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THE WELFARE OF INVERTEBRATE ANIMALS SUCH AS INSECTS, SPIDERS, SNAILS AND WORMS

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ABSTRACT

The concept of welfare applies to all animals but not to plants or inanimate objects. Hence we can evaluate and discuss the welfare of invertebrate animals such as snails, insects, spiders and worms, but this does not mean that they have all of the capabilities of more complex animals, or that we wish to protect them in the same way. In considering how we treat animals, one key question is "Should we respect the life of this animal?" A second, linked question is "Should we consider the needs of the animal if we interfere with its life?" A third is "Should we use anaesthetics and analgesics if we damage the tissues of this animal?" There are further questions about the level of awareness that the animal has. For many people, the answers to the questions are affected by whether or not the animal is perceived to be a food item, or likely to harm humans or their resources, or to be considered a beautiful living being. However, when a limpet, a swimming nudibranch, a butterfly, a honeybee, a jumping spider, or a phyllodocid worm is considered objectively, many people would answer yes to two or more of the questions. Information about the various aspects of sentience: perceptual ability, systems for pain and other feelings, learning ability, and various indicators of cognition and awareness is relevant to decisions about protection of animals. The concepts, and some evidence concerning these qualities in invertebrate animals, are presented here. The invertebrate groups most likely to be considered sentient, other than cephalopod molluscs and decapod Crustacea which are reviewed in other papers, are discussed. Whilst cognitive ability in some spiders is high and that in bees, ants and some gastropods is quite high, we cannot be sure that any of these animals feel pain, or that they do not. There is a case for some degree of protection for spiders, gastropods and insects. However, the case is not as strong as that for vertebrates, cephalopods and decapod Crustacea at present.

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1. INTRODUCTION: HUMAN OBLIGATIONS TO ANIMALS

Moral systems have evolved, in humans and other species, because cooperation and tolerance are successful strategies, especially in social species[1]. Most people would

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say that we have moral obligations to humans and animals of other species. If we use a living animal in a way that gives us some benefit, we have an obligation to that animal. It is my view that human behaviour and laws should be based on the obligations of each person to act in an acceptable way towards each other person and to each animal that is used. It is better to base strategies for living on our obligations rather than to involve the concept of rights because some so-called rights can result in harm to others.

With increasing knowledge and increasing efficacy of communication there has been a change in attitudes to people with a broadening of the range of people for whom we have concerns. We also now consider that a wide range of animals **deserve moral consideration**. One view of animal protection occurs because the animals are considered to have some intrinsic value. For many people, certain animals are valued because of evidence for their cognitive abilities, awareness, mental aspects of needs and feelings such as pain, fear and pleasure. Animals vary in the extent to which they are aware of themselves[2] and of their interactions with their environment, including their ability to experience pleasurable states such as happiness and aversive states such as pain, fear and grief. The concept of sentience affects our decisions about which animals to protect. A **sentient being** is one that has some ability: to evaluate the actions of others in relation to itself and third parties, to remember some of its own actions and their consequences, to assess risk, to have some feelings and to have some degree of awareness[3].

Human opinion as to which individuals are sentient has changed over time in well-educated societies to encompass, first all humans instead of just a subset of humans, and then: (a) certain mammals that were kept as companions, (b) animals which seemed most similar to humans such as monkeys, (c) the larger mammals, (d) all mammals, (e) all warm blooded animals, (f) all vertebrates and (g) some invertebrates. **Awareness**, a key aspect of sentience, is defined here as a state in which complex brain analysis is used to process sensory stimuli or constructs based on memory[4]. Its existence can be deduced, albeit with some difficulty, from behaviour in controlled situations. Awareness has been described using five headings: unaware, perceptual awareness, cognitive awareness, assessment awareness and executive awareness[5]. In **perceptual awareness**, a stimulus elicits activity in brain centres but the individual may or may not be capable of modifying the response voluntarily, e.g. scratching to relieve irritation. Examples of **cognitive awareness** include a mother recognising her offspring and an individual responding to a known competitor, ally, dwelling place, or food type. An individual is showing **assessment awareness** if it is able to assess and deduce the significance of a situation in relation to itself over a short time span, for example vertebrate prey responding to a predator recognised as posing an immediate threat but not directly attacking. **Executive awareness** exists when the individual is able to assess, deduce and plan in relation to long-term intention. In order to have intentions, the individual must have some capability to

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[1] Broom, D.M. 2003. *The Evolution of Morality and Religion*. Cambridge University Press: Cambridge, UK.

[2] DeGrazia, D. 1996. *Taking Animals Seriously: Mental Life and Moral Status.* Cambridge University Press: New York, USA.

[3] Broom, D.M. 2006. The evolution of morality. *Applied Animal Behaviour Science*, 100: 20-28.

[4] Broom, D.M. 1998. Welfare, stress and the evolution of feelings. *Advances in the Study of Behavior* 27: 371-403.

