the retro-fitting of precipitators on uncontrolled incinerators, or perhaps the installation of electrostatic precipitators on uncontrolled incinerators, or perhaps the retro-fitting of precipitators on units equipped with low pressure/efficiency scrubbers.

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Minireview

Do insects feel pain? – A biological view

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The question of whether insects, or indeed other invertebrates, have a pain sense has received little attention in the literature, despite its obvious biological interest and the ethical implications of the human treatment of insects and other invertebrates. The relevance of this question is that, whilst we could scarcely conceive of a world in which pest insects are not regularly damaged and killed in vast numbers by human design and many others killed incidentally in our daily activities, the experimental biologist still has to face decisions on how to handle his insect material.

Pain, as understood in humans, is a variable, subjective experience involving a class of sensations with which is associated a characteristic 'negative affect and aversive drive'[15]. Its quality and severity may be strongly modified by factors including previous experience, non-nociceptive sensory information, focussing of attention by the subject, and the perceived significance of the experience[15,16]. The unpleasant emotional qualities and strong motivation to remove the source of stimulation appear largely to comprise the experience known generally as 'suffering'. The occurrence of 'suffering' in other animals is usually inferred from physiological and behavioral changes such as flexor reflexes, blood pressure increases, tachypnoea and vocalisation[25], all of which are normally concomitants of severe pain experiences in humans. This inference becomes progressively less defensible as animals phylogenetically more remote from man are considered. The standard reference work on the structure and function of the nervous systems of invertebrates[3] suggests only that pain is inferred if an animal shows behavioral reactions resembling those of a human in pain, the decreasing similarity of reaction in simpler animals being taken to indicate a gradual evolution of a pain sense with the appearance of increasingly complex animals.

Although there is no conclusive proof as to whether an insect can experience something akin to human pain, logical analysis of known examples of insect behavior and physiology may facilitate a rational decision. In the only published examination of the possibility of insect pain known to us, Wigglesworth[24] has, by inference from his observations of insect behavior, concluded that while most of the manipulations to which insects are commonly subjected probably do not cause them pain, certain stimuli, such as high temperature and electric shocks, apparently do so. We here examine the question from three aspects: firstly, the adaptive role of pain in mammals and the relevance of this to insect biology; secondly, the neural basis of nociception and pain perception in mammals and its relation to the insect nervous system; and thirdly, the similarities and contrasts between the behavior of insects and mammals undergoing trauma or noxious stimulation.

Pain may induce a suffering mammal to withdraw from or otherwise neutralize the causative agent and to protect 'hurt' parts from further injury[16]: the individual (and perhaps nearby conspecifics) may learn to avoid that agent in future. In some circumstances, presumed pain has also been shown to stimulate aggressive behavior towards conspecifics or other animals or objects, and it has been suggested that pain may produce conditioning such that aggression is elicited by stimuli which have in the past been associated with it[6]. Thus several distinct classes of behavioral response are involved, including 'withdrawal', 'protection', 'aggression' and 'learned avoidance or aggression'. The potential adaptive value of such responses is clear and since mammals, especially man, have limited genetic pre-programming of their behavior patterns, learning from pain (and pleasure) experiences has a vital role to play in the development of their adaptive behavior.

By contrast, most insect behavior patterns are to a large extent pre-programmed[10], leaving much less scope for individual learning of appropriate behavior from noxious and 'pleasant' stimuli, although there is a capacity for learning[1], (including avoidance) in both intact[21,22] and decapitated[12] insects and in isolated ganglia[7]. The high situation specificity of learning in insects[1] is an additional factor limiting the possible adaptive value of hypothetical pain-activated learning.

Mammalian pain seems to be an alerting and motivating 'sub-programme' of neural function, occurring in organisms having considerable behavioral plasticity. It provides warning of body damage and incorporates response motivation, whilst allowing, apart from the purely reflexive or 'wired-in' elements of nocifensive response, flexibility of action influenced by the overall sensory context, past experiences and the quality of the pain experience itself. Insects, however, with their largely pre-programmed behavior patterns and limited learning capacity appear to be reliant on relatively rigid, programmed avoidance and escape responses, such as occur widely in motile organisms (including bacteria[2]), triggered by traumatizing stimuli such as heat, electrical currents, damaging chemicals and mechanical compression or restraint. Vigorous cleaning and violent struggling by insects which are restrained in spiders' webs typify more complex stereotyped escape reactions.

