

Neuroscience and Animal Sentience

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A. Introduction

To what degree do non-human animals experience emotion? How sophisticated are primates' cognitive capabilities? Do our companion pets experience consciousness? These are some of the questions that shape the intriguing interdisciplinary research field of animal sentience. Roughly defined as the capacity for emotion, pleasure and pain, sentience is related to other brain capabilities of intelligence and consciousness. Together these shape a growing field that pushes the boundaries of knowledge and carries moral and practical implications for humans' use of animals.

Research into animal sentience is emerging from neuroscience, evolutionary biology, zoology and philosophy, employing a variety of approaches and methods. Neuroscientists have conducted experimental brain lesioning and stimulation to map the neuroanatomy and neurochemistry of emotion. Researchers have done brain scanning on monkeys performing cognitive tasks, electrical recording on neural cells of shrews and post-mortem analyses of the brains of whales. Biologists have observed species' behavioural and physiological responses to potentially emotional or painful situations and have employed experimental studies to assess animals' preferences and choices. Evolutionary scientists, psychologists and philosophers have examined the adaptive value of emotion, of pleasure and of pain for motivation and for survival. Sentience has both broad and narrow definitions, but may be applied to species which philosopher Tom Regan (2006) calls subjects-of-a-life, aware of what happens to them and that events affect their lives. One working definition is that "sentient creatures are those who have feelings – both physical and emotional -- and whose feelings matter to them" (D'Silva, 2006, xxiii).

Paradoxically, many studies demonstrating animal sentience and awareness have been performed using captive mammals including primates. The results from these studies beg questions about

humans' use of animals for research as well as for other purposes such as animal agriculture. The findings suggest the need for scientific methods that rely less on animal subjects and underscore the necessity for increased awareness of animal sentience.

B. Evidence for sentience

B.1. Emotional brains are similar across species.

The past few decades have seen an explosion of research in comparative neuroanatomy, findings from which have altered scientific views of animals' abilities and of evolution itself. Analyses of brains across many species have demonstrated even greater structural and functional similarities than had previously been assumed. The research emphasizes continuity across species and suggests that humans are not so different from other animals after all.

The central nervous system, with the brain and spinal cord, exists in all vertebrates from apes to bats to fish (Butler, 2008). Even some invertebrates such as insects and snails have central nervous systems. Although these are relatively simple they can take in sensory information, they can learn and can initiate action. A few large invertebrates such as octopi have particularly impressive nervous systems (Butler and Hodos, 2005). All vertebrates including fish have brains with the same major structures and divisions (Butler, 2008a; Squire *et al.*, 2002), reflecting a "common ancestry and the need to perform similar vital functions" (Laberge, 2006, 177). The genes underlying nervous system development have been virtually unchanged throughout evolution (Butler, 2008a). Even the recently-evolved neocortex exists in some form in all vertebrates including birds and reptiles (LeDoux, 1996).

One glance at post-mortem brains in the lab shows that the human brain is larger than that of most species – mostly due to an enlarged cerebrum or cortex both in absolute size and relative to the rest of the brain. This evolutionary 'encephalization' has produced more complexity and more interconnections than in most species. But the human brain is not the largest among species and some animals also have a complex cerebrum, a topic furthered discussed in section C.1 below. The human cortex contains neurons numbering in the trillions (about 1.2×10 to the 10^{th} power) but large cetaceans and elephants have almost as many (Roth and Dicke, 2005a). Despite the elaboration of the human brain, research today suggests that animal species are structural and functional variations on a theme.

Neurons, the brain's building blocks, are also similar across species. Some complex neurons have been considered unique to humans, but even this is questionable following studies demonstrating that humpback whales possess cortical spindle cells (Hof and Van der Gucht, 2006) specialized for emotional processing and that macaque monkeys have mirror neurons that assist in empathic behaviour and learning (Damasio and Meyer, 2008). Some scientists caution against overstatement of human-animal similarities, however, and Premack (2007) points to structures and connections that may still suggest humans are unique.

Just as for the brain as a whole, it is clear that for the brain's emotion systems humans and animals are alike. There is no single, easily-delineated part of the brain that produces happiness, sadness, jealousy and pain. But the brain region best understood to mediate emotion is called the limbic system, located atop the spinal cord and brainstem, roughly between the ears. Both the limbic system, and the sensory input to it, are "strikingly similar" among vertebrates (Butler, 2008a, 6). Joseph LeDoux, a neural scientist and author of the acclaimed book *The Emotional Brain* (1996), says all animals have some form of that brain. According to Jaak Panksepp (2005), an expert in affective neuroscience, raw emotional experience may reflect "an ancient form of consciousness" (57) because the underlying systems are so alike between humans and other animals. For animal scientist Temple Grandin, it is clear that all animals and people have "the same core emotion systems in the brain" (2009, 5).

