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Commentary

Do insects feel pain? A question at the intersection of animal behaviour, philosophy and robotics

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Insects are common model organisms for studies in animal behaviour, genetics, molecular biology and other fields. They are also the focus of pesticide research, a subspecialty devoted to devising chemicals capable of killing them. These studies would raise animal welfare concerns, if insects were thought capable of suffering (i.e. experiencing pain). Four disparate areas of research touch on the question of whether insects feel pain: (1) philosophy, (2) insect neurobiology and behaviour, (3) artificial intelligence and robotics and (4) evolution. Using the perspectives provided by these fields, I assess what we know about whether insects feel pain.

PHILOSOPHICAL ISSUES

Philosophers typically make a distinction between the capacity to respond to potentially damaging stimuli (i.e. nociception), and the experience of pain (e.g. Allen, 2004, 2011). Nociception is ubiquitous in the animal kingdom (Sneddon, Elwood, Adamo, & Leach, 2014). For example, insects have specialized sensory neurons (nociceptors) designed to respond when tissue is damaged or exposed to extreme conditions (e.g. Johnson & Carder, 2012). When nociceptors are stimulated, insects move away from the stimulus (e.g. Johnson & Carder, 2012). Whether 'pain' is equally ubiquitous in animals is another matter. Pain is different from nociception because pain is primarily a subjective experience of discomfort, despair and other negative affective states (e.g. see Allen, Fuchs, Shriver, & Wilson, 2005). In humans it is possible to have nociception without pain, and pain without any activity in nociceptive fibres (Hardcastle, 1997). For example, after ingesting morphine people can still sense pain, but do so without a sense of suffering or producing characteristic pain behaviours (e.g. wincing) (Hardcastle, 1997). The difficulty in demonstrating whether animals experience pain, as opposed to nociception, lies in our ability to assess whether animals experience subjective states such as despair (Allen, 2011; Allen et al., 2005; Sherwin, 2001; Shriver, 2006). This is one of the most fraught areas in both philosophy and neuroscience. Also known as the 'hard' problem of consciousness, we do not know how the brain produces subjective experiences such as pain (e.g. see Allen, 2011; Merker, 2007; Reggia, 2013). This void in our understanding makes it impossible to determine the cognitive skills and neural connections needed to support subjective experiences such as pain. For example, does an organism need self-awareness to feel pain? What types of functional connectivity within the central nervous system are required to produce the emotional experience of pain? Without answers to these questions we cannot definitively demonstrate that insects feel pain, because we do not know which behaviours or neurobiological activities indicate the sensation of pain.

However, it is possible to assess the relative likelihood that animals experience pain using the argument-by-analogy (Allen et al., 2005; Sherwin, 2001; Shriver, 2006). Animals have both physiological and behavioural responses to nociception that correlate roughly with the experience of pain in humans (Allen et al., 2005). Although not definitive, these similarities can suggest that an organism experiences pain (e.g. rodents, Allen et al.,

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2005). However, the argument is valid only in so far as the two phenomena being compared are essentially the same. Unfortunately, invertebrates such as insects are used as examples of animals for which the argument-by-analogy is invalid (e.g. Allen, 2011), primarily because their nervous systems are different from ours (Bullock, Orkand, & Grinnell, 1977). Nevertheless, others contend that the argument-by-analogy can be extended to invertebrates by applying a functional and evolutionary perspective to their neurobiology and behaviour (e.g. by determining the possible selective advantage of the emotional experience of pain, e.g. Sherwin, 2001).

EVIDENCE FROM INSECT NEUROBIOLOGY

A major objection to the idea that insects experience pain rather than nociception is the size and organization of their central nervous system (Eisemann et al., 1984). Insects have small nervous systems (typically less than a million neurons), consisting of several distributed brains (ganglia) (Bullock et al., 1977). This distributed organization is thought to limit the capacity for advanced information processing (Bullock et al., 1977). Nevertheless, their principal brains (e.g. supraesophageal ganglia) contain complex neuroanatomical features (e.g. mushroom bodies, Strausfeld, 2002) that have an intricate neural architecture (Giurfa, 2013). The functions of these complex neural arrangements are still under investigation, but insects do have areas that are functionally equivalent to reward circuits in vertebrates (Giurfa, 2013). These complex structures allow insects to vary the activity of different neural circuits, providing insects with the capacity to learn and to have 'motivated' behaviour (Giurfa, 2013).

Insects can modify their nociceptive input (Johnson & Carder, 2012). This ability is often given as evidence that an animal experiences the emotional component of pain (e.g. Sneddon et al., 2014). However, this is not a compelling argument, because all sensory systems in insects are modifiable (Chapman, 1998). It is unclear why nociception should be an exception.

