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Abstract
This paper briefly considers the broad social and scientific background to research into the possibility of insects experiencing pain sensations analogous to our own. There has been increasing use of insects in pain experiments generally, as ethical constraints on the use of other animals increased through the last century. The ways in which scientists have tackled the question of insect pain, particularly in trying to distinguish between nociception and pain are then selectively summarised. These include opioid, hormonal, evolutionary, neurophysiological and behavioural approaches, as well as experiments designed to elucidate the difficult area of insect consciousness, from the 1980s to the present.

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In the early 1980s I took two courses in Entomology at the University of Queensland. The broad assumption then was that, although we could not be certain, insects probably did not experience pain. The thinking was quasi-Cartesian: insects were automata where noxious or physically negative stimuli were concerned – programmed to recoil, certainly, but this recoil was purely reflexive and did not involve any physical, or obviously, psychological, pain. In 1914 Harry Weiss had tentatively raised the question of insect pain without ruling the possibility out; but not a great deal of scientific inquiry into the subject had been undertaken. What work there was cast doubt on the possibility that insects might experience pain on anatomical, physiological and behavioural grounds. These findings were usually associated – directly or indirectly, with a normative classificatory bias. In the primary division between animals, the invertebrates, animals without backbones, were far simpler creatures than the vertebrates – i.e. with backbones. The assumption of invertebrate simplicity thus consciously or unconsciously militated against the expectation of something as complex as pain experience (based on what was known about humans and some other mammals) in invertebrate groups such as those of the class Insecta.

Although wary of lapsing into anthropomorphism, I was not entirely convinced. I felt that even if insects did not experience pain as we did, they must still be aware of a radical 'wrongness,' a fundamental disorientation akin perhaps to human dementia, or a loss of an unselfconscious-being-in-the world, only vaguely analogous to the way in which injury, old age, the threat of sudden annihilation precipitate our passage out of our everyday taken-for-granted being into a bodily awareness that is isolating and unpleasant in itself, even without accompanying pain. But any experiment designed to test pain hypotheses in insects did, of course, involve inflicting pain on them should they in fact experience it – and this I was reluctant, as well as ill-equipped, to do.

Even today, the physiological and psychological mechanisms of pain experience in humans remain enigmatic, so it is not surprising that even less was known about pain neurophysiology in either group in the 1980s. Insect behaviours in the face of life threatening or what we would find as grotesquely painful injuries could often seem analogous with our own; but that assumption smacked of a misguided, if not deluded, anthropomorphism. In support of the opposite view that relatively primitive neurophysiology in insects could not include pain reactions, scientists also turned to insect behaviours.

In 1984 C.H. Eisemann et al. published what would become over the next couple of decades, a very influential article on this question. Though they concluded their findings with Wigglesworth's[1] caution that insect pain could not be entirely disproven, they attributed to insects 'purely reflexive or "wired-in" responses' with 'largely pre-programmed behaviour patterns and limited learning capacity'(Eisemann et al.165). Invertebrates in general they noted, had, relative to vertebrates, 'fewer neurones' and far less complex nervous systems (Eisemann et al.166). Investigation of insect pharmacology had detected the presence of endogenous opioids (built-in pain ameliorators/suppressors) but opioids are associated with other functions in animal bodies, so their possession was by no means conclusive. Qualified as it was, their conclusion that insects did not suffer pain drew primarily on behaviour. They noted that, for example:

> An insect walking with a crushed tarsus [limb]... will continue applying it to the substrate with undiminished force... A locust continued to feed whilst being eaten by a mantis; a tse-tse fly which flew in to feed although half-dissected; caterpillars which continue to feed whilst tachinid larvae bore into them; many insects which go about their normal life [sic] while being eaten by internal parasitoids; and male mantis which continue to mate while they are being eaten by their partners (Eisemann et al.166).

