed that 9-month-old infants are capable of forming relational representations between a face and a complex background in a visual recognition memory procedure. Thus, it seems unlikely Robinson and Pascalis' (2004) findings can be attributed to the onset of the hippocampal involvement in recognition memory after the first year of life. Rather, it is more likely that the developmental changes in representational flexibility observed reflect, at least in part, the proposed age-related changes that occur *within* the hippocampus (Nelson, 1995).

What is the nature of this change? As Robinson and Pascalis (2004) observe, one potential explanation for the apparent disparity in the representational flexibility of 12-month-old infants observed across paradigms likely stems from the type of context change that have been employed. Studies with the deferred imitation and operant conditioning paradigms have employed a change of environment or social context as the key variable (e.g. Hartshorn et al., 1998; Hayne et al., 2000; Klein & Meltzoff, 1999), whilst a change of immediate background has been employed in the VPC task (Robinson & Pacalis, 2004). Possibly, the proximity of contextual features to the to-be-recognized item influences the strength of the association formed between those contextual features and the central item. Indeed, in adults the proximity of a contextual feature to an item has clear effects on the magnitude of a subsequent context-shift effect, suggesting that stronger associations are formed between items and more proximate

contextual features in the mature brain (Dalton, 1993; Russo, Ward, Geurts, & Scheres, 1999).

Infants may find it even harder to dissociate an item from proximal contextual features such as its immediate background, reducing the flexibility of the item-context association in their memory representation. Development in the ability to separate an item from its context across the first year of life, potentially mediated by maturation of the hippocampus and its connections with neocortical association areas (Atallah, Frank & O'Reilly, 2004), may thus play a critical role in the development of representational flexibility.

In two experiments we address whether separating an item from its context in memory is important in the development of representational flexibility in infant visual recognition. Specifically, we examined whether the constraining effects of a change of context on infant visual recognition in the VPC paradigm could be alleviated by facilitating separation between the 'to-be-remembered' item and the manipulated contextual feature. In Experiment 1, a large physical separation was created between the central item and the manipulated contextual features by employing a change of room between encoding and retrieval, whilst leaving the immediate stimulus background unchanged. If the separability of an item from a particular contextual feature is an important determinant of early representational flexibility across a change in that contextual feature, recognition across a change in room should emerge prior to 18-months of age (the age at which recognition across a change of immediate stimulus background was observed in Robinson and Pascalis, 2004). The results of this first experiment, however, will not necessarily indicate if representational flexibility in early infancy is affected by the separation of the item and contextual features during *encoding*. Rather, it may be that proximate contextual features (such as the immediate stimulus background) provide stronger *retrieval* cues than distal contextual features (such as the room of testing), perhaps because the infant is more likely to

notice proximal cues during the test session. In order to examine whether the item-context relation during *encoding* is a constraining factor in visual recognition across a change in proximal contextual features like the immediate stimulus background (as in Robinson & Pascalis, 2004), Experiment 2 explored whether experience with an item on multiple immediate backgrounds during encoding would facilitate recognition of that item on a novel immediate background at test. If associations made during encoding are critical to the development of representational flexibility in infancy, presentation of an item on multiple backgrounds during familiarization should enable recognition of that item on a novel background before 18-months of age.

Experiment 1: Recognition memory across a room change

In Experiment 1, we assessed the influence of a change of global environment on visual recognition memory in 6-, 9-, 12- and 18-month-old infants. The experiment was conducted across two laboratory rooms which were both unfamiliar to the infant, ensuring that any contextual influence on memory resulted only from information encoded within the experimental setting. Testing occurred one minute after familiarization, a delay interval which did not exceed the retention abilities of the youngest age group tested in a VPC procedure with static stimuli (e.g., Diamond, 1995) and also provided sufficient time for the parent and infant to move locations in the Different Room condition.

. We predicted that if the type of contextual feature manipulated was a critical feature in determining the timescale of the emergence of representational flexibility across a change in that contextual feature in infancy, 12- and 18-month-old infants would recognize a stimulus across a change of environment, whilst 6- and 9-month-old infants would not. This would follow the

pattern seen in experiments with the deferred imitation and operant conditioning procedures.