At a detailed level, neurologist Antonio Damasio (2001) outlines the brain's chief emotion systems as being within the hypothalamus, an area called the basal forebrain just above the chin, the

brainstem and other limbic areas including the amygdala. The latter is known to mediate fear in both humans and animals. All vertebrates have a hypothalamus containing at least some of the important nuclei present in the human brain (Butler and Hodos, 2005). All mammals have an amygdala as do all vertebrates including amphibians (Barton *et al.*, 2003; Laberge *et al.*, 2006), though there are small differences in how cell groups operate (Dumont *et al.*, 2002). Fish have a brain region in the medial pallium or mid-cortex which appears to be homologous to the amygdala (Broglia *et al.*, 2005) meaning with common evolutionary ancestry and purpose. Most experiments on the amygdala are performed in rats and other mammals because the similarities are so strong that the research can be extrapolated to humans (Berridge, 2003; LeDoux and Schiller, 2009).

When humans or animals experience emotion, higher regions of the cortex may sometimes be involved. For example, one area called the ventromedial prefrontal cortex can trigger emotion (Damasio, 2001). Yet cortical areas are not required for most basic emotion, which supports the idea that animals without a large cortex can be sentient. Emotion is generated largely from sub-cortical, internal brain regions that are similar across species (Damasio, 2001; Berridge, 2003; LeDoux, 1996). Damasio (2001) distinguishes between emotions and feelings – emotions as automatic physical responses from lower and middle brain regions, versus feelings as higher-order mental representations resulting from emotion. Case studies from psychology support the contention that emotion is a product of lower brain areas. Clinical cases show that humans with higher cortical damage continue to experience emotion, but often have trouble mustering socially acceptable responses and instead show anger and frustration (Pinel, 2007).

A few researchers have suggested that animals need significant cortex to experience emotion such as suffering (Bermond, 2003). But most do not agree and Berridge (2003) points out that while research on humans can show cortical involvement in emotion, that may be an artifact of methodology, which can “exaggerate the perceived difference between humans and other animals” (26).

B.2. Animals experience pain.

To be sentient, animals need to be able to process pain. For that, they need pain receptors or ‘nociceptors’ near the body surface, as well as the chemicals, nerve pathways and brain structures to record and interpret the information and cause the organism to act. As with the whole brain and the emotional brain, many species possess the neural structures for awareness of pain. Neuroanatomists Butler and Hodos (2005) say that although most pain research has been conducted on mammals, other simpler vertebrates have the neuroarchitecture to allow them to identify stimuli that hurt.

A fascinating question for sentience is: Where do we draw the line? (Kirkwood, 2006). Fish are considered rather lowly creatures, but it turns out that fish have the biological requirements for pain sensitivity (Sneddon, 2002, 2004; Chandroo *et al.*, 2004). Evidence from anatomy, pharmacology and behaviour suggest that numerous teleosts or bony fishes have the capability to experience pain (Chandroo *et al.*, 2004; Braithwaite and Huntingford, 2004). Lynne Sneddon (2004) found that fish have pain receptor systems similar to those of complex vertebrates, that they produce natural pain-killing opioids, and that they respond to morphine. A few researchers contend that fish merely exhibit “behavioural responses to noxious stimuli” (Rose, 2002, 1) and lack brain regions essential for pain. But others vociferously disagree. For example, Broom (2008) points out that when fish receive input from their nociceptors their brains are active. Furthermore, Webster (2005) suggests that while fish may not have pain-related brain regions identical to those of mammals, the data are clear that fish know fear and pain. He argues that: “It now becomes the responsibility of the neuroanatomist to seek out sites in the fish brain that do respond to painful stimuli” (61).

The degree to which invertebrates experience pain is less certain. Worms, snails and octopi have been thought to lack the neural hardware and to have less need for pain awareness because they are short-lived and rely on pre-programmed behaviour. But Sherwin (2001) summarizes intriguing studies showing that cockroaches, flies and slugs show “behavioural and physiological responses indicative of pain” (103). Mather (2001) has demonstrated that large-brained cephalopod molluscs

such as octopi may have “the potential for pain and suffering” (151). A report for the Norwegian Scientific Committee for Food Safety showed that numerous invertebrates produce opioids (Somme, 2005). It said the evidence for invertebrate pain awareness is insufficient but that cephalopods such as octopi should perhaps be given the benefit of the doubt.

Chickens have provided evidence for animal sentience, after researchers demonstrated that lame birds can learn to self-medicate pain-killers. Working with chickens in commercial flocks, Danbury *et al.* (2000) showed that lame animals voluntarily chose to consume feed containing the analgesic carprofen, rather than regular feed. Lame chickens consumed significantly more of the therapeutic feed than did other birds, and the medicated feed improved their gait. Field observations of various species have supported this idea. Chimpanzees with stomach upset have sought out particular shrubs, later analyzed and found to have medicinal properties, and monkeys have rubbed themselves with chili plants to kill disease-carrying insects (Engel, 2002). The evidence therefore converges to demonstrate that many non-human animals experience pain.

B.3. Neurochemical evidence supports animal sentience.

Neurotransmitters, hormones, and chemicals, the software of neural communication, are much the same in non-human animals as in people. As well, species after species has been shown to respond like humans to drugs classified as psychoactive, affecting emotion, cognition, or behaviour. This provides strong evidence that non-human animals experience emotion, pleasure and pain, all of which are physically transmitted through the body and brain by chemicals.