Eisemann et al. concluded that while such examples do not prove unequivocally that insects do not feel pain, they 'strongly suggest that if a pain sense is present, it does not have any adaptive influence on behaviour' and hence 'insect neurobiology does not involve a "pain" sub-programme' (166).

Much has changed since the early 1980s in both invertebrate and vertebrate pain research, with interest in the neurophysiology of the human brain (and human pain control) increasing

1. Wigglesworth, V.B. (1980) recommends that insects have their nervous systems inactivated before pain experiments are conducted on them, even though so far no proof of their experiencing pain has been found.

exponentially over the last twenty to thirty years. There has also been increasing interest in the possibility of pain presence and its mechanisms in the Insecta, both in terms of direct curiosity about insects themselves, but also because of what we might learn about ourselves from experiments on them. I turn to the particulars of a small sample of this research later in the paper, but it is first important to consider the social 'background noise' against which biological research takes place.

Science gains its place as the primary interpreter of life in this world for us because of its adherence to the principles (and practice) of apparent objectivity. Its current authority in the West and western-influenced countries derives from its unequivocal rejection of a subjective approach to matter and being. For Biology and Zoology in particular, this has meant, at least until very recently, an outright rejection of anything that smacks of anthropomorphism. Were we to judge animal form and behaviour by our own, science taught, we do non-human animals a disservice in failing to regard them (and thus understand them), as very different creatures; and secondly, and even more significantly, we would be likely to fall into gross errors in our conclusions, since their structures and modes of living are so radically different from our own. While regarding anthropomorphism, then, as anathema, science nevertheless takes place within human society. Further, the West is by no means alone in its assumption of anthropocentrism, that is, that humans are the apex of biological development and their interests – be they occupational, financial, survivalist – necessarily trump those of all other species. (Arguments for the preservation of biodiversity, for instance, can often rely on our preference for a world of variation, and our still shamefully weak attempts to halt climate change ultimately privilege ourselves as well).

While anthropocentrism is more or less unconsciously accepted in the societies out of which scientists work, anthropomorphism has usually been rejected. But the rise of ecological thinking and even evolutionary biology (with its constant reminder of our connections to other species in the recapitulation of phylogeny in our own ontogeny) suggest ways of conceiving the world which make anthropomorphism seem a less outrageous proposition, certainly in relation to other mammals. Moreover, the unexpectedly high percentages of DNA all animals share also suggests that science may have been too quick to dismiss anthropomorphism at least if judiciously applied.

As ethics replaced religion in the West during the twentieth century as arbiter of rules governing human behaviour, various ironies in the relationships between humans and animals, ethics and animal experimentation and anthropocentrism and anthropomorphism have begun – or are beginning to – emerge. These various shifts, broad as they are, have had a marked impact on the interest in and understanding of the nature and possibility of insect pain.

Although objections to in vivo experiments on animals – including other primates and mammals - gained purchase only in the late nineteenth century, there had always been minority voices speaking against it. Most of these experiments were not undertaken in the interests of the animals concerned but for the understanding and thus betterment of the human condition. But there was always an unperceived or deliberately unacknowledged irony. As the American Veterinary Association belatedly acknowledges, if we can use animals to tell us about ourselves, then the reverse must also hold true. Or as philosopher Bernard Rollin puts the question slightly differently:

> One can well believe that only by thinking of animal pain in terms of Cartesian, mechanical processes devoid of an experiential, morally relevant dimension, could scientists have done the experimental work which has created the neurophysiology we have today. But given that science, the neurophysiological analogies that have been discovered between humans and animals … are powerful arguments against the Cartesianism which made it possible. In a dialectical irony which would have pleased Hegel, Cartesianism has been its own undoing by demonstrating more and more identical neurophysiological mechanisms in humans and animals, mechanisms which make it highly implausible that animals are machines if we are not (Rollin 86).