However, if another factor (such as the task used to assess memory) is a critical feature in determining representational flexibility, only the 18-month-old infants should recognize an item across a change of environment. This would follow the pattern seen in Robinson and Pascalis (2004).

Participants

Twenty-four 6-month-old, 24 9-month-old, 24 12-month-old and 24 18-month-old infants were recruited from a database of infants born at the Jessops Maternity Ward of the Hallamshire Hospital, Sheffield. Each group contained equal numbers of male and female infants. Infants were tested within ten days of their 6-, 9-, 12- or 18-month birthday. No infant was born more than 3 weeks premature, and no infant had experienced birth complications. Testing was discontinued on 28 additional infants who were excessively fussy or cried during testing (n=10), failed to look at the test pictures for long enough (n=5), exhibited side bias during the test session (n= 10), or due to experimenter error (n=3). This 23% attrition rate is comparable to that observed in previous visual recognition memory studies employing static stimuli with infants of this age range (e.g. 22% - 43%, Haaf et al., 1996; 34%, Richmond & Nelson, 2009; 27%, Robinson & Pascalis, 2004). Infants were Caucasian (n=88), Asian (n=2) and Afro-Caribbean (n=6) and all were from families of moderate to high socio-economic status. The study was approved by the Department of Psychology ethical committee.

Apparatus and stimuli

Testing was conducted in two rooms located immediately next to each other, which served as the two contexts. One room was a large sound-proof chamber which had walls covered with dark blue material, and was dimly lit (Context A). The second room was a typical university room which had pale yellow walls and was brightly lit (Context B). In both rooms, infants were tested whilst seated on their parent's lap. Before testing commenced in each location, the lights in the rooms were turned off, rendering them equivalent in terms of illumination. In the first room, stimuli were back-projected onto a screen positioned 60cm in front of the infant. In the second room, stimuli were presented on a computer monitor positioned 60cm in front of the infant. In both rooms, infants' eye-movements were recorded with a camera positioned centrally above the location of the stimulus presentation.

The stimuli were color photographs of faces, approximately 15cm by 15cm in size. The faces were presented on a plain black background. Four different sets of faces were used to ensure the findings were not stimulus specific. Infants were randomly assigned to one of the four sets.

Procedure

Infants were randomly assigned to either the Same Room or the Different Room condition, with the constraint that within each age group there should be equal numbers of male and female infants in each group. After the study was explained and informed consent was obtained in a separate reception room, each infant participated in one VPC session, consisting of a familiarization and a test. The familiarization and test were separated by a one minute retention interval. Half the infants were familiarized in Context A and half the infants were familiarized in Context B. Infants in the Same Room condition received both familiarization and test sessions in

the same room. Infants in the Different Room condition were moved from one room to another during the retention interval, such that the familiarization and test sessions occurred in two different rooms. For infants in the Same Room condition, during the one minute retention interval the experimenter turned on the lights and interacted with parent and infant in the same way as for infants in the Different Room condition.

The familiarization session

During the familiarization session infants were presented with a single image until they had accumulated a fixed amount of looking time to the picture. To account for age-related changes in information processing speed, 6- and 9-month-old infants received 20 seconds of familiarization time while 12- and 18-month-old infants received 10 seconds of familiarization time, consistent with the procedure used by Robinson and Pascalis (2004). Fixation was assessed online by the experimenter, and confirmed offline from a video-recording of the infant's eye movements.

The test session

One minute after the familiarization session, infants were presented with two 5-second recognition tests in which the familiarization image was presented alongside a novel stimulus. In the second test, the lateral position of the images was reversed to prevent any subtle side bias from confounding novelty scores. The initial lateral positions of the stimuli were counterbalanced between infants. Infants' eye movements were recorded on a video for later analysis.

Results and Discussion

Looking times to the novel and familiar images were calculated offline by frame-by-frame analysis of the video recordings. A second observer coded 50% of the video recordings; inter-observer reliability was 96%.

Figure 1 shows the amount of time infants spent fixating on the novel image as a percentage of the total looking time during the test session. Preliminary analyses indicated that the picture set, the specific room in which the test session occurred (Room A or B) or the gender of the infant had no significant effect on novelty preferences, so the data was collapsed across these variables.