Research on human neurochemistry is often conducted using animals, some of which have been shown to produce endorphins or natural opiates, epinephrine (adrenaline) and the neurotransmitters dopamine and serotonin, all key to emotional states (Panksepp, 1998; Pinel, 2007). Dopamine is produced during pleasurable activities, in people and in some species. Rats and other animals release dopamine during eating and sex and goldfish prefer to swim in locations where they have received amphetamine, which stimulates the release of dopamine in their brains (Balcombe, 2006c). These neurochemicals have existed in their current forms virtually unmodified throughout evolution, though their functions may have altered (Butler and Hodos, 2005). Even the sea pansy, a relative of the jellyfish, uses dopamine (Balcombe, 2006c).

Drug research offers further evidence that animals are endowed with neurochemical emotion systems. Routinely used as subjects in pharmaceutical studies, many mammals have human-like molecular brain receptors that respond to therapeutic and recreational drugs. Hundreds of studies have been conducted on Prozac alone, administering the antidepressant to animals and assessing their mood. Some mice given fluoxetine (Prozac) display less anxiety and depression afterward (Dulawa *et al.*, 2004). Heroin, cocaine and other socially problematic substances have also been studied in species that voluntarily self-administer drugs in the same situations as human addicts. Animals' personalities even affect their drug-taking, and impulsive rats tend to self-administer more cocaine than do non-impulsive rats. (Dalley *et al.*, 2007). Non-human neurochemistry offers strong data in support of animal sentience.

B.4. Animals behave emotionally.

Anyone with a dog has witnessed behaviour suggesting animal emotion. In the home, in the lab, or in the wild, animals display by their actions that they have likes and dislikes, and that events affect them positively or negatively. Sceptics dismiss single observations as unscientific, but the sheer number of reports is notable. Scientific assessment of animal emotion has been considered inhibited by the language barrier. But emotion is difficult to assess even in humans who often have trouble clearly articulating emotional experience.

Neuroscientists, nevertheless, regularly assess animal emotion to test the effectiveness of psychoactive drugs. Popular tests for depression and anxiety are the ‘tail suspension’ and ‘forced swim’ procedures (Dulawa *et al.*, 2004). In a tail suspension test, mice are suspended from a lever to see how long they will fight to regain a normal posture in this situation of inescapable stress.

After a time, the mice stop writhing and become immobile. Antidepressant drugs “reverse the immobility” (Cryan *et al.*, 2005, 571) and increase the escape attempts. In the forced-swim test, mice are put into pools from which they cannot climb out. The animals exhibit what scientists describe as vigorous activity, which others might call panic, then freeze into immobility. Antidepressant medications encourage the animals to continue their attempts at escape. Anxiety is also assessed in rodents, including by their willingness to explore a frightening open area and by their tendency to eat when hungry even in new and unknown environments (Dulawa *et al.*, 2004). These methods provide strong evidence that animals are capable of experiencing emotion.

Other scientists have developed alternative means for assessing animal emotion, and have demonstrated that animals have preferences. Oxford University professor Marian Dawkins pioneered motivation analysis, allowing humans to ask what animals want and how much they want it (Dawkins, 2006a, 2006b; Webster, 2005). Such methods can determine whether animals tend to choose one situation or another and how much effort or resources they are willing to expend. So it has been shown that rats will lever-press more to get into a cage containing other rats than to get into larger cages or cages containing pillars or novel objects, illustrating rodents’ social needs (Patterson-Kane *et al.*, 2002; Dawkins, 2006b). Mink which are farmed for their fur will perform difficult tasks including pushing heavy doors to gain access to water baths (Mason *et al.*, 2001; Dawkins, 2006b). When frustrated from swimming, their favourite activity, mink release the stress hormone cortisol (Mason *et al.*, 2001). Animals press levers for food if they are hungry enough, and seek companions of one sex or the other depending on their state of sexual receptivity (Kirkden and Pajor, 2006).

Some preferences are powerful. Temple Grandin (2009) comments that hens will do virtually any amount of work to reach a nest box in which to lay their eggs. As prey animals, chickens get anxious when potentially exposed to predators, illustrating that captive animals can suffer even when not in physical pain simply from being denied the opportunity to perform natural behaviours (Grandin, 2009; Balcombe, 2006a). The drive of laying hens to seek nest boxes has also been demonstrated experimentally, suggesting that “the presence of a suitable nesting site for laying hens is a clear behavioural need, indeed a necessity of life” (Webster, 2005, 54).

Even invertebrates such as locusts, slugs and snails have been subjects in preference and consumer demand studies, and have shown that they too have priorities and take opportunities to make choices. Sherwin’s (2001) review showed feeding preferences in *Drosophila*, habitat preferences in beetles, and host selection preferences in some insects.

Animal welfare has motivated many studies, some of which have yielded poignant reminders of animals’ non-physical needs. In one study horses, given the choice of different bedding materials in two separate boxstalls, chose instead to stand in the intervening passageway – which offered the horses a view, albeit limited, of the yard and the outside world (Webster, 2005). Other studies have aimed to improve animal welfare by examining controversial practices. One such practice in factory farming is the castration of pigs without anaesthetic, routinely done in many countries producing pigs for meat. One research group measured the vocalizations of piglets undergoing such castration and found they screamed during the incisions, and even more as their spermatic cords were pulled and severed, producing much louder vocalizations than control animals that were not castrated (Taylor and Weary, 2000). The data are not surprising, though for common-sense observers the practice would be.

