NUFFIELD COUNCIL ON BIOETHICS

Animal sentience and consciousness

A review of current research

Prepared by Arzoo Ahmed with Claudia Corradi

March 2022

Table of Contents

Summary

- Animal sentience and consciousness are capacities which feature prominently in debates concerning the moral status of animals. These aspects of the mental lives of animals offer a basis for establishing their interests and have moral relevance for assessing the mental and physical welfare implications of the human treatment of animals.
- Sentience is the capacity for consciously experiencing positive and negative affective states, such as joy, pleasure, desire, pain, and fear. Consciousness refers to the subjective or phenomenological experiences of the world and one's body, the capacity to experience a rich range of mental states, have an awareness of internal and external stimuli, and possess a sense of self, and includes abilities such as self-recognition, episodic memory, metacognition, and mindreading.
- Questions about sentience and consciousness have historically been approached through philosophical inquiry and some scientific investigation. A significant body of past research has been shaped by an interest in the study of negative emotions, as well as anthropocentric models of study and interpretation. The emergence of positive psychology and affective neuroscience demonstrate a shift in focus, beyond pain and suffering, towards other positive states and experiences which matter to animals and contribute to their quality of life and flourishing.
- Since there is no single test for establishing sentience or consciousness in animals, the study of these capacities is faced with several unresolved challenges on issues of definition, scope, methods of study, interpretation of findings, as well as on the origins and distribution of consciousness across species.
- The field of animal sentience has an emerging interdisciplinary community of researchers from different disciplines (such as comparative psychology, behavioural studies, neuroscience, animal welfare science, and philosophy), which is focused on developing the behavioural, cognitive, and neuronal criteria which could attribute conscious states to animals.
- There is a growing sense that for consciousness to exist in animals, it does not need to have an equivalent form to consciousness as it is found in humans. Emerging research is focused on moving away from assigning the same consciousness criteria we observe in humans to animals and promotes an understanding of animal minds with the exploration of a wider range of affective states in animals. Research directions have shifted away from asking whether any nonhuman animals are conscious to questions of which animals are conscious and what form their conscious experiences take.
- Animals display cognitive and emotional complexity, as well as the propensity for positive and negative affective states. There is a growing body of research on the emotions, cognition, social interaction, and time perception across animals including cows, sheep, pigs, chicken, as well as some invertebrates.
- New approaches proposed for characterising sentience and consciousness in animals include the development of multi-dimensional scales or 'distinctive profile scales' of consciousness instead of a unidimensional sliding scale for different species, on which some species are more or less conscious than others.
- There is a growing consensus amongst the scientific research community, owing to conceptual and methodological advances, that animals possess a wider range abilities for complex thinking and social behaviours, and experience feelings which matter to them (birds and fish included). The question raised by current research is what experiences comprise a 'good life', and to what extent different animals have the capacity for these experiences.

Background

1. In our fact-finding meeting in 2019, we heard about research on animal sentience and consciousness, capacities that feature prominently in debates concerning the moral status of animals. These aspects of the mental lives of animals offer a basis for establishing their interests and have moral relevance for assessing the mental and physical welfare implications of the human treatment of animals.[1] On some ethical accounts, the level of respect afforded to animals is premised on an understanding of their capacities for conscious experience or the forms of consciousness which are accessible to different animal species.[2] For others, the capacity in animals to feel pleasure and pain is sufficient as a criterion for moral consideration and for establishing nonhuman animal interests.[3] According to the latter view, the problem of consciousness does not need to be solved in order to establish a science of animal welfare.[4]

2. Whilst there exists ambiguity and differences in how these capacities are defined and understood, broadly speaking, consciousness, refers to the subjective or phenomenological experiences of the world and one's body, the capacity to experience a rich range of mental states, have an awareness of internal and external stimuli, and possess a sense of self.[5] In a being that possesses the capacity for consciousness, an intentional relation is assumed between it and an object of which it has awareness.[6] Self-consciousness, a higher level of consciousness, is 'an organism's capacity for second-order representation of its own mental states.'[7] This level of consciousness includes abilities such as self-recognition, episodic memory, metacognition, and mindreading.

3. Sentience, a lower form of consciousness or first-order consciousness,[8] is widely accepted as common to humans and most animals (with a sufficiently developed nervous system) and refers to the 'subjective states of animals.' Sentience includes the capacity of animals for 'experiencing positive and negative affective states'[9] (also referred to as positively or negatively 'valenced' feelings)[10] or their conscious 'ability to feel and experience emotions such as joy, pleasure, desire, pain and fear.'[11] This is also referred to as 'affective sentience' and means that sentient animals have the capacity to feel good or bad about the positive or negative affective states which they experience.[12] Cognitive capacities and conative attitudes (such as, aims, intentions, desires, and

---

[1] In his paper 'What is suffering and what sorts of beings can suffer?' David DeGrazia writes 'beings who are capable of suffering in at least the broad sense have interests, and beings who have interests have moral status.' See also Article 13 of the Lisbon Treaty which states 'Member States shall, since animals are sentient beings, pay full regard to the welfare requirements of animals.'