Insert Figure 1 about here

The effects of age (6, 9, 12 and 18 months) and condition (Same Room or Different Room) on novelty preferences across the two test periods were assessed using a two-way Analysis of Variance (ANOVA). There was a significant main effect of Age ($F(3, 95) = 3.96, p = 0.011$), indicating that with increasing age, overall novelty scores decreased. Post-hoc Tukey tests indicated that the 12- and 18-month-olds showed significantly smaller novelty preferences than the 6-month-olds ($p = 0.008$); no other groups significantly differed from each other. There was also a significant effect of Condition ($F(3, 95) = 38.57, p < 0.001$), indicating that infants in the Different Room condition fixated the novel stimulus for significantly less time than infants in the Same Room condition. The interaction effect did not reach significance ($F(3, 95) = 1.80, p = 0.15$).

Whilst an ANOVA reveals group differences, it does not indicate which groups of infants showed recognition memory. Recognition memory is evidenced by preferences that differ

significantly from chance. One sample t-tests were used to compare the percentage fixation to the novel stimulus to the chance level of responding (0.5). Infants in all age groups showed significant novelty preferences in the Same Room condition (6 month-olds: $t(11) = 12.26, p < 0.001$; 9 month-olds: $t(11) = 3.75, p = 0.003$; 12 month-olds: $t(11) = 2.50, p = 0.03$; 18-month-olds: $t(11) = 2.50, p = 0.03$). Novelty preferences are commonly taken to indicate recognition memory for the familiar stimulus. Thus, infants of all ages exhibited evidence of recognition memory for the familiar stimulus when testing occurred in the learning context (i.e. in the Same Room condition).

There were age-related differences in memory performance when infants were tested in a different room from where learning occurred. The looking patterns of 6- and 9-month-old infants in the Different Room condition was not significantly different from chance levels (6-month-olds: $t(11) = 1.21, p = 0.25$; 9-month-olds: $t(11) = 0.38, p = 0.71$). In contrast, 12- and 18-month-old infants showed a significant preference for looking at the familiar item (12-month-olds: $t(11) = 4.19, p = 0.02$; 18-month-olds: $t(11) = 3.93, p = 0.02$). Thus, older infants clearly discriminated between the familiar and novel items in a novel environment.

In contrast to the familiarity preference observed with 18-month-old infants after a room change in the present study, recognition was evidenced by a novelty preference when the same age-group was tested across a change of background by Robinson and Pascalis (2004). What can account for the different direction of the recognition response across these studies? Although interpretations of the direction of preferences (novelty or familiarity) remain controversial (for review see Houston-Price & Nakai, 2004; Pascalis & de Haan, 2001), familiarity preferences have been proposed to result from a weaker representation of the item, which the individual is motivated to update (Bahrick & Pickens, 1995; Richmond, Colombo & Hayne, 2007). For

example, Richmond et al. (2007) found that adults show a delay-related shift from a novelty to a familiarity preference in a VPC task that is coupled with lengthening reaction times in a forced-choice recognition task, supporting the contention that representational strength or accessibility may be a critical factor in preference direction. Possibly, 18-month-old infants have learned to more heavily weight in memory the location in which a person or object is experienced than its immediate background, leading to greater effects on memory when location is changed. Indeed, the similar novelty preferences observed in the Same Background (0.61) and Different Background (0.64) conditions for 18-month-olds tested by Robinson and Pascalis (2004) provides no evidence that the background upon which the item was presented was encoded by this age group. Directly comparing preferences for the familiar object presented on a novel versus familiar background would be one way to examine this proposal.

Alternatively, memory may be expressed as a familiarity preference when infants are tested in a novel room because the familiar item is now the more incongruous with the remainder of the testing environment. For example, 4-month-old rats prefer to explore a previously familiar object when first tested in a novel environment, but as the environment becomes familiar begin to preferentially explore a novel object (Sheldon, 1969). Encountering a familiar item in a new room may be more ‘unexpected’ than encountering a novel item in an unfamiliar room, thus driving a familiarity preference. A related possibility is that the relation between novelty and looking preferences is curvilinear in human infants, with moderate levels of discrepancy driving the strongest preferences (for a recent presentation of this argument, see Kagan, 2008). A novel item in a familiar room or a familiar item in a novel room may thus produce greater attention than a novel item in a novel room, or a familiar item in a familiar room, because only the former two conditions produce moderate levels of discrepancy from encoded information. A

background change may be insufficient to alter preference direction, since the majority of the environment remains consistent. Further work would be required to evaluate these possibilities, such as evaluating the effect of providing familiarization with the second testing room prior to the test session on preference direction.