Behavioural research has demonstrated that animals show empathy, and have the capacity to recognize the moods or needs of another. Empathy has been reported extensively in primates (de Waal, 2005) and in a classic 1935 study of a chimpanzee in Russia (Kohts, 2002). Working in isolation in Stalinist Russia with the chimpanzee Joni, Kohts demonstrated scores of capabilities in the chimp, including empathy toward herself and others. Empathy has been widely observed in companion animals (de Waal, 2005; Bekoff, 2007). One recent series of experiments caused a stir by demonstrating that mice feel more or less pain depending on the situations of their cagemates. Langford *et al.* (2006) showed that mice exhibited increased or decreased pain response depending on whether they could see their cagemates being administered a noxious stimulus.

Commenting that empathy had been “thought to be unique to higher primates, possibly to humans alone” (1967), the authors suggest an alternative point of view.

B.5. Sentience is adaptive.

Emotion and its counterparts are not simply useful, but necessary for an animal to survive and reproduce. Whether to seek pleasurable situations or avoid painful ones, emotions motivate individuals and direct them to effective action. Damasio (1994) first noticed this phenomenon in a neurological patient whose brain damage disallowed emotion. Though highly intelligent, the patient had made “a succession of mistakes, a perpetual violation of what would be considered socially appropriate and personally advantageous” (xv).

Pain is highly adaptive. The rare individual who is unable to experience pain is in constant danger. Among humans, one young woman with congenital pain insensitivity suffered constant physical trauma. She once bit off the tip of her tongue while chewing food and she received third-degree burns kneeling on a radiator to look out a window. She died young of tissue damage and infections (Pinel, 2008).

Consciousness is also likely to be adaptive, in assisting with the problem of information overload – a problem not specific to human beings – and in helping summarize relevant information for the brain’s decision circuits (Pinker, 2007). One adaptive value of consciousness may be to produce the best possible interpretation of a situation and to make it available to areas of the brain that plan movement, speech, and other responses to the demands of the environment (Crick and Koch, 1998).

The evidence for animal sentience has helped shape recent evolutionary views that brain capabilities emerged independently in many different lineages. This disputes long-held notions of evolution as a unilinear phenomenon culminating in *Homo sapiens*. Neuroanatomical and other findings have resulted in a “reversal of the 19th century view that a dramatic change in brain evolution occurred with the evolution of mammals in general and humans in particular” (Butler and Hodos, 2005, xv). Today the taxonomy is seen not as an ascending scale, but as a branching tree in which competence developed in parallel among many species (Marino *et al.*, 2007; Patton, 2008).

C. Intelligence and consciousness

C.1. Intelligence and its relevance to sentience

Sentience is intertwined with other brain phenomena of intelligence and consciousness. Animal intelligence is a topic of fascination and vigorous research, from which new findings are constantly emerging. Animal consciousness is intriguing to neuroscientists and philosophers, and its role in sentience is a topic of debate.

Intelligence can be considered a collection of abilities that allow an animal to survive and thrive in its environment. Both for humans and animals, intelligence is assessed through tests of memory, problem-solving, abstract thinking, ability to plan and other related tasks. Intelligence is relevant to sentience in reflecting brain capacity and complexity, yet the two capabilities are not equivalent. Cognition may even help alleviate suffering by allowing animals to control their responses or give meaning to painful events (Webster, 2005). This ability is not solely human since rats are able to suppress pain when distracted or threatened. Just as human athletes in competition, and dancers in performance, can ignore and even fail to consciously register pain until they have the luxury of attending to it, so rats exposed to a cat will fail to notice painful heat applied to their tails (LeDoux, 1996). Cognition and sentience are rightly linked, in complex ways, in both the popular and the scientific imagination.

Brain size is commonly considered an indicator of intelligence and “the term ‘birdbrain’ is often used in a pejorative sense to insult someone’s intellect” (Butler and Hodos, 2005; 514). But like

other expressions dismissive of animals (it is usually derogatory to call someone a snake, a dog, a turkey, a donkey, or even a monkey) this one is unfair to winged creatures. Birds have sizeable brains relative to their bodies and according to recent studies, a long list of cognitive abilities.

Larger brains do have more neurons and interconnections, therefore more capacity for mental processing. But brain size may not indicate an individual's or a species' capacity to survive and thrive. Humans dominate the planet yet human brains are, on average, smaller than those of whales and elephants, consistent with the rough correspondence in vertebrates between brain and body size (Butler and Hodos, 2005; Pinel, 2007). Historically, researchers searched for measures indicating human superiority, and suggested that the most intelligent creatures might be those with the largest percentage of brain weight to body weight. This put people (2.33%) in front of elephants (0.20%) but still had humans, even scientists, trailing behind the shrew (3.33%) (Roth and Dicke, 2005a; Pinel, 2007). Other measures use mathematical allometry to indicate which animals have brains that are larger than expected for their body size. This puts primates on top but not much above other mammals and produces further surprises such as that cartilaginous fishes including sharks have brains that are relatively large (Butler and Hodos, 2005). This analysis reveals that birds have impressive cerebra and that the brains of parrots would be typical of a small primate of the same body weight. Brain size is therefore an uncertain measure of either intelligence or of sentience.