[5] Sommerville, B.A. and Broom, D.M. 1998. Olfactory awareness. *Applied Animal Behaviour Science 57*, 269-286.

prepare for the future. This requires that information received now can be related to a concept of events that will occur in the future. Executive awareness may involve deductions about choices of action available to that individual (retroduction), the feelings of others, imagination, and the mental construction of elaborate sequences of events.
The complexity of brain organisation is greater for animals that have to contend with a varied environment. Such animals have an elaborate motivational system that allows them to think about the impacts of that environment and then take appropriate decisions. Some kinds of feeding methods and predator avoidance demand a great cognitive capacity, but the most demanding thing in life for humans and many other species is to live and organise behaviour effectively in a social group[6]. Animals which live socially, are generally more complex in their functioning and in their cognitive capacity than related animals that are not social. When deciding whether animals are sentient, a first step is the analysis of the degree of complexity of living that is possible for the members of the species. Without a capability for brain functioning that makes some degree of awareness possible[7], an animal could not be sentient.

One obligation is to avoid causing poor welfare in the animal except where to do so would lead to net benefit to that animal, or to other animals including humans, or to the environment. Hence some aims in animal protection are associated with concerns about animal welfare. We can consider the welfare of all living animals, including humans, but the term is not applicable to inanimate objects, plants, bacteria or viruses. Every living organism is likely to be the subject of more reverence than an inanimate object because living organisms are qualitatively different from inanimate objects in complexity, potential and aesthetic quality. This can affect decisions about whether to kill the organism and whether to conserve such organisms. Animals can respond adaptively and behave using neural control so their welfare can be evaluated.

The **welfare** of an animal is its state as regards its attempts to cope with its environment[8]. Welfare is a characteristic of an individual animal whilst animal protection is a human activity. Welfare includes both the ease of coping, or difficulty in coping, and any failure to cope. It varies over a range from very good to very poor and can be evaluated scientifically[9]. Coping mechanisms can be physiological, behavioural, brain systems including those that lead to feelings, and responses to pathology. Most feelings, for example pain, fear, eating pleasure, sexual pleasure, are adaptive and are components of the mechanisms for attempting to cope with the

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[6] Humphrey, N.K. 1976. The social function of intellect. In *Growing Points in Ethology,* ed. P.P.G. Bateson and R.A. Hinde, 303-317. Cambridge: Cambridge University Press: Humphrey, N.K. 1992. *A History of Mind.* London: Chatto and Windus.; Broom, D.M. 1981. *Biology of Behaviour*. Cambridge University Press: Cambridge, UK; Broom, D.M. 2003. *The Evolution of Morality and Religion*. Cambridge University Press: Cambridge, UK.

[7] Sommerville, B.A. and Broom, D.M. 1998. Olfactory awareness. *Applied Animal Behaviour Science 57*, 269-286.

[8] Broom, D.M. 1986. Indicators of poor welfare. *British Veterinary Journal* 142: 524-526.

[9] Broom, D.M. and Johnson, K.G. 2000. *Stress and Animal Welfare*. Kluwer: Dordrecht, Netherlands; Broom, D.M. and Fraser, A.F. 2007. *Domestic Animal Behaviour and Welfare, 4th edn.* Wallingford: CABI; Fraser, D. 2008. *Understanding Animal Welfare: the Science in its Cultural Context.*Chichester: Wiley Blackwell.

environment and regulate life[10]. Feelings are an important part of welfare but are not all of it. **Health** is the state of an individual as regards its attempts to cope with pathology so health is also an important part of welfare but not all of it[11].

Concern for animal welfare is increasing rapidly and is a significant factor affecting whether or not animal products are bought. If a product is perceived to be associated with bad effects on human health, animal welfare or the environment, sales can slump dramatically[12].

Our knowledge of the functioning of the brain and nervous system and of animal welfare has advanced rapidly in recent years[13]. New knowledge has tended to show that the abilities and functioning of non-human animals are more complex than had previously been assumed so there should be some re-appraisal of which animals should be protected[14].

2. HOW DO WE DECIDE WHICH ANIMALS SHOULD BE RESPECTED AND WHICH PROTECTED?

We can evaluate and discuss the welfare of invertebrate animals such as snails, insects, spiders and worms. All of these animals have sensory ability, escape and defence responses and some degree of analytical brain function. They also have means of defending against pathogens, for example insects have an immune system with pattern recognition proteins, a toll pathway for synthesis of anti-microbial peptides, C-type proteins that bind to particular carbohydrate sequences in pathogens and serpins that regulate cascade reactions[15]. These are energetically costly responses but can be used when energy availability is not limiting. Like vertebrates, the animals have a range of mechanisms for coping with their environment so it is entirely logical to talk about their welfare. However, the abilities do not mean that these invertebrates have all of the capabilities of vertebrates, or that we wish to protect them in the same way. There are several questions about animals whose answers will affect how people

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[10] Cabanac, M. 1979. Sensory pleasure. *Quarterly Review of Biology*, 54, 1-129.