The occurrence of these reactions does not in itself indicate any pain experience[4] - a sufficient explanation for them can be advanced in terms of excessive or abnormally-patterned non-nociceptive sensory input activating central nervous system programmes which produce avoidance or escape outputs. Certain types of very mild stimulation, such as light touch of the outside of pupal Lepidoptera, which by mammalian standards could not be considered noxious, evoke strong motor output. Even human flexor reflexes remain when consciousness (and pain perception) are surgically or pharmacologically blocked[4]. Thus we conclude that 'avoidance' or 'withdrawal' responses, although often accompanying pain in conscious humans, are not reliable signs for determining the presence of pain.

Although a detailed neural basis of pain and suffering in mammals has still to be fully formulated, considerable progress has been made towards a general understanding of the structures involved. Pain experiences are generally based on central processing of input from nociceptors, which travels in along nerve fibers of the 'A delta' and 'C' classes[25]. These carry information from receptor endings, whose adequate stimuli either cause tissue damage, such as intense heat, strong mechanical deformation, ischemia and irritant chemicals, or are certain of the chemical products of pathological conditions of skin, muscles and viscera. Most pain receptor endings are responsive to several types of stimulus[25].

Nociceptive nerve fibers have been estimated to comprise about half of the afferents entering the cord via the dorsal roots, while others enter at the ventral roots[25]. At the spinal level, nociceptive input may participate in protective (somatic and sympathetic) reflexes as well as being projected to higher centers, apparently after considerable modulation. The dorsal horns of the spinal cord, which receive the central terminals of many nociceptive fibers, are the site of much processing of the afferent information, integrating it with input from non-nociceptive afferents and descending fibers[25,17]. After processing in the cord, the output is transmitted towards the brain by fibers in the ventro-lateral spinal cord from where it projects via separate fiber tracts into 2 major brain systems. It is suggested that one system provides, at least in part, a sensory-discriminative basis for pain, whilst the other underlies the adjunctive unpleasant affect and motivational drive[16,17]. Both systems are influenced by neocortical processes, which interact with them to provide a multidimensional experience embracing sensory perception, affect, motivation towards response, and cognitive functions resulting from integration of the somato-sensory and motivational systems with memory of past experience and evaluations of possible responses. The central nervous system state resulting from these processes can then initiate effector mechanisms to produce responses[16] such as non-reflexive 'withdrawal', 'protection', 'aggression', and 'learned avoidance or aggression'.

The apparent absence from insects of any known or likely candidate nociceptors is of doubtful significance. Whilst it could be argued that the evolution of specific nociceptors accompanies a developing capacity to experience pain states, alternative mechanisms could possibly subserve this function. For example, nociceptive information could be decoded from abnormally high-frequency discharges from non-nociceptive mechano-, chemo-, and thermo-receptors, such as has been proposed for nociception in some mammalian viscera[25]. On the other hand, the presence of receptors specialized to receive noxious stimulation (such as the high-threshold mechanoreceptive 'N' cells of the leech[19]) would, if demonstrated, have no necessary bearing on pain perception, as they could well mediate reflexive avoidance behavior without the involvement of a sense of pain.

Similarly, the absence in invertebrates of identified central pathways analogous to those implicated in mammalian pain experience is inconclusive, as other means of producing a comparable experience could possibly exist. However, the invertebrate CNS generally has a relatively simple organisation, and fewer neurones (10^5–10^6 neurones in insects of which some 80% are concerned with the immediate integration of sensory input, as against 10^{10} in higher mammals[13]). This at least raises the question of whether any experience akin to human pain could be generated. A recent examination of relevant behavioral evidence produced no indication of conscious experience in insects[10]. Could any state occurring in the absence of at least a rudimentary consciousness meaningfully be labelled pain?