Systematic research has confirmed that many animals possess cognitive abilities previously considered unique to humans. Numerous species are now known to make and use tools including chimpanzees and crows (Goodall, 1993; Hunt and Gray, 2003). The tool use of New Caledonian crows is sophisticated, as the crows improve their tools over time and teach other members of the group to copy good designs (Hunt and Gray, 2003; Patton, 2008). Face recognition has been demonstrated in sheep, which remember a large number of other individual sheep and humans, and behave differently toward those they know (Kendrick *et al.*, 2001). Young pigs have the cognitive capacity to distinguish particular other pigs (McLeman *et al.*, 2008). Mirror self-recognition, suggesting self-awareness, has been shown in numerous species from elephants to magpies (Plotnik *et al.*, 2006; Prior *et al.*, 2008).

Scrub-jays can plan for the future and manage complex environmental conditions to make sure they will have the right kinds of food in the right kinds of places. Raby *et al.* (2007) showed that jays will cache food in locations where they have learned they will be hungry the following morning and they cache particular foods in locations where they have learned that food will not be available later. Jays are among the wider group of corvids that have impressive cognitive abilities (Emery and Clayton, 2004). Researcher Irene Pepperberg (2006) has shown that Grey parrots such as Alex can solve problems and use language like young children do.

Further studies have revealed that monkeys possess abstract notions of numerical quantity (Merten and Nieder, 2009); that whales and dolphins engage in cultural learning passed through generations (Rendell and Whitehead, 2001); and that chickens learn from watching each other and learn more from watching dominant conspecifics than nondominant ones (Nicol, 2006). Learning in animals has been demonstrated in many contexts and may go beyond classical conditioning to demonstrate an understanding of causation (Penn and Povinelli, 2007). Problem-solving by animals has been achieved in numerous contexts. Even in the early 20th century, Wolfgang Kohler showed that chimpanzees improvise by piling boxes so that they can climb and reach hanging bananas (Bernstein *et al.*, 2008). This contradicted the belief that animals use solely trial-and-error, and demonstrated that animals can have insight.

C.2. Consciousness and its relevance to sentience

Consciousness, that elusive first-person subjective experience that creates, or that is, awareness, is a topic of considerable research into who or what possesses this state of being. Humans do, and many researchers among them assume that at least some animals possess at least some levels of consciousness (Crick and Koch, 1998, 2003).

There is considerable evidence for animal consciousness. Griffin and Speck (2004) show that animals have sophisticated communication; that consciousness-related brain structures or processes are not unique to humans; and that animals respond to novel challenges for which they have not been prepared either genetically or through prior learning. A highly-developed cortex does not appear to be necessary for consciousness. Merker (2007) shows that mammals without large cortexes exhibit “purposive, goal-directed behaviour” (63) and that children born without a cortex are conscious. Pinker adds that language is not required for consciousness and that babies, “many animals” and some brain-damaged persons are conscious (Pinker, 2007, 1). Damasio (1999) sees animals as having a core consciousness providing a sense of self and depending on neither reasoning nor language. Crick and Koch (1998, 2003) specifically chose the macaque monkey on which to research consciousness.

Neuroscientists assume that consciousness is completely brain-based, though others have not been so certain. In an influential paper entitled *What is it like to be a bat?* (1974) philosopher Thomas Nagel argued that consciousness and similar phenomena are unlikely to be reducible to biology. Consciousness may not be necessary for sentience, which rests on the capacity to experience emotion, much of which is generated unconsciously (Damasio, 2001).

Consciousness is not necessarily present or absent, but may be more or less present in a situation, as demonstrated in psychological research (Bernstein *et al.*, 2008). When sleeping, adult humans are nevertheless monitoring the world and may waken even to a soft cry from their newborn child. We have all experienced driving a familiar route while day-dreaming, but we are nevertheless not driving entirely without consciousness. Even hospital patients under deep general anesthetic can later demonstrate awareness of conversations from the operating room (Schwender *et al.*, 1995). Consciousness therefore exists on a spectrum, supporting the idea that it could also exist to greater or lesser degrees among animal species. Richard Dawkins (1993) has criticized what he calls “the discontinuous mind” (81) which seeks to put beings or objects in categories rather than seeing complex phenomena as continuous. Humans are apes, says Dawkins, and should admit other great apes to “the charmed circle of human privilege” (87) to which they rightfully belong.

D. Conclusion

What is the minimum that animals need to qualify as sentient? Sentience involves the capacity for emotion and for pain, whether or not the experience is cognitively sophisticated or human-like. Sentience therefore requires the neural structures, networks and systems to register important stimuli and react to them as pleasant or aversive. As this paper has attempted to summarize, many species have such capacities. For this there is extensive converging evidence from experiments in neuroanatomy and neurochemistry, from behavioural studies of animals’ preferences and aversions, and from evolutionary understandings of the necessity for emotion if animals are to survive and thrive. All vertebrates appear to qualify as sentient, and some invertebrates may also.