[10] Broom, D.M. 1998. Welfare, stress and the evolution of feelings. *Advances in the Study of Behavior* 27: 371-403; Panksepp, J. 1998. *Affective Neuroscience. The Foundation of Human and Animal Emotion.* New York: O.U.P.

[11] Dawkins, M.S. 2004. Using behaviour to assess welfare. *Animal Welfare,* 13, 53-57; Broom, D.M. 2006. Behaviour and welfare in relation to pathology. *Applied Animal Behaviour Science,* 97, 71-83.

[12] Bennett, R.M. (Ed) 1994. *Valuing Farm Animal Welfare.* Reading: University of Reading; Broom, D.M. 2010. Animal welfare: an aspect of care, sustainability, and food quality required by the public. *Journal of Veterinary Medical Education,* 37, 83-88.

[13] Broom, D.M. and Johnson, K.G. 2000. *Stress and Animal Welfare*. Kluwer: Dordrecht, Netherlands; Broom, D.M. and Zanella A.J. 2004. Brain measures which tell us about animal welfare. *Animal Welfare* 13: S41-S45 Supplement.

[14] EFSA (European Food Safety Authority) Animal Health and Welfare Scientific Panel. 2005. Aspects of the biology and welfare of animals used for experimental and other scientific purposes. *The EFSA Journal* 292: 1-136; Broom, D.M. 2007. Cognitive ability and sentience: which aquatic animals should be protected? *Diseases of Aquatic Organisms,* **75**: 99-108.

[15] Nation, J.L. 2008. *Insect Physiology and Biochemistry, 2nd edition.* CRC Press: Boca Raton, FL; Broom, D.M. 2007. Cognitive ability and sentience: which aquatic animals should be protected? *Diseases of Aquatic Organisms,* **75**: 99-108.

treat them. One key question is: “Should we respect the life of this animal?” A second, linked question is “Should we consider the needs of the animal if we interfere with its life?” A third is “Should we use anaesthetics and analgesics if we damage the tissues of this animal?” Further questions concern the level of awareness that the animal has.

For many people, especially when invertebrates are considered, the answers to the questions are affected by whether or not the animal is perceived to be a food item, or be used in another way, or likely to harm humans or their resources. For example, oysters, e.g. *Ostrea edulis*, and escargots, edible snails *Helix pomatia*, are thought of as items of food rather than individual beings whose welfare may be considered. Similarly, researchers studying crickets, e.g. *Gryllus*, or the swimming marine sea-slug *Aplysia* think of them principally as subjects for study and most people think of wasps *Vespa* spp as a somewhat dangerous nuisance. Ethical decisions about how an animal should be treated should not be dominated by these factors.

A further factor that affects people’s judgements about how animals should be treated is the aesthetic question of whether or not they are perceived to be beautiful. A butterfly may be pleasing to look at for many people. Those who look closely at marine worms like *Phyllodoce maculata* or many tubeworms, or at nudibranch molluscs in the sea, or at the head of a honeybee or spider, usually find them beautiful. This response may make it more likely that individuals and populations of the animals will be preserved.

Other arguments about which animals to protect have involved analogy with humans in that if the animals seem to be more like us they are considered to be more worthy of protection. The argument advocated here and by Broom[16], views the qualities of the animal on an absolute scale that includes known animals but would also be relevant to unknown living beings such as those that might be found on another planet. Criteria based on scientific evidence are listed in Table 1 which incorporates points made by Sherwin[17] who outlined the likelihood of suffering in various invertebrate groups.

Table 1. Evidence which can be used to decide about the animals that should be protected[18]

- complexity of life and behaviour,
- ability to learn relatively difficult tasks especially in a social situation e.g. discrimination, recognition and deception,
- functioning of the brain and nervous system,
- indications of pain and other feelings/emotions,
- indications of awareness based on observations and experimental work

Some of those who have sought to compare the cognitive abilities of animals of different species have reported on total brain size or the size of some part of the

[16] Broom, D.M. 2007. Cognitive ability and sentience: which aquatic animals should be protected? *Diseases of Aquatic Organisms,* **75**: 99-108.

[17] Sherwin, C.M. 2001. Can invertebrates suffer? Or, how robust is argument-by-analogy? *Animal Welfare* 10: S103-S118 (Supplement).

[18] Modified after Broom, D.M. 2007. Cognitive ability and sentience: which aquatic animals should be protected? *Diseases of Aquatic Organisms,* **75**: 99-108.

brain[19]. However, some animal species or individuals function very well with very small brains. The brain can compensate for lack of tissue or, to some extent, for loss of tissue, by cell growth. There are many anomalies in relationships between ability and brain size so no comparative conclusions can be reached except in relation to grossly aberrant individuals or within small taxonomic groups[20]. Studies of complexity of brain function, on the other hand, can give much information about ability as well as about welfare[21].