Although Rollin is here referring to Vertebrates in particular, the irony to which he draws attention can potentially apply to Invertebrates. As ethical constraints on live and/or unanaesthetised animal experimentation have been formalised as laws (at least in some countries), these constraints have also moved from Primates to mammals (with the exception, of those perpetual experimental victims, rats and mice) and even octopi – insects (and spiders) have become experimental subjects.[2] And just as the keeping of octopi for experimentation and the experiments themselves revealed human/octopus analogies, so too have insect/human analogies, particularly in the area of pain experience, gained increasing credence. As we learn about human pain from crickets, spiders or fruit flies, we begin to credit the possibility that they too might indeed experience pain. Insects are now the subject of neurophysiological, pharmacological, evolutionary and behavioural experiments designed either to reveal the nature of pain in general – in humans, or in the insects themselves.

The physiological and psychological processes involved in experiencing pain is one of the hardest subjects for science to tackle. Pain has always been, and to a degree remains, enigmatic in humans, let alone in the Insecta. The primary difficulty, of course, is that pain experience is not even species specific but is in fact personal and subjective. This means that science, with its mantra of objectivity, seems ill-placed at the outset to investigate a subjective condition as fugitive as pain experience. Weiss, in his work published in 1914, was not the first scientist to raise the issue of potential pain in insects as well as the difficulties inherent in such inquiry, but he set out a number of pertinent questions: 'How does one distinguish between what is "painful" and what is "unpleasant" in our own species? What constitutes a symptom of pain in Insects? Who is qualified to judge? Can we assume insects feel no pain because they exhibit no signs of suffering?' After all, he notes, many humans who are suffering pain 'go about their duties without exhibiting any signs of pain other than changes in facial expression' (Weiss 270).

One hundred years later, many of these questions remain unanswered, even for humans where we know that the combined effects of physical and psychological/emotional factors complicate the understanding and treatment of pain. In insects it has proven difficult to distinguish between 'pain' and what is termed 'nociception'. Martin Kavaliers (1988) quotes Sherrington (1906) in explaining the term 'nociception'. It is characteristic of all animals to respond to negative stimuli, and 'this capability of animals to detect and react to stimuli that may compromise their

2. Spiders are not insects as such, but they are often considered so closely aligned as to shed equal light on insect behaviour, neurotransmission [2]etc.

integrity is embodied in the term "nociception".' But aversive reactions to such noxious stimuli may be purely reflexive or, alternatively, conscious, with the latter implying the potential or actuality of pain feelings, while the former – the reflexive – does not. Thus the simple presence of nociceptors and/or nociceptor-responsive behaviours does not necessarily involve pain sensations. As Kavaliers also explains, it is difficult for human observers to interpret animal behaviours objectively. 'Descriptions of postures, movements and vocalisations that are associated with nociception can be quantitative and objective, but *interpretations* . . . are in words with connotations of human experience' (emphasis added). He cautions that 'too often scientists working with non-human animals considered 'nociception' and 'pain' as equivalent' (Kavaliers 923). Quoting Merskey's definition of pain as 'an unpleasant sensory and emotional experience associated with either actual or potential tissue damage, or described in terms of such', Kavaliers distinguishes it from the nociceptive behaviours of all animals, primarily, it would seem, through its emotional component and thus the question of insect consciousness.

Few investigators today– whether scientists or philosophers –would argue against pain experience in mammals or vertebrates more generally. And although in-vivo eye/brain experiments continue on Cephalopods in many countries, most researchers would be wary of ruling out pain experience – even including its conscious component – in the invertebrate octopus. Kavaliers quotes the Eisemann article as a reasonably authoritative one, but he does note, citing Bodman (1986), that 'some insects have been proposed to display hormonally-mediated responses to stressful environmental conditions; responses which, in certain respects, appear similar to the hormonally-mediated stress responses in mammals' (Kavaliers 925). These hormonal responses would certainly indicate a complex neurophysiological pathway from nociceptor to nerve centre to catalysing hormonal secretions, but would again not necessarily provide firm evidence of pain. It might, however, be indicative, in its similarity to human hormones, of an evolutionary continuation (across the vertebrate/invertebrate 'divide') of mechanisms – chemical as well as neurophysiological – that might include pain registration as a response to injurious stimuli. Thomas Eisner & Scott Camazine's work (1983) on spider leg autotomy (the shedding of a limb to avoid more lethal damage) in Argiope spp. is also of interest here, since 'the sensing mechanisms whereby spiders detect harmful venom' – injected by prey – 'may be fundamentally similar to the mechanisms in humans that are coupled with the perception of pain' (Eisner and Camazine 25).

