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Review

Defining and assessing animal pain

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The detection and assessment of pain in animals is crucial to improving their welfare in a variety of contexts in which humans are ethically or legally bound to do so. Thus clear standards to judge whether pain is likely to occur in any animal species is vital to inform whether to alleviate pain or to drive the refinement of procedures to reduce invasiveness, thereby minimizing pain. We define two key concepts that can be used to evaluate the potential for pain in both invertebrate and vertebrate taxa. First, responses to noxious, potentially painful events should affect neurobiology, physiology and behaviour in a different manner to innocuous stimuli and subsequent behaviour should be modified including avoidance learning and protective responses. Second, animals should show a change in motivational state after experiencing a painful event such that future behavioural decision making is altered and can be measured as a change in conditioned place preference, self-administration of analgesia, paying a cost to access analgesia or avoidance of painful stimuli and reduced performance in concurrent events. The extent to which vertebrate and selected invertebrate groups fulfil these criteria is discussed in light of the empirical evidence and where there are gaps in our knowledge we propose future studies are vital to improve our assessment of pain. This review highlights arguments regarding animal pain and defines criteria that demonstrate, beyond a reasonable doubt, whether animals of a given species experience pain.

Bateson's (1991) seminal review on the assessment of pain has been influential in inspiring numerous researchers investigating pain in animals. Bateson set out a clear framework upon which hypothesis-driven research questions could be derived regarding the capacity for pain in any species. Indeed, the criteria suggested have been applied to numerous species, particularly non-mammalian vertebrates (e.g. fish, Sneddon, 2011) and more recently invertebrates (e.g. crustaceans, Barr, Laming, Dick, & Elwood, 2008). Well-defined criteria were proposed and it was suggested that animals that fulfilled all criteria should be considered capable of pain. These criteria were: possession of nociceptors, receptors that detect damaging stimuli on or in the body; pathways from nociceptors to the brain; brain structures analogous to the human cerebral cortex that process pain; opioid receptors and endogenous opioid substances in a nociceptive neural system; a reduction in adverse behavioural and physiological effects after administration of analgesics or painkillers; learning to avoid potentially painful stimuli and that this learning is rapid and inelastic. Sneddon (2004) added that animals should suspend normal behaviour for a prolonged period rather than show a reflex response, with adverse changes in behaviour reflective of signs of 'discomfort' as shown by long-term motivational change. These robust scientific approaches can provide evidence strongly suggesting that an animal is capable of experiencing pain and we can then seek to reduce or ameliorate that condition by reducing the invasiveness of any procedures to which we subject animals or, when this is unavoidable, providing pain relief. However, Bateson's review has been recently criticized as being outdated (Rose et al., 2014). Given the advances made in the scientific study of pain, the technologies now at our disposal and more recent evidence from a wider variety of taxonomic groups, this review provides a timely update on the definition, assessment and importance of animal pain.

PAIN: A COMPLEX ISSUE

Nociception, the capacity to respond to potentially damaging stimuli, is a basic sensory ability (Purves et al., 2012), and even

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occurs in bacteria (Berg, 1975). Testing whether animals are able to respond to noxious stimuli is typically straightforward, even though many nociceptors are multifunctional (Tsagareli, 2011). Philosophers and scientists, however, make a distinction between pain and nociception (Allen, 2011) because pain is primarily a subjective experience of anguish, despair and other negative affective states (e.g. see Allen, Fuchs, Shriver, & Wilson, 2005). The difficulty in demonstrating whether animals feel pain, as opposed to just nociception, lies in our ability to recognize negative internal mental states in other species (Broom, 1998).

Animals have both physiological and behavioural responses to nociception that parallel those that accompany the experience of pain in humans and this is the basis for the argument by analogy (Allen et al., 2005; Sherwin, 2001). However, there are weaknesses to this concept. Clearly animal pain behaviour differs from human pain behaviour, as does the underlying neuroanatomy. When are these differences important (i.e. rendering the argument by analogy invalid) and when are they inconsequential? Understanding the biology of a given species may be helpful here. Some suggest animals may behave as though they are in pain, but this behaviour may reflect nociception without suffering (e.g. Allen, 2004). Thus, analogous behavioural and physiological responses need not imply identical mechanisms. Allen et al. (2005) reviewed the evidence for pain in rodents and compared it with data from humans, concluding that the evidence is not conclusive. However, Shriver (2006) reviewed similar evidence and concluded that it was 'beyond a reasonable doubt' that most mammals feel pain. We review here data that has led to a consensus that it is beyond a reasonable doubt that pain can be experienced in animals (Allen, 2011). This review presents a combination of behavioural, physiological and evolutionary evidence and arguments, which taken together demonstrate, beyond a reasonable doubt, that animals from different phyla experience pain.