Historically, animal capabilities have at times been widely accepted, as evidenced by Charles Darwin’s (1872) *The Expression of the Emotions in Man and Animals*, a best-seller in his day. However, animal emotion drew scientific scepticism for most of the 20th century, influenced by behaviourism (Duncan, 2006; Bernstein *et al.*, 2008), which disregarded internal brain processes. Scepticism may also have been fueled by socio-cultural trends including the industrialization of food and expansion of factory farming, along with the growth of scientific research relying on animal subjects. These factors remain, but are counterbalanced today by environmental concerns and rising recognition of the interconnection of humans with the natural world. Animal sentience is now a respected and energetic topic of research.

Scientific attitudes toward sentience - then and now - illustrate the power of cultural context. The methods of science ensure procedural objectivity but science cannot escape subjectivity in interpretation of data and in the research questions it chooses to ask. Science is also influenced by prevailing norms and views. Jane Goodall recalls, in graduate school in the 1960s, being roundly criticized by scientists for naming the Gombe chimpanzees and for suggesting they might

sometimes be happy or sad (Goodall, 2007). One pertinent example of cultural preconceptions involves who or what is capable of suffering. In the 19th century United States, anaesthetic was not used for patients considered insensitive to pain: recent immigrants, blacks, alcoholics and the poor, but was reserved for those considered pain-sensitive: whites, women, and the wealthy (Weary *et al.*, 2006).

Science provides much evidence in support of the argument for animal sentience. In the process it raises questions about the ways that humans use animals. Scientific evidence increasingly supports the notion that humans and other animals are on a spectrum of capabilities, and that humans have opportunities and even imperatives to recognize animals' potential for emotion, for pleasure and for pain. As Jane Goodall has said, the distinction between human and animal is blurred and becoming more so all the time.

References

- Balcombe, J. (2006a) Laboratory environments and rodents' behavioral needs: a review. *Laboratory Animals*. 40: 217-235
- Balcombe, J. (2006c) *Pleasurable Kingdom: Animals and the Nature of Feeling Good*, Macmillan, London
- Barton, R. A., Aggleton, J. P. and Grenyer, R. (2003). Evolutionary coherence of the mammalian amygdala. *Proc. R. Soc. Lond. B*. 270: 539-543
- Bekoff, M. (2007) *The Emotional Lives of Animals: A Leading Scientist Explores Animal Joy, Sorrow, and Empathy, and Why They Matter*. New World Library, Novato California
- Bermond, B. (2003) The Myth of Animal Suffering. In *The Animal Ethics Reader*, Armstrong, S. and Botzler, R. (eds.) Routledge, New York, pp77-85
- Bernstein, D. *et al.* (2008) *Psychology*. Houghton Mifflin, Boston
- Berridge, K. (2003) Comparing the emotional brains of humans and other animals. In *Handbook of Affective Sciences*, Davidson, R. J., Scherer, K. R. and Hill Goldsmith, H. (eds.) Oxford University Press, Toronto
- Braithwaite, V. and Huntingford, F. (2004) Fish and welfare: Do fish have the capacity for pain perception and suffering? *Animal Welfare* 13(1): 87-92
- Broglio, C. *et al.* (2005) Hallmarks of a common forebrain vertebrate plan: Specialized pallial areas for spatial, temporal and emotional memory in actinopterygian fish. *Brain Research Bulletin*, 66(4-6): 277-281
- Broom, D. (2008) Minority Opinion: Scientific Opinion of the Panel on Animal Health and Welfare on a request from the European Commission on Animal Welfare Aspects of Husbandry Systems for Farmed European Eel. *The EFSA Journal*, 809: Annex II, 1-19
- Butler, A. (2008a) Brain Evolution and Comparative Neuroanatomy. In *Encyclopedia of Life Sciences (ELS)*. John Wiley and Sons, Ltd, Chichester
- Butler, A. and Hodos, W. (2005) *Comparative Neuroanatomy: Evolution and Adaptation*. John Wiley and Sons, Inc., New Jersey
- Chandroo, K., Duncan, I. and Moccia, R. (2004) Can fish suffer? Perspectives on sentience, pain, fear and stress. *Applied Animal Behaviour Science*, 86: 225-250
- Crick, F. and Koch, C. (1998). Consciousness and neuroscience. *Cerebral Cortex*. 8(2): 97-107.
- Crick, F. and Koch, C. (2003) A framework for consciousness. *Nature Neuroscience*. 6(2) : 119-126
- Cryan, J. F., Mombereau, C. and Vassout, A. (2005) The tail suspension test as a model for assessing