Where there is reference to the brain of animals in discussions of their complexity, there has sometimes been an assumption that nearness in structure to humans is the best estimate of sophistication. Rose[22], argues against the existence of pain and awareness in animals other than mammals on the basis that these other animals do not possess the brain structures needed for awareness in mammals However, such arguments should take account of function rather than anatomy alone. We may also over-emphasise visual analysis, even though other senses have a more primary role in the lives of many animals. Rose[23] also points out that associative learning occurs in decorticate mammals and that decorticate humans can show aversive responses to noxious stimuli.

Awareness is a state in which complex brain analysis is used to process sensory stimuli or constructs based on memory[24]. There are degrees of awareness: perceptual, cognitive, assessment and executive, with different levels of sophistication of concepts[25]. For example, in assessment awareness the individual is able to assess and deduce the significance of a situation in relation to itself over a short time span. The individual would not only be sensible to stimuli but would have memory of events and mental images of non-current events that could be used when taking appropriate action, both to avoid the negative and to increase positive consequences. This definition of awareness includes the somewhat imprecise concept "complex brain analysis" but a more accurate definition is not yet available.

Does ability to learn indicate a level of awareness? Animals are more likely to be considered sentient if they can learn much, learn fast and make few errors once they have learned. However, isolated ganglia from various organisms show changes commensurate with learning and a headless locust can learn aversive foot-shock conditioning[26]. Learning is not, in itself, evidence for awareness but is an indicator

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[19] Jerison, H.J. 1973. *Evolution of Brain and Intelligence.* Academic Press: New York, USA; Hemmer, H. 1983. *Domestikation.* Braunschweig: Viewig. (Translated 1990. Cambridge University Press: Cambridge, UK).

[20] Barton, R.A. and Dunbar, R.I.M. 1997. Evolution of the social brain. In: *Machiavellian Intelligence II* pp.240-263. (Eds) Whiten A. and Byrne R.W. Cambridge University Press: Cambridge, UK; Broom, D.M. 2003. *The Evolution of Morality and Religion*. Cambridge University Press: Cambridge, UK.

[21] Broom, D.M. and Zanella A.J. 2004. Brain measures which tell us about animal welfare. *Animal Welfare* 13: S41-S45 Supplement.

[22] Rose, J.D. 2002. The neurobehavioral nature of fishes and the question of awareness and pain. *Review of Fisheries Sci*ence, 10, 1-38.

[23] *Ibid*.

[24] Broom, D.M. 1998. Welfare, stress and the evolution of feelings. *Advances in the Study of Behavior* 27: 371-403.

[25] Sommerville, B.A. and Broom, D.M. 1998. Olfactory awareness. *Applied Animal Behaviour Science 57*, 269-286.

[26] Carew, T.J., Sahley, C.L. 1986. Invertebrate learning and memory: from behavior to molecules. *Annual Review of Neuroscience 9*: 435-487.

that further investigation of cognitive ability might reveal the existence of awareness commensurate with sentience.

In consideration of the welfare of animals, their abilities to cope with their environment and the ways in which they might be harmed are clearly relevant. The qualities listed in Table 1, including cognitive ability, awareness and capacity to have feelings are key issues.

3. WHAT LEARNING, COGNITION AND AWARENESS HAVE BEEN DEMONSTRATED IN INVERTEBRATES?

There are many descriptions of conditioning, habituation and associative learning in a wide range of invertebrate taxa. For example, classical conditioning and operant conditioning can occur in the swimming sea-slug *Aplysia*[27], This would require at least cognitive awareness.

Fruit flies *Drosophila* have been demonstrated to show associative conditioning, incidental learning, contextual learning and second order conditioning[28]. Context specific learning has also been described in the swimming sea-slug *Aplysia* and in the pond snail *Lymnaea.*

Cockroaches can show place learning[29] which may indicate an awareness of a place when the animal cannot detect it directly, implying assessment awareness. Is there other evidence of awareness of a place or object in the absence of cues from that place or object? Both honeybees *Apis mellifera*[30] and ants[31] have been described as having the ability to form cognitive maps. This implies that information obtained at different points on a journey is gathered together in an allocentric representation[32], thus the individual has a concept of spatial relationships without being able to perceive cues relevant to them at the time. The ability of the jumping spider *Portia* to look at a maze, move out of sight of it and then choose the optimal route through the maze when they can only see the entry point[33] is impressive evidence for awareness in the absence of a cue, perhaps even executive awareness.

Reznikova also described ants learning by observation, counting while foraging and transmitting learned information to other ants. The ability of honeybees to transmit

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[27] Lorenzetti, F.D., Mozzachiodi, R., Baxter, D.Q., Byrne, J.H. 2006. Classical and operant conditioning differentially modify the intrinsic properties of an identified neuron. *Nature Neuroscience* 9: 17-19.