The opposition to the idea that animals experience pain has sparked fierce debates over the capacity of nonprimate animals for pain (e.g. Bermond, 1997, 2001; Rose, 2002; Rose et al., 2014). However, although it cannot be proven that animals experience pain, it also cannot be proven that they do not. We propose that if animals fulfil our criteria below then they should be considered capable, beyond a reasonable doubt, of experiencing pain with implications for their health and welfare.

FUNCTION OF PAIN

Nociception is a fundamental sensory system that alerts an animal or human to potential damage. Nociceptive pathways connect with brain areas important for motivation, and animals are motivated to avoid the injurious stimulus and protect themselves from further damage (Bateson, 1991). Therefore, it would be adaptive to evolve such a system and many diverse taxa possess specific receptors, i.e. nociceptors that detect damaging stimuli, for example *Drosophila melanogaster* and *Caenorhabditis elegans* (Im & Galko, 2012; Neely et al., 2010; Wittenburg & Baumeister, 1999). However, different species are likely to show specific differences in how these nociceptors operate.

Evolutionary heritage and life history place very different pressures on animal groups and they are exposed to different types of nociceptive stimuli (e.g. high mechanical pressure, extremes of temperature, noxious chemicals). Therefore, animals will have evolved their nociceptive and possible pain systems to meet the demands of their environment (Broom, 2001; Rutherford, 2002).

The advantage of nociception seems clear. However, some animals also have an associated aversive motivational state similar to many of the aspects of pain in humans. It is the existence of this aversive motivational state that leads us to propose that, beyond a reasonable doubt, at least some animals experience pain. We should consider the function of this aversive motivational state because it might guide us in establishing how pain might be better defined and shown to be likely in particular taxa. The key function appears to be that the aversive experience of pain creates a strong and lasting motivation that enables the animal to avoid getting into a similar situation in the future. That is it increases fitness by assisting long-term protection from further damage (Bateson, 1991; Elwood, 2011; Sneddon, 2004). Thus, while nociception typically allows for an immediate reduction of tissue damage, pain typically allows for longer-term protection. Unfortunately this single criterion, on its own, does not prove that an animal experiences pain. Nociception can also have long-lasting effects without invoking higher-order neural processes (e.g. long-term nociceptive sensitization, Chase, 2002; Smith & Lewin, 2009). Therefore, such long-term behavioural changes, although consistent with the concept of pain, require further evidence as we discuss below.

DEFINITION OF ANIMAL PAIN

Because it is impossible to know how other humans feel when they are in pain, we rely upon their ability to communicate their experience of pain. This illustrates how difficult it is to measure pain in humans that cannot speak (e.g. neonates) or animals that do not share our language. Therefore, the commonly used definition of human pain cannot be directly applied to animals because it relies on either knowing how animals feel or requiring them to be able to communicate their subjective experiences to us. The International Association for the Study of Pain defined human pain as 'An unpleasant sensory and emotional experience associated with actual or potential tissue damage, or described in terms of such damage' (IASP, 1979, p. 249). However, the IASP (1979, p. 249) also refers to adults unable to communicate, neonates and infants and adds that 'The inability to communicate verbally does not negate the possibility that an individual is experiencing pain' and so we believe this can be applied to animals.

It is vital that an animal-based definition of pain allows rigorous scientific investigation of disparate species and also allows us to detect, assess and alleviate pain in animals where possible. The most commonly used definition for animals is 'an aversive sensory experience caused by actual or potential injury that elicits protective and vegetative reactions, results in learned behaviour, and may modify species specific behaviour' (Zimmerman, 1986, p. 2). Sneddon (2009, p. 338) refined this definition suggesting that animals in pain should 'quickly learn to avoid the noxious stimulus and demonstrate sustained changes in behaviour that have a protective function to reduce further injury and pain, prevent the injury from recurring, and promote healing and recovery.' We use these definitions as the foundation for our criteria by which possible pain experience might be judged.

Pain provides strong motivation for animals to learn to avoid damaging stimuli within a few trials (Carlsson et al., 2006). The aversive experience associated with pain is probably an important driver in ensuring that animals survive in a dangerous habitat avoiding injury that may otherwise lead to ill health and mortality. Instead of considering pain to be a special property of humans, it is likely that pain, and its associated motivational state, has an adaptive survival function for animals. We believe that the aversive affective component of pain, therefore, is integral to its evolutionary function (Dawkins, 1980, 2012), otherwise animals would frequently damage themselves in the same manner and be incapable of altering their behavioural decisions to learn to avoid injury. A negative internal state can produce robust and repeatable changes in behaviour induced by damaging stimuli in animals. However, other mechanisms might also produce some similar