Even when insect behaviours are similar to those that would suggest an emotional experience of pain if observed in a mammal, they may be mediated by much simpler neural mechanisms in insects. One example is 'learned helplessness', which is interpreted as a state of 'hopelessness' in mammals (Eisenstein & Carlson, 1997). In 'learned helplessness', an animal is given inescapable electric shocks. Eventually it no longer exhibits escape behaviour and loses the ability to learn how to escape the shock (Eisenstein & Carlson, 1997). Similar effects can be observed in the surgically isolated locust leg attached to a single thoracic ganglion. Either a neuronal population of about 1000 neurons is capable of an emotional state similar to 'utter despair' in humans, or the behaviour is superficially similar but does not contain the emotional component (Eisenstein & Carlson, 1997).

Without an understanding of the neural architecture or minimum brain size required to support subjective experience, we are left with no neurobiological method of determining whether insects experience pain (also see Elwood, 2011). Merely pointing out that insect brains have a different neuroanatomical structure than mammals does not demonstrate that they are incapable of experiencing an emotional response to pain; insects could use different neurobiological mechanisms (Sherwin, 2001). The difficulty, then, is demonstrating the existence of these internal mental states without being able to examine neurobiologically analogous areas. In the future, when there is a consensus as to the type of neural architecture that supports subjective experience (e.g. see Merker, 2007; Tononi & Koch, 2015), then neuroethological studies could examine whether insects have the necessary neural organization. For the present, researchers have turned to behavioural criteria (see Tables 1 and 2 in Sneddon et al., 2014) to search for evidence that might suggest a subjective response to nociception in invertebrates (e.g. Elwood, 2011; Horvath, Angeletti, Nascetti, & Carere, 2013; Sherwin, 2001).

EVIDENCE FROM INSECT BEHAVIOUR

There is no doubt that insects have nociception. For example, locusts will writhe when sprayed with DDT (Eisemann et al., 1984). However, they also exhibit complex behavioural responses to noxious stimuli. Like vertebrates, insects alter their behaviour when faced with threatening or damaging stimuli (e.g. predator exposure, Hedrick & Dill, 1993). These changes can be long-lasting (Slos, Meester, & Stoks, 2009), suggesting a motivational shift, possibly mediated by their stress response system (Adamo & Baker, 2011; Roeder, 2005). Other invertebrates show a similar motivational shift when exposed to potentially damaging stimuli (e.g. crustaceans, Elwood & Adams, 2015). As in vertebrates, noxious stimuli can be used to train insects to perform a variety of tasks (Giurfa, 2013; Tedjakumala & Giurfa, 2013). Insects are capable of attentional modulation, concept learning and navigation (Giurfa, 2013) and, therefore, may have other advanced neural processing abilities sufficient to support an emotional response to pain (Carruthers, 2004a, 2004b). However, insects may solve complex problems using simpler information processing principles than we would use to solve the same problems (Giurfa, 2013).

Studies suggesting that insects experience an emotional response to nociception tend to be equivocal. For example, negative stimuli appeared to induce 'pessimistic' cognitive biases in bees (Bateson, Desire, Gartside, & Wright, 2011). However, Giurfa (2013) pointed out that Bateson's et al. (2011) data also support the interpretation that shaking (i.e. the negative stimulus used in Bateson's study) makes bees better discriminators of a food reward. This alternative explanation is appealing because shaking alters octopamine concentrations in the haemolymph (Bateson et al., 2011), and octopamine levels modulate sensory function (Roeder, 2005). Therefore, the results can be explained without requiring that bees have emotional states.

Insects show some differences in their responses to nociception compared to vertebrates. For example, insects tend to continue to use damaged limbs (Eisemann et al., 1984), will eat their own innards (Miller, 2012; http://www.radiolab.org/story/185551-killer-empathy/) and will continue to feed while being consumed by another insect (Eisemann et al., 1984). However, the observation that insect behaviour differs from human behaviour when exposed to noxious stimuli does not necessarily mean that they do not have a pain-like experience. Being able to experience the emotional component of pain may not be an all-or-none phenomenon. Insects could have some aspects of an emotional experience but still lack the full subjective experience (Anderson & Adolphs, 2014). Moreover, this capacity may vary across species, depending on the whether or not a subjective experience of pain would provide a fitness advantage.

Despite these interpretational issues, insect behaviour does provide examples of behaviour (also see Sherwin, 2001) that, if observed in a vertebrate, would be interpreted as evidence of an organism experiencing pain (Sneddon et al., 2014). For some researchers, this similarity is sufficient to convince them that insects feel pain (Horvath et al., 2013). However, there is an alternative perspective to consider.

ARE INSECTS MORE LIKE LITTLE PEOPLE OR COMPLICATED ROBOTS?

Using the same type of argument-by-analogy reasoning, we can also compare insects to entities not thought to experience