But such suggestive findings remained inconclusive, failing to rule out the possibility of pain, but not unequivocally demonstrating its presence either. Over the next thirty years different approaches were adopted, some directly concerned with pain in insects, but many more investigating the nature of pain in general, particularly as this might be useful in its application to humans. Hari Manev and Nikola Dimitrijevic (2005) explain why insects have become so important to pain researchers:

> Because pain can predict tissue damage by noxious stimuli it appears to be a sensation common to complex living systems. Furthermore, it appears that different species use common mechanisms of temperature and pain sensation or perception. Because reducing pain is a human activity that typically requires pharmacological interventions, in-vivo experimentation appears to be the only methodology that can lead to successful discovery of new analgesics. This type of research is bound by ethical concerns and most commonly relies on in-vivo mammalian models (de Bars et al 2001). However, no serious ethical controversies have arisen regarding in-vivo experiments on insects.

Thus it appears that for the time being a Drosophila [fruit fly] model for screening putative analgesics and characterisation of antinoceptive mechanisms and novel drug targets would be advantageous (Manev and Dimitrijevic 2404).

From this, one can see that the literature on the ethics of animal experimentation has itself burgeoned in philosophical and animal welfare circles, though only very recently bringing with it any ethical questions about insects and insect pain. Interestingly, Manev & Dimitrijevic, summarising previous work on Drosophila in terms of memory and learning conclude that: 'These studies clearly point out the complexity of Drosophila behaviour and suggest that [fruit] flies are sufficiently complex organisms and can be used in pain research' (2406). As far as other scientists were concerned, however, a broad claim of insect 'complexity' did not necessarily imply insect pain. Many scientists certainly continued, through the 1990s, to disagree with its presence and/or likelihood.

In their attempts to apply objective methodologies and to assess results objectively, scientists sought proof in a number of ways: First, the presence (or lack thereof), of endogenous opioids in insects together with exogenous opioid experimentation with morphine (as pain ameliorator/suppressor and nociceptor inhibitor) i.e. the antinociceptor effect; second, neurological complexity in terms of both ganglionic and brain function demonstrated through learning and memory experiments especially as applied to nociception and the vexed question of the nature of consciousness; and third, evolutionary continuation of hormonal and molecular responses across the vertebrate/invertebrate divide.

Drosophila melanogaster has long been an experimental favourite in genetic research. Its recruitment to pain studies is relatively recent but has obviously been facilitated by its long history as an experimental subject. In order to determine 'a pain condition in animals, in addition to a response to … noxious stimuli e.g. heat, one has to demonstrate the capacity of an *antinociceptive* procedure treatment that can attenuate this response'(emphasis added, (Manev and Dimitrijevic). In 2003 Daniel Tracey et al. isolated a mutant gene in Drosophila (which they rather confusingly dubbed 'painless') that could be used to demonstrate antinociceptive responses consistent with pain experience in Drosophila and Drosophila larvae. Their interest was in broader pain investigation, with their results published in *Cell*. Zabala and Gomez (1991) had already used the cricket (Pteronemobius sp) to test morphine analgesia, tolerance and addiction in insects. The presence of endogenous opioids in insects had already been demonstrated but since opioids can have a number of functions aside from pain amelioration, their particular effect as a pain suppressor in insects remained unproven. However, 'the same antinociceptive behavioural effects' as those reported in vertebrates, had already also been observed in some invertebrates … 'like the honey bee, praying mantis and crickets' (Zabala and Gomez). Zabala and Gomez used a previously untried methodology to effectively demonstrate pain suppression through morphine analgesia in Pteronemoibus. Continuing work on the role of endogenous opiods, V.E. Dyakonova (2001) pursued a more evolutionary approach, arguing that 'comparative data indicate that the most conservative and ancient function of opioids is control of an adequate level of protective reactions' (Dyakonova 253) and that other functions have been added in the course of evolution, such as 'stress-induced analgesia, regulation of feeding and mating behaviour and aggression'. They further suggested that 'the main events in the formation of functions of the endogenous opioid system occurred in the lower invertebrates', though 'these had been the least studied' (Dyakonova 253).