The recent discovery of endogenous opioid peptides[8] and their receptor sites[20] in various invertebrates (including insects) may encourage the belief that these animals can experience pain[9], in view of the analgesic role of opioid peptides in mammals. However, the various functions, unrelated to pain experience, which are mediated by opioids in mammals[5], as well as the known occurrence of two such compounds in a protozoan[14], suggest that the endogenous opioids of invertebrates may function in regulating physiological[20] or behavioral[11] activities unconnected with pain phenomena. The presence of opioids can therefore not be taken as necessarily indicating a capacity for pain perception in an animal.

Observation of the behavior of insects which have recently suffered a variety of injuries provides more direct evidence bearing on the question. No example is known to us of an insect showing protective behavior towards injured body parts, such as by limping after leg injury or declining to feed or mate because of general abdominal injuries. On the contrary, our experience has been that insects will continue with normal activities even after severe injury or removal of body parts. An insect walking with a crushed tarsus, for example, will continue applying it to the substrate with undiminished force. Among our other observations are those on a locust which continued to feed whilst itself being eaten by a mantis; aphids continuing to feed whilst being eaten by coccinellids; a tsetse 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 whilst being eaten by large internal parasitoids; and male mantids which continue to mate as they are eaten by their partners. Insects show no immobilisation equivalent to the mammalian reaction to painful body damage, nor have our preliminary observations of the response of locusts to bee stings revealed anything analogous to a mammalian response. Wigglesworth[24] has provided additional examples of insect non-response to treatment which would certainly produce both pain and violent reactions in humans. Whilst these examples do not prove that insects do not suffer pain, they strongly suggest that if a pain sense is present it is not having any adaptive influence on the behavior, such as causing a damaged part to be protected until healed. This suggests to us the possibility that insect neurobiology does not involve a 'pain' sub-programme.

Some insect behavior, such as the writhing of insecticide-poisoned insects, the struggling of restrained living insects, and the production of sounds, repellent secretions and alarm pheromones by insects under attack, although superficially resembling that of higher animals responding to painful stimuli, no more requires the presence of a pain sense than do reflexive withdrawal responses. Most such examples can be explained adequately as adaptive behavior patterns elicited reflexly by certain kinds of stimulation; for example, the activation of neural circuits for escape and cleaning behavior as a result of mechanical stimulation during handling. The increase in both general grooming activity and specific grooming of a wound site observed after experimental puncturing of the abdominal wall of the cockroach *Periplaneta americana* (L.)[11] may be attributable to mechanoreceptive input from the wound site similar to that indicating lodgement of foreign material on the body surface, especially in view of the apparent contra-adaptiveness of this response in relation to wound healing. Other examples are explicable as merely the direct consequences of abnormal neural activity. The hyperexcitability, ataxia and convulsions characteristic of insects poisoned by DDT and pyrethroid insecticides, for example, have been attributed directly to abnormal repetitive discharges in a variety of neurones[18] – no underlying motivation for this behavior, based on a perception of pain, seems called for. It would seem, therefore, that little evidence exists for the occurrence of a generalized pain experience caused by a wide range of damaging stimulation, as it is difficult to envisage the natural selection of a capacity for pain, without a corresponding capacity for adaptive responses.

The implications of the foregoing discussion, for insects and other invertebrates, need to be considered with caution. Clearly, it is not possible to provide a conclusive answer to the problem of pain in lower animals, as any subjective experience of an organism cannot be directly experienced by another and a means of communicating with lower organisms is not available to us. On balance, however, the evidence from consideration of the adaptive role of pain, the neural organisation of insects and observations of their behavior does not appear to support the occurrence in insects of a pain state, such as occurs in humans. It is likely that the same could be said of other invertebrates having less complex nervous systems, though more caution would be needed in other cases, notably that of the cephalopod molluscs, which have a considerably more complex nervous system[23]. We consider that the experimental biologist would be advized to follow, whenever feasible, Wigglesworth's recommendation that insects have their nervous systems inactivated prior to traumatizing manipulation. This procedure not only facilitates handling, but also guards against the remaining possibility of pain infliction and, equally important, helps to preserve in the experimenter an appropriately respectful attitude towards living organisms whose physiology, though different, and perhaps simpler than our own, is as yet far from completely understood.

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