[28] See review by Greenspan, R.J., van Swinderen, B. 2004. Cognitive consonance: Complex brain functions in the fruit fly and its relatives. *Trends in Neurosciences* 27: 707-711.

[29] Mizunami, M, Okada, R., Li, Y., Strausfeld N.J. 1998. Mushroom bodies of the cockroach : activity and identitities of neurons. *Journal of Comparative Neurology*, 519, : 501-519.

[30] Menzel, R., Greggers, U., Smith, A., Berger, S., Brandt, R. 2005. Honeybees navigate according to a map-like spatial memory. *Proceeding of the National Academy of Sciences,* 102, 3040-3045.

[31] Reznikova, Z. A. 2003. Government and nepotism in social insects: new dimension provided by an experimental approach. *Eurasian Entomology Journal*, 2, 1-12; Reznikova, Z.A. 2007. *Animal Intelligence: from individual to social cognition.* Cambridge: Cambridge University Press.

[32] Shettleworth, S, J. 2010. *Cognition, Evolution and Behavior, 2nd edition.* Oxford: Oxford University Press.

[33] Tarsitano, M. S., Jackson, R. R. 1994. Jumping spiders make predatory
detours requiring movement away from prey. *Behaviour* 131: 65-73. Tarsitano, M.S. and Jackson, R.R. 1997. Araneophagic jumping spiders discriminate between detour routes that do and do not lead to prey. *Animal Behaviour* 53: 257-266.

information on returning to the hive after foraging has been known for many years. The ants and the bees must be remembering information about their spatial movements when transmitting such information to others. Bees are able to discriminate patterns, generalise, e.g. sameness versus difference or symmetry versus asymmetry, and use information in a novel situation[34]. There are reports that bees can be trained to locate and indicate land mines by their odour. It would seem that these insects have assessment awareness.

Predatory fireflies *Photuris* mimic the signals of other flrefly species, attract males and eat them. The flashing pattern used in this deception is changed to that of another potential prey species if the flashing of that second species is the most frequent in a given location. In addition, when prey use counter-measures, the predator also changes signals and behaviour[35]. The complexity of these responses cannot be accounted for by automatic processes so quite sophisticated cognitive ability is indicated. Stomatopod Crustacea, such as *Squilla*, also use deception in contests with other individuals[36].

In other studies of the jumping spider *Portia,* Jackson and Wilcox[37] have found them to have a very sophisticated ability to evaluate when to jump, to assess where to jump accurately onto the prey, and also to show deception and modify movements in accordance with the circumstances. During predation on other spiders, *Portia* and other arachnophagic species deceive the prey while gaining information which optimises their attack strategy[38]. These spiders must have some awareness of themselves in relation to the environment and of an event to come in the future, i.e. the jump onto the prey, so again, executive awareness is implied. The cognitive ability exhibited by these spiders is great but they require a much longer time for the brain analysis than would a vertebrate, which has a much larger brain. The occurrence of play behaviour has been suggested as evidence for assessment awareness. Pruitt et al[39] reported that the spider *Anelosimus studiosus* showed repeated behaviour before mating, that could be regarded as practice or play, and were more successful at mating as a consequence. The term "play" here is often taken to imply a positive feeling in the mammalian literature.

4. ARE THE TERMS EMOTION, FEELING, PAIN AND SUFFERING APPROPRIATE FOR ANY INVERTEBRATES?

[34] Giurfa, M., Eichmann, B., Menzel, R. 1996. Symmetry perception in an insect. *Nature* 382,458 *-461;* Giurfa M., Zhang S., Jenett A., Menzel R., Srinivasan M.V. 2001. The concepts of 'sameness' and 'difference' in an insect. *Nature.* 410: 930-931; Giurfa, M. 2007. Behavioral and neural analysis of associative learning in the honeybee: a taste from the magic well. *Journal of Comparative Physiology,* 193, 801-824.

[35] Lloyd, J. E. 1986. Firefly communication and deception, oh what a tangled web!. In *Deception,* ed. R.W. Mitchell and N.S. Thompson, 113-128. SUNY Press: Albany, N.Y.

[36] Caldwell, R.L. 1986. The deceptive use of reputation by stomatopods. In *Deception,* ed. R.W. Mitchell and N.S. Thompson, 129-145. SUNY Press: Albany, N.Y.

[37] Jackson, R.R. and Wilcox, R. S. 1994. Spider flexibly chooses aggressive mimicry signals for different prey by trial and error. *Behaviour*, 127, 21–36. Wilcox, R.S., R.R. Jackson. 1998. Cognitive abilities of araneophagic jumping spiders. In *Animal cognition in nature*. I. Pepperberg, R. Balda, A.Kamil, eds. 411-433, San Diego: Academic Press.

[38] Jackson, R.R., Cross, F.R. 2011. Spider cognition. *Advances in Insect Physiology,* 41, 115-174.