Whilst null preferences observed at younger ages in the room change condition may not reflect complete forgetting (Courage & Howe, 1998, 2001), it indicates that we have no evidence that 6- and 9-month-old infants remembered the familiarization stimulus in the Different Room condition. It is unlikely that behavioral inhibition in the novel environment could account for these results, as there was no significant difference between the total time infants spent looking at the test pictures in the Same Room and Different Room conditions in these age-groups (for 6-month-olds, $t(22) = 0.03$, $p = 0.98$; for the 9-month-olds $t(22) = 1.18$, $p = 0.25$).

It is possible that physically changing location during the retention interval in the Different Room condition may have impaired memory performance at the younger ages, rather than the lack of congruency of contextual details at encoding and retrieval. Infants in the Same Room condition had, in contrast, remained seated in the same location throughout the session. To assess the possibility that leaving the room may have impacted on recognition memory, an additional group of 9-month-old infants (12 infants: 6 male, 6 female) were tested in a Room Disruption condition. In this condition, familiarization and test sessions occurred in the same room, but infants left the testing room during the 1-minute retention interval. Infants in this condition showed a significant novelty preference (mean novelty score = 0.56 (SE 0.02); $t(11) = 2.39$, $p = 0.038$) and there was no difference in performance between the Room Disruption and Same Room groups ($p > 0.05$). This result suggests that infants in the Room Change condition did not fail to recognize the test item because of events occurring during the retention interval.

Rather, the effect is more likely to be driven by the disparity in contextual information present at encoding and retrieval.

The results of the current study are consistent with research conducted with other memory procedures showing that by 12-months of age, infants are able to retrieve their memories across changes in global environment (e.g., Hartshorn et al., 1998; Hayne et al., 2000; Klein & Meltzoff, 1999). Thus, the late emergence of representational flexibility observed in Robinson and Pascalis (2004) likely reflects the way context was defined (as the background to the stimulus), rather than the task used to assess memory.

Why might a change of background create particular difficulty in generalization for 12-month-old infants? In the Introduction, we argued that the degree of separation between an item and a particular contextual feature during encoding may influence the representational flexibility infants demonstrate across a change in that contextual feature between learning and test. A distinctive background may be more difficult to separate in memory from the central item during encoding, such that the negative effect of a background change persists until later in development. If this is the case, helping infants to separate the item from its background by pairing the item with multiple backgrounds during familiarization should facilitate recognition of this item on a novel background. This proposal was the focus of Experiment 2.

Of note, it is important to recognize that there is an alternate way to characterize this issue. Specifically, a distinctive background may have a greater effect on recognition memory because infants interpret the background as a part of the central item, rather than as a proximal contextual feature. Indeed, data from the deferred imitation task indicate that changes to features of a central item have a more negative impact on memory than changes to (perhaps) more clearly contextual features such as the location of testing (Hayne et al., 2000). Do infants perceive an

item and its background holistically in a visual recognition memory procedure? Data from Haaf et al (1996) indicate that this is not the case: the authors show that 6-month-old infants treat an item and its background in a visual habituation procedure as “separable but interactive components” (Coldren & Haaf, 1999, page 132). Specifically, Haaf et al. (1996) demonstrated that a) habituation occurs more rapidly to the background than to a central item, and b) that multiple central items do not distract attention from a background pattern, whilst multiple backgrounds do distract attention from a central item. Given this, it is likely that the background of an item was appropriately characterized as a contextual feature by the authors of previous work in this area (Haaf et al., 1996; Coldren & Haaf, 1999; Robinson & Pascalis, 2004).