- antidepressant activity: Review of pharmacological and genetic studies in mice. *Neuroscience & Behavioral Reviews*. 29(4-5): 571-625
- Dalley, J. et al. (2007) Nucleus Accumbens D2/3 Receptors Predict Trait Impulsivity and Cocaine Reinforcement. *Science*. 315(5816) 1267-1270
- Damasio, A. (1994) *Descartes' Error: Emotion, Reason, and the Human Brain*. Penguin, New York
- Damasio, A. (1999) *The Feeling of What Happens*. Harcourt, New York
- Damasio, A. (2001) Fundamental feelings. *Nature*. 413: 781
- Damasio, A. and Meyer, K. (2008) Behind the looking-glass. *Nature*. 454: 167-168
- Danbury, T., et al. (2000) Self-selection of the analgesic drug carprofen by lame broiler chickens. *Veterinary Record*. 146: 307-311
- Darwin, C. (1872) *The Expression of the Emotions in Man and Animals*. Re-published 1965. University of Chicago Press, Chicago
- Dawkins, M. (2006a) Through animal eyes: What behaviour tells us. *Applied Animal Behaviour Science*. 115: 4-10
- Dawkins, M. (2006b) A user's guide to animal welfare science. *Trends in Ecology and Evolution*. 21(2): 77-82
- Dawkins, R. (1993) Gaps in the Mind. In *The Great Ape Project: Equality Beyond Humanity*. Cavalieri, P. and Singer, P. (eds.) St. Martin's Press, New York, pp80-87
- De Waal, F. (2005) The evolution of empathy. *Greater Good*. Fall/Winter 2005/06: 6-9
- D'Silva, J. (2006) Introduction. In *Animals, Ethics and Trade: The Challenge of Animal Sentience*, Turner, J. and D'Silva, J. (eds.) Earthscan, London, pp xxi-xxvi
- Dulawa, S. et al. (2004) Effects of chronic fluoxetine in animal models of anxiety and depression. *Neuropsychopharmacology*. 29: 1321-1330
- Dumont, E.C. et al. (2002). Physiological properties of central amygdala neurons: species differences. *Eur J. Neurosci.*, 15(3): 545-552
- Duncan, I. (2006) The changing concept of animal sentience. *Applied Animal Behaviour Science*. 100: 11-19
- Emery, N. and Clayton, N. (2004) The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science*. 306: 1903-1907
- Engel, C. (2002) *Wild Health: How Animals Keep Themselves Healthy and What We Can Learn From Them*. Weidenfeld and Nicolson, London
- Goodall, J. (1993) Chimpanzees – Bridging the Gap. In *The Great Ape Project: Equality Beyond Humanity*. Cavalieri, P. and Singer, P. (eds.) St. Martin's Press, New York, pp 10-18
- Goodall, J. (2007) Foreword. In: *The Emotional Lives of Animals: A Leading Scientist Explores Animal Joy, Sorrow, and Empathy- and Why They Matter*, Bekoff, M. New World Library, Novato California
- Grandin, T. (2009) *Animals Make Us Human: Creating the Best Life for Animals*. Houghton Mifflin, Boston
- Griffin, D. and Speck, G. (2004) New evidence of animal consciousness. Review. *Animal Cognition*. 7: 5-18
- Hof, P. and Van Der Gucht, E. (2006) Structure of the cerebral cortex of the humpback whale, *Megaptera novaeangliae* (Cetacea, Mysticeti, Balaenopteridae). *The Anatomical Record Part A*. 290(1): 1-31
- Hunt, G. and Gray, R. (2003) The crafting of hook tools by wild New Caledonian crows. *The Royal Society. Biology Letters*. 2003. S88-S90