Focussing on pain in insects per se, Ayse Yarali et al. in *Animal Behaviour* (2008) again used Drosophila in experiments in pain relief learning – using odours before and after electric shock – to demonstrate that Drosophila experienced pain and 'that "relief learning" showed that in terms of *psychological* [my italics] mechanisms it established genuinely associative conditioned approach behaviour' (Yarali et al. 1173). Gregory Neely et al. (2011) – again using thermal nociception in Drosophila – isolated a gene, 'TrpA1' as a 'bona fide "pain" gene in both adult and larval fly nociception paradigms'. All genes require expression in animal bodies and Neely's group were able to demonstrate 'its expression within the Drosophila nervous system, specifically within multi-dendritic (md) sensory neurones'. Therefore, they concluded, 'our analysis identifies the channel TRPA1 as a conserved regulator of nociception'. Both endogenous opioid presence and morphine-induced analgesia thus seemed to demonstrate, for many scientists, pain experience in insects who, it seemed evinced responses to analgesic effects not unlike our own. But many scientists still felt that a presumed lack of consciousness in the Insecta necessarily militated against this possibility. Text books are by definition more conservative than investigative research, and in *Neuroscience – From Molecule to Behaviour* (2013) published by the reputable Verlag Press in Heidelberg, Maria P. Abbracchio and Angelo M. Reggiani concluded that in addition to humans, 'the only animals capable of feeling pain are those that can feel emotions such as fear, anxiety, distress' (445). All vertebrates show 'typical signs of pain' while 'the balance of evidence suggests that most invertebrates do not'. For Abbracchio and Reggiani the capacity to experience emotion is inseparable from the experience of pain, and 'only the brain recognises and gives "meaning" to the pain messages, while the "mind" evaluates how bad the pain is' (Abbracchio and Reggiani 446). Invertebrates as a whole, for these researchers, thus lacked the brain capacity/complexity to both experience emotion and evaluate injury.

Brain/neurological complexity in invertebrates as a whole and the Insecta in particular is at issue here. But well before 2013, a number of scientists had identified various cognitive and often complex abilities and behaviours in insects. Though cognition and consciousness are not considered identical, they have been closely related in terms of the investigation of insect neurophysiology. But 'identifying hallmarks of consciousness' is, as David B. Edelman et al. (2004) point out, a particularly difficult task in non-mammalian species. 'More creative means', they suggest, 'must be developed for eliciting behaviours consistent with consciousness'.

Strategies available for 'amassing evidence for consciousness in non-human species include searching for evolutionary homologies in anatomical substrates and measurement and physiological correlates of conscious states' (Edelman et al. 180). The potential for evolutionary development/continuity across the vertebrate/invertebrate divide is an interesting one and one raised not only by the neurobiologists, but, as noted above, in opioid/analgesic studies as well.