Experiment 2: Variability training

Providing young infants with the opportunity to experience a stimulus in multiple environments facilitates the flexibility of memory retrieval in the mobile conjugate reinforcement task (e.g., Amabile & Rovee-Collier, 1991; Boller & Rovee-Collier, 1992; Rovee-Collier & DuFault, 1991). For example, training 3- and 6-month-old infants to kick their foot to move a mobile in the presence of more than one crib liner enhances their responding in the presence of a novel crib liner (Amabile & Rovee-Collier, 1991; Rovee-Collier & DuFault, 1991), and mere exposure to the moving mobile in the presence of crib liner B after two training sessions with crib liner A enables infants to respond to the mobile in the presence of crib liner C 24-hours later (Boller & Rovee-Collier, 1992). However there has been little evidence for the effectiveness of this type of variability training using other memory procedures (e.g., Jones & Herbert, 2008). Thus, it is unclear whether the facilitative effects of variability training are a general principle of memory retrieval in infancy, or are specific to a particular type of paradigm or learning experience.

In the only previous study to provide variability training in a recognition memory procedure, Haaf et al. (1996) initially determined that presenting 6-month-old infants with a fixed familiarization period of 30 or 45-seconds resulted in background-dependent recognition. In a second experiment using an infant-control procedure (in which familiarization with a stimulus occurs until looking time decreases to a pre-set criterion), infants were familiarized with either the same background on each trial (no variability training), or a different background on each trial (variability training). Infants were then tested with the familiarization item on a novel background. In this experiment, infants who received variability training showed evidence of recognition memory for the familiarized item, but so did infants who did not receive variability training. This ceiling level of responding precludes assessment of the effects of variability training on representational flexibility. The critical test of the effect of variability training requires conditions in which infants do not show a novelty preference in the absence of variability training, such as those employed by Robinson and Pascalis (2004).

Robinson and Pascalis' (2004) research demonstrated that infants younger than 18-months fail to recognize a previously seen stimulus when it is presented on a new background. In the present study, infants saw one object appear on five different colored backgrounds during learning, for 5-seconds each. During the test, infants saw the familiarized object and a novel object on a background that was not presented during the learning phase. We predicted that if variability training is effective at promoting flexible recognition memory, infants should show recognition memory for the familiar item. However, if variability training is not effective, infants should show no preference for either item, following Robinson and Pascalis (2004) and Haaf et al. (1996). As in Experiment 1, we tested infants aged 6-, 9-, 12-, and 18-months of age

to determine whether there were age related changes in the effectiveness of this training procedure.

Participants

Twenty 6-month-old (7 male), 20 9-month-old (8 male), 20 12-month-old (8 male) and 20 18-month-old (11 male) infants were recruited from a database of infants born at the Jessops Maternity Ward of the Hallamshire Hospital, Sheffield. Infants were tested within ten days of their 6-, 9-, 12- or 18-month birthday. No infant was born more than 3 weeks premature, and no infant had experienced birth complications. Testing was discontinued on 23 additional infants (22% attrition rate) who were excessively fussy or cried during testing (n=9), failed to look at the test pictures for long enough (n=5), exhibited side bias during the test session (n= 7), or due to experimenter error (n=2). Infants were Caucasian (n=73), Asian (n=1), Afro-Caribbean (n=4) and mixed race (n=2) and all were from families of moderate to high socio-economic status. The study was approved by the Department of Psychology ethical committee.

Apparatus and Stimuli

Infants were tested while seated on their parent's lap in Context A from Experiment 1. Stimuli were back-projected onto a flat screen which was positioned 60cm in front of the infant. The infants' eye movements were recorded by a camera set centrally above the screen.

The stimuli were colored photographs of children's toys, each item measuring approximately 10cm by 10cm. They were sorted into pairs which were matched for size, brightness, and complexity and the items were shown on plain colored backgrounds. Colors used were red, blue, yellow, green, pink and white. Four complete stimuli sets were used to

ensure that any effects found were not due to characteristics of a specific stimulus item.

Procedure

Each infant participated in one VPC testing procedure, comprising of a familiarization session immediately followed by a test session.

Familiarization:

A single image was projected centrally onto the screen for 5 seconds whilst the infant was visually fixating on the object. Fixation was assessed online by a trained experimenter, and defined by the corneal reflection of the stimulus. The first familiarization trial was followed immediately by four other familiarization trials. All infants received the same amount of familiarization, irrespective of age. On each trial, the object was presented on a randomly chosen new colored background.