- Kendrick, K. *et al.* (2001) Sheep don't forget a face. *Nature*. 414(6860): 165-6
- Kirkden, R. and Pajor, E. (2006) Using preference, motivation and aversion tests to ask scientific questions about animals' feelings. *Applied Animal Behaviour Science*. 100: 29-47
- Kirkwood, J. (2006) The Distribution of the Capacity for Sentience in the Animal Kingdom. In *Animals, Ethics and Trade: The Challenge of Animal Sentience*, Turner, J. and D'Silva, J. (eds.), Earthscan, London, pp12-26
- Kohts, N. (2002) *Infant Chimpanzee and Human Child: A classic 1935 comparative study of ape emotions and intelligence*. Oxford University Press, Toronto
- Laberge, F. *et al.* (2006) Evolution of the Amygdala: New Insights from Studies in Amphibians. *Brain Behaviour and Evolution*. 67(4): 177-187
- Langford, D. *et al.* (2006) Social modulation of pain as evidence for empathy in mice. *Science*. 312: 30 June 2006: 1967-1970
- LeDoux, J. (1996) *The Emotional Brain: The Mysterious Underpinnings of Emotional Life*. Simon & Schuster, Toronto
- LeDoux, J. and Schiller, D. (2009) The Human Amygdala: Insights from Other Animals. In *The Human Amygdala*, Whalen, P., Phelps, E. (eds.), ch. 2. Guilford Press, New York
- Marino, L. *et al.* (2007) Cetaceans Have Complex Brains for Complex Cognition. *PLoS Biology*. 5(5): 966-972
- Mason, G. J., Cooper, J. and Clarebrough, C. (2001) Frustrations of fur-farmed mink. *Nature*. 410: 35-36
- Mather, J. (2001) Animal suffering: An invertebrate perspective. *J Applied Animal Welfare Science*. 4(2): 151-156
- McLeman, M. *et al.* (2008) Social discrimination of familiar conspecifics by juvenile pigs, *Sus scrofa*: Development of a non-invasive method to study the transmission of unimodal and bimodal cues between live stimuli. *Applied Animal Behaviour Science*. 115: 123-137
- Merker, B. (2007) Consciousness without a cerebral cortex: A challenge for neuroscience and medicine. *Behavioral and Brain Sciences*. 30: 63-81
- Merten, K. and Nieder, A. (2009) Compressed scaling of abstract numerosity representations in adult humans and monkeys. *Journal of Cognitive Neuroscience*. 21(2): 333-346
- Nicol, C. (2006) How animals learn from each other. *Applied Animal Behaviour Science*. 100: 58-63
- Nagel, T. (1974) What is it like to be a bat? *The Philosophical Review*, LXXXIII: 435-50
- Panksepp J. (1998) *Affective Neuroscience: the foundations of human and animal emotions*. Oxford University Press
- Panksepp, J. (2005) Affective-Social Neuroscience Approaches to Understanding Core Emotional Feelings in Animals. In: *Mental Health and Well-Being in Animals*. McMillan, D. (ed) Chapter 5. P. 57. Wiley-Blackwell
- Patterson-Kane, E., Hunt, M., and Harper, D. (2002) Rats demand social contact. *Animal Welfare*. 11(3): 327-332(6)
- Patton, P. (2008) One World, Many Minds: Intelligence in the Animal Kingdom. *Scientific American*. Dec 23, 2008
- Penn, D., and Povinelli, D. (2007) Causal Cognition in Human and Non-Human Animals: A comparative, critical review. *Annu. Rev. Psychol.* 2007. 58: 97-118
- Pepperberg, I. (2006) Cognitive and communicative abilities of Grey parrots. *Applied Animal Behaviour Science*. 100: 77-86

- Pinker, S. (2007) The Mystery of Consciousness. *Time*. Fri., Jan. 19, 2007. Pp 1-9.
<http://www.time.com/time/magazine/article/0,9171,1580394,00.html> (Accessed January 26, 2009)
- Pinel, J. (2007) *Basics of Biopsychology*. Pearson, Boston
- Plotnik, J., de Waal, F. and Reiss, D. (2006) Self-recognition in an Asian elephant. *PNAS*. 103(45): 17053-17057
- Premack, D. (2007) Human and animal cognition: Continuity and discontinuity. *PNAS*. 104(35): 13861-13867
- Prior, H., Schwarz, A., and Gunturkun, O. (2008) Mirror-induced Behavior in the Magpie (*Pica pica*): Evidence of self-recognition. *PLoS Biol*. 6(8): e202, doi:10.1371/journal.pbio.0090202
- Raby, A., et al. (2007) Planning for the future by western scrub-jays. *Nature*. 445(22), doi:10.1038/nature05575
- Regan, T. (2006) Sentience and Rights. In: *Animals, Ethics and Trade: The Challenge of Animal Sentience*. Turner, J. and D'Silva, J. (eds.), Earthscan, London, pp79-86
- Rendell, L., Whitehead, H. (2001) Culture in whales and dolphins. *Behavioral and Brain Sciences*. 24: 309-382
- Rose, J. (2002) The Neurobehavioral Nature of Fishes and the Question of Awareness and Pain. *Reviews in Fisheries Science*. 10(1): 1-38
- Roth, G. and Dicke, U. (2005a) Evolution of the Brain and Intelligence. Review. *Trends in Cognitive Sciences*. 9(5): 250-257
- Schwender, D. et al. (1995) Awareness during general anesthesia. Definition, incidence, clinical relevance, causes, avoidance, and medicolegal aspects. *Anaesthesist*. 44(11): 743-754
- Sherwin, C. (2001) Can invertebrates suffer? Or, How Robust is Argument-by-Analogy? *Animal Welfare*. 10(1): 103-118
- Sneddon, L. (2002) Anatomical and electrophysiological analysis of the trigeminal nerve in a teleost fish, *Oncorhynchus mykiss*. *Neuroscience Letters*. 319(3): 167-171
- Sneddon, L. (2004) Evolution of nociception in vertebrates: comparative analysis of lower vertebrates. *Brain Res Rev*. 46(2): 123-130
- Somme, L. (2005) *Sentience and Pain in Invertebrates*. Report to the Norwegian Scientific Committee for Food Safety. <http://jillium.nfshost.com/library/pain.htm>. Accessed February 1, 2009
- Squire, L. et al. (2002) *Fundamental Neuroscience*. Academic Press, Toronto
- Taylor, A. and Weary, D. (2000) Vocal responses of piglets to castration: identifying procedural sources of pain. *Applied Animal Behaviour Science*. 70(1): 17-26
- Weary, D., et al. (2006) Identifying and preventing pain in animals. *Applied Animal Behaviour Science*. 100: 64-76
- Webster, J. (2005) Sentience, Sense, and Suffering. In: *Animal Welfare: Limping Toward Eden*. Webster, J. 2005. Oxford: Universities Federation for Animal Welfare. Ch 3. Pp. 46-76