For Abbracchio and Reggiani in their 2013 textbook, vertebrate/invertebrate classification still tended to dominate thinking about the Insecta, coupled, as always, with conscious or unconscious assumptions about complexity (us and our relatives) and simplicity – the Insecta. A 2014 textbook specifically on insects, however, while leaving the question of pain experience open, notes that 'insect behaviour can be complex, involving integration of neural information within the ganglia' and that 'insect neurones release a variety of chemicals at synapses to both stimulate or inhibit effector neurones or muscles. Important neurotransmitters include acetylcholine … and dopamine as in vertebrates' (Gullan 64).

Animal welfare proponents and philosophers have also been aware, of course, of the difficulties of proving unequivocally that insects experience pain sensations comparable to ours. As Jane A. Smith (1991) states, 'the further we move away from the mammalian plan, the more difficult it becomes to infer pain in other species' (Smith 25). There are, she notes, no 'easy answers' to the difficult question of assessing pain in invertebrates given its 'subjective nature' and it is unlikely 'that any clear cut definitive criteria will ever be found to decide the question'. C.M. Sherwin in *Animal Welfare* (2001) investigates, from a philosophical perspective, the robustness – or otherwise – of 'argument by analogy'. Because suffering is a 'negative mental state – a private experience – …it cannot be measured directly'. Although we may now know that 'invertebrates such as cockroaches, flies and slugs have short and long-term memory' it does not prove they suffer pain although 'invertebrates openly behave in a strikingly analogous manner to vertebrates' and therefore 'the similarity of these responses may indicate a level of consciousness not normally attributed to invertebrates'. For Sherwin this indicates that 'we should either be more cautious when using argument by analogy or remain open minded to the possibility that invertebrates are capable of suffering in a similar way to vertebrates' (Sherwin 115).

Jennifer Mather approaches the subject through both a history of standard animal classifications – those which, like the Scala Naturae or the vertebrate/invertebrate distinction imply judgements of simplicity and complexity. Classification itself also tends to emphasise differences rather than similarities, competition rather than cooperation. Mather also gives a summary of the standard philosophical approaches to human – nonhuman animal relations from the contractarian to rights based perspectives. In conclusion, she writes:

> Although theorists have not necessarily thought specifically of invertebrates in postulating humans' attitudes towards animals, human attitudes are important to the welfare of these (and all) animals. Contractarian theorists value our humanness in caring about animals, utilitarians consider the importance of the 99% of animals that invertebrates represent, and rights theorists' concentration on animals' essential needs is useful/or enriching the everyday lives of invertebrates (Mather 211).

In a 2015 article Mather argues for the extension of our 'anthropocentric' consideration for the welfare of mammals (and other vertebrates) to the invertebrates. A 'morality of care' rather than one of rights, and 'the damage humans do to themselves by cruel treatment of animals both argue for the extension of consideration to all animal species' (Mather 211).

Robert Elwood (2011) in *ILAR Journal* summarises previous scientific work on invertebrate pain, focussing, in contrast to Mather (who appears to conflate pain and nociception) on the differences between pain and nociception. Using criteria similar but not identical to those scientists had explored in the last three decades, he concludes his article by stating that:

> Braithwaite (2010) was confident enough to state that fish feel pain but invertebrates do not. I do not share the confidence to make that discrimination. Neither do I feel confident in stating unequivocally that some of them do feel pain, although it is clear that the responses described above cannot be explained just by nociceptive reflexes. While awaiting the results of further relevant studies, perhaps all who use invertebrates should consider the possibility that at least some might suffer pain and as a precaution, ensure humane care of these animals (Elwood 182).

Given that Elwood's account is perhaps the most comprehensive on scientific findings to 2011, it is particularly interesting to note that having considered experimental work over the last forty years in relation to: suitable receptors; a suitable central nervous system; responsiveness to opioids, analgesics and anaesthetics; protective motor reactions; tradeoffs between stimulus avoidance and other activities; and cognitive ability and sentience, he comes to the conclusion – so focal in Eisemann et al.'s influential 1980s paper – that behaviour provides the greatest insights into likely experience of pain (Eisemann et al.182). Moreover, the inconclusive nature of the sum of the results to 2011, and the caution that we should apply humane treatment in our dealings with insects – since pain remains neither proven nor disproven – also seems to take us back to Weiss's questions at the beginning of the twentieth century. But while the accumulated findings of the last thirty or forty years may not have produced scientific proof of pain experience in the Insecta, it has nevertheless provided a solid foundation for the groundbreaking 2016 results of insect neurobiologist Andrew Barron and philosopher Colin Klein.