Test:

The familiarization was immediately followed by two 5-second recognition tests, during which the original stimulus was presented alongside a new one, on an unfamiliar color of background. In the second recognition test the lateral position of the images was reversed to prevent any subtle side bias from confounding novelty scores. Infants' eye movements were recorded on a video for later analysis. Looking times to the novel and familiar images were calculated offline by frame-by-frame analysis of the video recordings. A second observer coded 50% of the video recordings; inter-observer reliability was 96%.

Results and Discussion

Table 1 shows the amount of time infants spent fixating the novel image as a percentage of the total looking time during the test session. Preliminary analyses indicated that the picture set or the gender of the infant had no significant effect on novelty preferences, so the data was collapsed across these variables. A one-way ANOVA of novelty preferences by Age revealed no main effect ($F(2,79) = 0.69, p = 0.56$), indicating that preference strength did not differ between the age groups.

One sample t-tests were used to compare the percentage fixation to the novel item to the chance level of responding (50%). Infants in all age groups showed significant novelty preferences (6 month-olds: $t(19) = 2.58, p = 0.02$; 9 month-olds: $t(19) = 2.57, p = 0.019$; 12 month-olds: $t(19) = 4.59, p < 0.001$; 18-month-olds: $t(19) = 4.19, p < 0.001$), indicating recognition memory for the familiar item.

Insert Table 1 about here

Previous results from our laboratory indicate that when 6- and 12-month-old infants receive 20 seconds familiarization with an object, they subsequently fail to show evidence of recognition memory for that object when it is presented on a different background (Robinson & Pascalis, 2004). In the present study, when infants received 25 seconds of familiarization during which the object was presented on five different backgrounds, all age groups tested recognized the object when it was presented on a final, novel background. The slightly longer familiarization period is unlikely to have driven the present effects, as habituation to a central cue takes longer when it is presented on a constantly changing background than when it is presented on a constant

background (Haaf et al., 1996), and background-dependent recognition has been found with 30 and 45 seconds of familiarization time for 6-month-old infants (Haaf et al., 1996). Rather, it is likely that the variability training provided during the familiarization period was effective in facilitating background-independent recognition in the first year of life.

General Discussion

The present experiments revealed that infants exhibit representational flexibility across changes in distal contextual features in a visual recognition memory task by the age of 12-months (Experiment 1), and that reducing the strength of an association between an item and proximal contextual features during encoding facilitates representational flexibility in infant visual recognition memory between 6- to 18-months of age (Experiment 2). Previous research had indicated that item recognition may be strongly dependent on the immediate background upon which that item is presented until the age of 18-months (Robinson & Pascalis, 2004). The present study shows that contextual dependency is not only seen in reference to the immediate background of an item, but also includes the environment in which it is presented. However, both maturation and experience reduce the influence of a change of context on recognition in the infancy period. Notably, this is the first study to empirically demonstrate that experience of a stimulus on multiple backgrounds can be effective in promoting background-independent visual recognition memory after a brief period of passive exposure to an item across the infancy period. This complements and extends work with the mobile conjugate reinforcement paradigm showing that after active experience with a physical contingency, variability training can facilitate generalization to a novel environment (e.g. Amabile & Rovee-Collier, 1991; Rovee-Collier & DuFault, 1991), or to a novel mobile (Amabile & Rovee-Collier, 1991; Boller & Rovee-Collier,

1992; Fagen et al., 1984; Hayne, Rovee-Collier & Perris, 1987; Rovee-Collier, Borza, Adler & Boller, 1993).

Age-related changes in representational flexibility were observed in the present study between 9- and 12-months using a form of the VPC task that is thought to require integrity of the hippocampal formation (Nemanic et al., 2004). Critically, 12- and 18-month-old infants showed evidence of both contextual encoding and contextual flexibility in this procedure. This is central to the definition of representational flexibility as originally conceptualized (Eichenbaum, 1997), because it indicates that infants were able to retrieve a memory representation from a partial subset of its elements. Increases in representational flexibility at the end of the first year of life have also been found with the deferred imitation task (e.g. Hayne et al., 2000), and this consistency across paradigms is consistent with the proposal that both paradigms rely on the medial temporal lobe memory system (for review see Hayne, 2004; Richmond & Nelson, 2007). Further, research with humans and animals shows that incidentally-presented environmental contextual information, like the room in which participants are tested, is likely to exert an influence on memory through hippocampally-based processes in the mature brain (e.g., Mumby, Gaskin, Glenn, Schramek & Lehmann, 2002). Thus, the present findings are compatible with the proposition that gradual functional maturation of the hippocampus over the first years of life supports an increasing ability to form flexible or relational associations between items and their contexts, and that these representations support the gradual emergence of representational flexibility (e.g., de Haan, Mishkin, Baldeweg, & Vargha-Khardem, 2006; Hayne, 2004; Richmond & Nelson, 2007; Robinson & Pascalis, 2004). Indeed, the timescale over which change was observed in the current study is congruent with the 8- to 12-month shift from ‘pre-declarative’ to ‘declarative’ memory systems proposed by Nelson (1995), supporting the