[39] Pruitt, J. N., G. Iturralde, L. Avilés, S. E., Riechert. 2011. Amazonian social spiders share similar within-colony behavioral variation and behavioral syndromes. *Animal Behaviour* 82:1449–1455.

A crucial issue in this discussion of possible sentience in invertebrates is whether or not the animals have emotions or feelings. A **feeling** is a brain construct involving at least perceptual awareness which is associated with a life regulating system, is recognisable by the individual when it recurs and may change behaviour or act as a reinforcer in learning[40]. Where feelings are described, it is sometimes possible to measure physiological aspects, in which case the term emotion can be used. An **emotion** is a physiologically describable condition in individuals characterised by: electrical and neurochemical activity in particular regions of the brain, autonomic nervous system activity, hormone release and peripheral consequences including behaviour.

The ability to feel pain is generally included amongst the capabilities of sentient animals. Pain is an important cause of poor welfare but the pain system also includes both simple sensory aspects and complex brain analysis. In humans, nociception is considered by some to be the physiological relay of pain signals; an involuntary, reflex process not involving the conscious parts of the brain. However, the separation of one part of the pain system from other parts by the use of the term nociception has been criticised because the system should be considered as a whole[41]. Pain leads to aversion, i.e. to behavioural responses involving immediate avoidance and learning to avoid a similar situation or stimulus later. Pain has a sensory component often related to injury but also requires complex brain functioning of the kind associated with a feeling. Kavaliers[42] suggested, based on the International Association for the Study of Pain definition[43], that for non-humans, pain is 'an aversive sensory experience caused by actual or potential injury that elicits protective motor and vegetative reactions, results in learned avoidance and may modify species specific behaviour, including social behaviour'. More simply, Smith and Boyd[44] considered pain to be the conscious, emotional experience that, in humans, involves nerve pathways in the cerebrum. A definition of pain should refer to the sensory and emotional aspects, and the reference to function and consequences is not needed as it may unnecessarily restrict its meaning. Accordingly, Broom[45] defined **pain** as an aversive sensation and feeling associated with actual or potential tissue damage. If pain occurs in an animal, it can cause poor welfare. The degree of awareness in animals that can feel pain will vary but many people consider that it is not necessary to protect a group of animals

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[40] Broom, D.M. 1998. Welfare, stress and the evolution of feelings. *Advances in the Study of Behavior* 27: 371-403.

[41] Wall, P.D. 1992. Defining "pain in animals". In: *Animal Pain*. 63-79. (Eds) Short, C. E. and van Poznak, A. Churchill Livingstone: New York, USA; Broom, D.M. 2001. Evolution of pain. In: *Pain: its nature and management in man and animals. Royal Society of Medicine International Congress and Symposium Series* 246: 17-25. (Eds) Soulsby E.J.L and Morton D.

[42] Kavaliers, M. 1989. Evolutionary aspects of the neuromodulation of nociceptive behaviors. *American Zoologist* 29: 1345-1353.

[43] P. Iggo, A. 1984. *Pain in Animals.* Universities Federation for Animal Welfare: Potters Bar, Hertfordshire, UK.

[44] Smith, J. A., K. M. Boyd. 1991. *Lives in the Balance: The Ethics of Using Animals in Biomedical Research* (Report of a Working Party of the Institute of Medical Ethics). Oxford: Oxford University Press.

[45] Broom, D.M. 2001. Evolution of pain. In: *Pain: its nature and management in man and animals. Royal Society of Medicine International Congress and Symposium Series* 246: 17-25. (Eds) Soulsby E.J.L and Morton D.

unless they have the capability to feel pain. The definition of pain used here depends on the term feeling, and that in turn depends on the definition of awareness. The issue of whether or not there is complex brain analysis in invertebrate animals is discussed here. There is a gradation in complexity of brain analysis so different scientists will put the threshold in different places.

Many kinds of aquatic and terrestrial animals have a pain system involving receptors, neural pathways and analytical centres in the brain. There is also evidence from many animal groups of physiological responses, direct behavioural responses and ability to learn from such experiences so that they are minimised or avoided in future. This suggests the existence of feelings of pain in many species. Feelings, such as pain, fear and various kinds of pleasure, will often be an important part of the biological mechanism for coping with actual or potential damage. Sometimes the response is to avoid whatever is causing the damage. Consequent learning allows the minimising of future damage and, where the pain is chronic, behaviour and physiology can be changed to ameliorate adverse effects. Pain systems have been identified by anatomical and physiological investigation and by studies of behavioural responses, particularly with the assistance of analgesic administration as an experimental probe.

Species differ in their responses to painful stimuli as different responses are adaptive in different species. The feeling of pain may be the same even if the responses are very different. However, even if immediate responses vary, avoidance of the painful stimulus and the effects of learning to avoid such stimuli on subsequent exposure to the stimulus, would be observable in invertebrates. Other feelings such as fear, anxiety and the various forms of pleasure may be deduced to exist by careful observation and experiment. The word suffering is used when the individual has one or more bad feelings continuing for more than a short period.