It is perhaps no accident that the most fruitful research to date on this topic has been produced not by scientists or philosophers alone but in the conjunction between the two disciplines. Addressing the issue of insect consciousness, Barron and Klein argue, in *Proceedings of the National Academy of Sciences*, that structures in the insect brain function similarly to the human midbrain, an area understood to be focal in subjective experience in humans where consciousness is thought to emerge. Drawing on existing research in insect intelligence and learning, Barron and Klein write that 'insect behaviour involves multiple layers of filtering of sensory information to support selective attention to stimuli that are salient and suppression of representation of irrelevant stimuli'.

It would have seemed unlikely in the 1980s that research on insect pain per se would have found its way into the popular press. And although Barron and Klein do mention a potential for human application their stress is on insects themselves. Both the *New York Times* (April 19, 2016) and the *Sydney Morning Herald* (April 24, 2016) published accounts of the findings. Klein told the papers that 'one of the things we are interested in is consciousness, and why consciousness might have evolved in the first place. What is really important about the origin of consciousness in this account is that it arises from integrating functions – taking together sensory information, the state of the body, memories of where the organism has been and putting these together into a single point of view that allows navigation in a complicated world.

Consciousness, they claim, may be very ancient, perhaps emerging in the Cambrian period (500 million years ago) – rather than something which evolved only in humans and the 'higher' vertebrates.

Writing of Klein and Barron's findings in the *New York Times*, James Gorman concludes that:

> Thus if consciousness is widespread through the animal kingdom ethical questions about how we treat even tiny household pests becomes a bit more complicated. It's long been recognised that there's a huge moral difference between slaughtering a lamb quickly and letting it die slowly even if in both cases the intention is to barbecue its meaty bits.... Does the same distinction thus apply between a cockroach stomped on, and one left to expire over time, fearful and pain-racked by pesticide? What of Louie's [the fly in the *Mortein* ad] cousin helplessly glued to fly paper, struggling until thirst and exhaustion take their fatal toll? He might be in trauma, but equally, Klein suggests, he may be in 'dim confusion'.

Barron and Klein's neurophysiological findings on the insect brain and its implications for consciousness in animals as a whole, together with earlier evidence such as opioid/analgesic responses, the presence of stress-related hormones in insects, evolutionary continuities across vertebrates and invertebrates and learning and memory – would seem to indeed argue for the presence of pain or something very closely related to it, in insects. These conclusions, and the manner of their dissemination are significant. Reported in both a reputable scientific publication, and in the popular press, these findings – though no doubt able to be used to elucidate the nature of consciousness in Homo sapiens – are expressed in terms of their significance for insects, and even more importantly, our treatment of them.

It is worth returning to the questions raised by Weiss in 1914: 'How does one distinguish between what is "painful" and what is "unpleasant"? .... What constitutes a symptom of pain in insects?' and perhaps, his most interesting question of all, 'who is qualified to judge?' While science continues – and indeed needs to continue – its objective investigation of the natural world, it is worth noting that the question of insect pain, illuminated by scientific advances, took many a detour through anthropocentric experiments along the way. In the end, however, a philosopher and a neurobiologist arrived at the most significant discovery – consciousness in insects – and therefore the likelihood of pain and suffering with a basis in anthropomorphic intuition: 'I do have the instinct that fly paper seems more cruel than swatting', Klein says 'even if it's more convenient for us. I think if you're governed by the idea that it's just a fly or just a bee, so it doesn't matter, then it's probably worth rethinking'.

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