proposal that changes in the structure of memory representations are likely a key feature of this shift.

The findings of Experiment 2 provide further indication that representations formed during encoding are vital in shaping representational flexibility at retrieval. When infants were provided with experiences during encoding that reduced the contingency between the central item and its background (variability training), representational flexibility across a change in background was facilitated. Notably, this was observed at all ages studied, indicating that the separability of an item and a contextual feature is important in determining the effect of a change of that contextual feature on recognition from at least 6- to 18-months of age. The effects of variability training have been widely documented with the mobile conjugate reinforcement paradigm with both 3- and 6-month-old infants (e.g. Amabile & Rovee-Collier, 1991; Boller & Rovee-Collier, 1992). However, under at least some conditions retrieval has been demonstrated in the mobile paradigm but not in a VPC procedure, despite equivalent learning periods (Gross, Hayne, Herbert & Sowerby, 2002; Wilk, Klein & Rovee-Collier, 2001). Thus, it is likely that the mobile task and the VPC procedure tap different types of recognition memory, or reflect the differential expression of recognition memory when tested through different output systems (leg kicking versus visual attention). The present demonstration that variability training is effective in the VPC task provides converging evidence that the relation between an item and particular contextual features during encoding has a pervasive effect on representational flexibility across a change in those contextual features in infant visual recognition.

The effects of 'variability training' may also explain the apparent disparity between the contextual specificity of infant recognition memory for novel stimuli, and infants' ability to recognize their mother in a variety of contexts from shortly after birth (e.g., Bartrip, Morton & de

Schonen, 2001; Bushnell, 2001; Bushnell, Sai & Mullin, 1989; Field, Cohen, Garcia & Greenberg, 1984; Pascalis, de Schonen, Morton, Fabre-Grenet & Dereulle, 1995). Although neonates clearly have very limited experience with their mother's face, the findings of Experiment 2 suggest that at least for older infants, a very brief period of variability training is sufficient to offset the negative impact of a context change on item recognition. If variability training is also effective for neonates, brief encounters with their mother in a range of contexts (for example, as the infant's position is shifted, the mother's face will appear against different backdrops) may facilitate the creation of an 'independent' representation of the mother's face, which can then be encoded and remembered with little influence from contextual variation (e.g., O'Reilly, 2001). Assessing the effectiveness of variability training in neonates would be a first-step towards evaluating this possibility.

With age (Experiment 1) or experience (Experiment 2), it appears that contextual features are less likely to be bound or fused with a target item and more likely to be encoded in flexible relational associations, reducing the impact of a context shift on retention. This may be related to increases in the strength of relational representations, as proposed by Richmond and Nelson (2009). Notably, these changes in representational composition would theoretically support the increasing use of recollective-based recognition memory for retrieval (Diana et al., 2007), although it is important to note that the contribution of recollection to infant VPC performance remains unclear. However, in conjunction with Robinson and Pascalis (2004), the present data suggests that factors such as the temporal or spatial separation between contextual features and the target item may influence the timescale over which representational flexibility is likely to be observed. Specifically, whilst 12-month-old infants showed flexible recognition memory across a change of room in the present study, they did not show flexible recognition across a change of

background in Robinson and Pascalis (2004). Infants may develop the ability to generalize across an environment change earlier than the ability to generalize across a change of background because aspects of the global environment are easier to separate from a central item than a proximal background, and are thus likely to be more flexibly associated with that item. In contrast to the background of an item, the global environment is both spatially distal and temporally non-contingent with the target item (since the global environment is present both before and after the item is seen), and a long history of associative learning research indicates that either factor would likely reduce the strength of context-item associations (e.g. Buehner, 2005; Chamizo, Manteiga, Rodrigo & Mackintosh, 2006; Wagner, 1981). Indeed, when, in Experiment 2, infants were provided with experiences during encoding that reduce the contingency between an object and its background (variability training), representational flexibility was facilitated (for similar findings in operant conditioning studies see Amabile & Rovee-Collier, 1991; Boller & Rovee-Collier, 1992). Examining retrieval across different context changes in a within-infant longitudinal study would be an important next step in evaluating the role of object-context associations in the development of representational flexibility.