Many invertebrate animals have elements of a pain system[46] so a first question is whether or not the animal under consideration has the components of a pain system. Have they got nociceptors (pain receptors), pathways and analysis potential. Nociceptors have high thresholds and show little or no adaptation with continuing stimulation. A second question is whether they show avoidance responses, other behaviours in response to tissue damage, or physiological responses such as increases in cortisol in body fluids. A third question concerns later responses such as in acute phase proteins, or immune system function, or longer term behaviour changes. A fourth mechanism is the suppression of responses, for example by endogenous opioids. If such a system exists it may be mimicked by analgesics. Anaesthetic activity implies blocking of receptors, pathways or analytical centres.

Leeches, e,g. *Hirudo* have mechanoreceptors that fulfil the criteria for nociceptors. It is likely that many other invertebrates have such receptors. However, vertebrate animals utilise both specialist nociceptors and normal receptors to gain information about actual or potential tissue damage. Hence, whilst the presence of specialist

[46] Sherwin, C.M. 2001. Can invertebrates suffer? Or, how robust is argument-by-analogy? *Animal Welfare* 10:S103-S118 Suppl.

nociceptors is evidence for the presence of part of a pain system, their absence does not mean that no pain sensation can occur. Behavioural avoidance of sources of potential or actual tissue damage is shown by sea anemones, earthworms and most other invertebrate animals[47]. However, this does not tell us that they feel the consequences of damage. It is of interest that leeches and the swimming sea slug *Aplysia* are used as models in vertebrate pain studies[48]. Clearly the similarities in the components of the pain system that they possess are sufficient for extrapolation to vertebrates. Studies of humans, mice and the fruit fly *Drosophila* have revealed the existence of genes that seem to be involved in aspects of pain in each animal[49]. Rather than using the word nociception for mechanisms in invertebrates and pain for similar processes in vertebrates, the central issue to consider is the degree of analysis of the incoming information?"

The receptors, transmission system and some analysis that could be part of a pain system are reported from many invertebrate groups, for example earthworms and other annelids, gastropod molluscs and insects[50]. Insects poisoned with DDT, or restrained, often struggle or show convulsions. Such a reaction could indicate pain but may not. If an animal has a substantial injury but continues to show attempts to carry out normal movements, does this mean that it does not feel pain consequent upon the injury? Several insect species have been observed to continue walking after their foot has been crushed. Locusts may continue eating when being consumed by a praying mantis and aphids may do the same when eaten by a coccinelid (ladybird) beetle[51]. This may mean that they feel no pain but there are parallels with mammals that do not show active responses when predators injure them even when physiological responses characteristic of pain are occurring[52]. The avoidance of an active response can be adaptive and save the life of the individual. Spiders, e.g. *Argiope*[53]can respond to mechanical pressure on the body by autotomising limbs. So can some insects whilst lizards may autotomise the tail. Does this mean that they do not feel pain? I see no logic in deducing this.

Opioids have an important role in the natural regulation of mammalian pain. These have many different functions in animals, almost certainly with some differences in the various phyla. However, they are present in most invertebrates and often seem to

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[49] Neely' G.G., Keene, A.C., Duchek, P., Chang, E.C., Wang, O-P., Aksoy, Y.A., Rosenzweig, M., *Costigan, M., Woolf, C.J., Garrity, P.A. and Penninger, J.M. 2011. TrpA1 Regulates Thermal* Nociception in *Drosophila. PLOS One,* 6, 1-9.

[50] Stefano, G.B., Cadet, P., Zhu, W., Rialas, C.M., Mantione, K., Benz, D., Fuentes, R., Casares, F., Fricchione, G.L., Fulop, Z., Slingsby, B. 2002. The blueprint for stress can be found in invertebrates *Neuroendocrinology Letters* 23: 85-93.

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[52] Broom, D.M. 2001. Evolution of pain. In: *Pain: its nature and management in man and animals. Royal Society of Medicine International Congress and Symposium Series* 246: 17-25. (Eds) Soulsby E.J.L and Morton D.

[53] Fiorito, G. 1986. Is there 'pain' in invertebrates? *Behavioural Processes,*12, 383-388.

be associated with suppression of responses to injury[54]. Earthworms show wriggling and escape responses when injured and these responses are suppressed by naloxone, an opioid inhibitor. The defensive response of the mantis shrimp *Squilla,* a stomatopod crustacean, is inhibited by morphine and blocked by naloxone[55]. Honeybees *Apis mellifera* and praying mantis *Stagmatophora biocellata* are among the insects known to produce opioids during defensive reactions and to have opioid receptors that are blocked by naloxone, as in humans and other vertebrates. Snails *Cepaea nemoralis* lift part of their foot if it is in contact with a surface that is being warmed to 40C[56]. Several opioids have been found to inhibit this response. Slugs and other molluscs have opioids and naloxone inhibits their action. It is unlikely that the opioid systems have arisen independently during the evolution of the various invertebrates and the vertebrates.

Ross et al[57] have produced a book that includes a variety of methods for using anaesthesia and analgesia for invertebrate animals. Some anaesthetics suppress movement in a way that would be useful for a veterinary surgeon or experimenter. However, such a book would be of little use if there were no pain in these animals. Analgesic action does imply that pain is occurring but in many cases we do not know how analgesics or anaesthetic is acting. As with humans and other vertebrates, stopping responses to tissue damage does not necessarily mean that there is pain or that pain is stopped. A worm or mollusc that is injured, and perhaps writhing, may be feeling pain but could be showing an automatic response. The change in scientific thinking is that the weight of evidence for some of these animals now indicates that they may be feeling pain. Walters and Moroz[58] review evidence for memory of injury in molluscs, principally *Aplysia*. If these animals can remember injury, their experience must be close to pain.

Experiments demonstrating cognitive bias have been carried out with several domestic animals species. These have been interpreted as evidence for positive and negative feelings in the animals involved. A study by Bateson et al[59] produced a similar result with bees. Mendl et al[60] concluded from this that bees may have an ability to have positive and negative feelings. Whilst this may be true, another explanation could be that a close look at the strategies used by the animals in the

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[54] Stefano, G.B., Salzet, B., Fricchione, G.L. 1998. Enkelytin and opioid peptide association in invertebrates and vertebrates: immune activation and pain. *Immunology Today* 19, 265-268; Dyakonova, V.E, 2001. Role of opioid peptides in behavior of invertebrates. *Journal of Evolutionary Biochemistry and Physiology* 37: 335-347.

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[60] Mendl, M., Paul, E.S., Chittka, L. 2011. Animal behaviour: emotion in invertebrates? *Current Biology*, 21: R463–R465.

course of this and other cognitive bias experiments could indicate a different reason for the cognitive bias result in both the vertebrates and the bees[61].

As explained above and by Broom[62] animals that are sentient have a wide array of ways in which their welfare can be poor. Actually or potentially harmful events might be more readily recognised and receive more attention as a result of the cognitive ability of the animal. For some sentient animals, pain can be especially disturbing on some occasions because the individual concerned uses its sophisticated brain to appreciate that such pain indicates a major risk. However, more sophisticated brain processing will also provide better opportunities for coping with some problems. For example humans may have means of dealing with pain that animals with simpler brains do not have and may suffer less from pain because they are able to rationalise that it will not last for long. As a consequence, in some circumstances humans who experience a particular pain might suffer more than other animals, whilst in other circumstances a certain degree of pain may cause worse welfare in those animals than in humans[63]. These arguments will also be valid for other causes of poor welfare. Fear is likely to be much greater in its impact if the context and risk cannot be analysed. In addition, more complex brains should allow more possibilities for pleasure and this contributes greatly to good welfare.

Some aspects of the pain system exist in leeches, insects, snails and swimming sea-slugs. However, we cannot be sure that these animals feel pain, or that they do not feel pain.

Conclusions from the data presented

1. Our knowledge of the functioning of the brain and nervous system and of animal welfare has advanced rapidly in recent years. Some of this new knowledge concerns invertebrate animals.

2.More sophisticated brain processing will provide better opportunities for coping with some problems, for example, dealing with pain. As a consequence, a certain degree of pain and other poor welfare may cause worse welfare in the simpler animals than in humans.

3.Spiders have substantial cognitive ability and perhaps executive awareness and some insects such as bees and ants have quite high cognitive ability and probably assessment awareness.

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[61] Broom, D.M. 2010. Cognitive ability and awareness in domestic animals and decisions about obligations to animals. *Appl. Anim. Behav. Sci,* 126, 1-11.

[62] Broom, D.M. 2006. The evolution of morality. *Applied Animal Behaviour Science*, 100: 20-28; Broom, D.M. 2007. Cognitive ability and sentience: which aquatic animals should be protected? *Diseases of Aquatic Organisms,* **75**: 99-108.

[63] Broom, D.M. 2001. Evolution of pain. In: *Pain: its nature and management in man and animals. Royal Society of Medicine International Congress and Symposium Series* 246: 17-25. (Eds) Soulsby E.J.L and Morton D.; Broom, D.M. 2006. *Ibid*.; Broom, D.M. 2007. Cognitive ability and sentience: which aquatic animals should be protected? *Diseases of Aquatic Organisms,* **75**: 99-108.

4. Some aspects of the pain system exist in leeches, insects, snails and swimming sea-slugs. However, we cannot be sure that these animals feel pain, or that they do not feel pain.

5.There is a case for some degree of protection for spiders, gastropods and insects. However, the case is not as strong as that for vertebrates, cephalopods and decapod Crustacea at present.

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