Although the present study focused on how experiences during encoding influence representational flexibility in infant visual recognition memory, it is also likely that there are other influential variables that act after the encoding period. For example, it is clear that the interval over which retention is assessed can impact the degree to which infants exhibit flexible memory in the mobile task and that the nature of the effect may change with age: representational flexibility across a change in a distinctive crib liner is more limited over longer versus shorter retention intervals for 3-month-old infants (Butler & Rovee-Collier, 1989; Rovee-

Collier, Griesler & Earley, 1985), but shows a U-shaped function of decreased flexibility both at the beginning and end of the forgetting curve in 6-month-old infants (Borovsky & Rovee-Collier, 1990). Changes in representational flexibility with retention interval are also apparent in human adults tested with a VPC procedure: Richmond et al (2004) found that the effects of a change of room on recognition are apparent over a 2-week retention interval, but not with a 3-minute retention interval. However, the effect of retention interval on representational flexibility in the VPC procedure with infants is unknown. Exploring how representational flexibility in recognition memory across different contextual changes varies with retention interval in infancy is thus an important topic for further work.

Conclusively linking developments in representational flexibility to specific brain regions such as the hippocampus will also require further investigation. Although analogies with procedures that appear hippocampally-dependent in primates or human adults is suggestive of the anatomical basis of performance in human infancy, it is also possible that performance in human infancy is subserved by different brain regions. Intriguingly, in rats the formation of context-object associations depends on different regions of the medial temporal lobe when context is defined as features of a testing box versus the presence of a second background object (Norman & Eacott, 2005), raising the possibility that the development of representational flexibility across different contextual changes involves the development of subtly different networks of brain regions. Longitudinal studies of structural and functional brain development, coupled with behavioral measures of flexibility that manipulate multiple contextual parameters, may begin to address the neuroanatomical regions that are central to the development of representational flexibility in infancy. Additionally, changing the parameters of existing computational models of brain function (e.g., Atallah et al., 2004; Norman & O'Reilly, 2003) in

order to test hypothesis about memory functions in development may also be a strategy for further research. Further, the implications of dual-process models of recognition memory for infant memory development have yet to be widely discussed, and further work is required to evaluate the characteristics of recollection and familiarity in the infancy period. Research techniques developed with nonverbal animals that have distinguished recollection from familiarity (e.g., Eacott & Easton, 2007) and ERP paradigms used to distinguish recollection and familiarity in adulthood (reviewed by Curran, Tepe & Piatt, 2006; Friedman & Johnson, 2000; Rugg & Yonelinas, 2003) may be useful in providing converging evidence in this area.

In summary, it appears that the ease with which a contextual feature can be dissociated from an item strongly influences representational flexibility in the infancy period. Experience within the experiment, experiences outside the experiment, and the maturation of the hippocampus and its connections are all likely to play a role in the flexibility of recognition memory in the first two years of life. Gradual changes in representational flexibility across development may stem from age or experience-related improvements in the dissociation of items from their contexts, and this process may be an important factor in the development of 'declarative' memory.

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Table 1.

Novelty preferences in Experiment 2, in which context-dependent recognition was tested after a period of variability training.

	6-month-olds	9-month-olds	12-month-olds	18-month-olds
Mean novelty preference	0.59	0.59	0.64	0.60
Standard Error	0.035	0.034	0.029	0.026

Figure caption

Figure 1

The effect of a change in place context on preferences in the VPC: Only 12- and 18-month-old infants show evidence of recognition memory in the Different Context condition. An asterisk indicates preferences were significantly different from chance ($p < 0.05$), which is indicated by the horizontal line. Error bars indicate ± 1 SE.

Figure 1