[2] Le Neindre P, Bernard E, Boissy A, Boivin X, Calandreau L, Delon N, Deputte B, Desmoulin-Canselier S, Dunier M, Faivre N, Giurfa M, Guichet J-L, Lansade L, Larrère R, Mormède P, Prunet P, Schaal B, Servière J, Terlouw C, 2017. Animal consciousness. EFSA supporting publication 2017:EN-1196. p.8

[3] Zuolo F (2019). Misadventures of Sentience: Animals and the Basis of Equality. *Animals 9*(12), 1044.

[4] Dawkins MS (2008) The science of animal suffering. *Ethology* 114(10), 937-945

[5] Le Neindre P *et al.* (2017) Animal consciousness. EFSA supporting publication 2017:EN-1196, p.160.

[6] Gulick RV (2012) Consciousness and cognition in The Oxford Handbook of Philosophy of Cognitive Science.

[7] Le Neindre P *et al.* (2017) Animal consciousness. EFSA supporting publication 2017:EN-1196, p.38.

[8] Andrews K and Beck J (2018) Routledge handbook of animal minds, p.170

[9] Duncan JH (2006) The changing concept of animal sentience *Applied Animal Behaviour Science* 100(1-2), 11-19.

[10] Powell R and Mikhalevich I (2020) Affective sentience and moral protection *Animal Sentience* 29(35).

[11] Proctor HS *et al.* (2013) Searching for Animal Sentience: A Systematic Review of the Scientific Literature *Animals 3*(3), 882–906; Ledger RA and Mellor DJ (2018) Forensic use of the Five Domains Model for assessing suffering in cases of animal cruelty *Animals* 8(7) E101.

[12] Powell R and Mikhalevich I (2020) Affective sentience and moral protection. *Animal Sentience* 29(35).

preferences) are also discussed in relation to, as part of, or as indicative of sentience and consciousness.

4. There is a growing sense that for consciousness to exist in animals, it does not need to have an equivalent form to consciousness as it is found in humans.[13] Since there is no single test for establishing sentience or consciousness in animals, discussions on animal sentience and consciousness are faced with several unresolved challenges in this constantly evolving field:

   - ***Definitional*** – how should sentience and consciousness be defined in animals? How do these features relate to the brain, body, and environment of animals?
   - ***Varieties of consciousness*** – Are there degrees, dimensions, or forms of consciousness? What are the levels and contents of consciousness? To what extent does consciousness differ in nonhuman animals and human animals?
   - ***Origins and evolution of consciousness*** – when, how, and why did consciousness evolve? Did it evolve gradually? Or did it emerge at different points in different species lines? What is the phylogenetic context of the evolution of consciousness?[14]
   - ***Methods of study*** – How can we know if a given species is conscious? How should properties such as sentience and consciousness be studied? What are the appropriate designs and methods of inquiry which can combine insights from different disciplines to reveal knowledge about animal sentience and consciousness?
   - ***Scope and distribution*** – What are the criteria for sentience and consciousness? How are these properties distributed in the living world and how can we know which species are conscious? What forms of consciousness are found in which species of animals within the large diversity of vertebrate and invertebrate species?
   - ***Interpretation*** – how should findings drawing judgements about animal sentience and consciousness be interpreted in the absence of narrative language in animals? How can interpretive methods move away from anthropomorphic and anthropocentric practices to understand animal minds on their own terms?
   - ***Moral significance –*** what is the moral significance of establishing sentience and consciousness in different species? What kinds of rights or duties are owed to animals who are classified as sentient or conscious?

5. Discussions in the field of sentience and consciousness have developed significantly over recent decades and are constantly evolving with new methods of investigation. With ongoing research characterised by different approaches and interpretive models, there continues to be disagreement about how to formulate and conceive of sentience, how to study and measure it, how to determine its distribution in the living world, and establish what moral significance sentience confers.[15]

Historical evolution of sentience and consciousness debates

6. Questions related to consciousness, which explore whether animals have consciousness and what (if anything) it 'might be like' to be those animals, have been approached both through philosophical and scientific inquiry.[16] The criteria and methods for studying

[13] Le Neindre P *et al.* (2017) Animal consciousness. EFSA supporting publication 2017:EN-1196, p.44.
[14] Godfrey-Smith P (2017) "The Evolution of Consciousness in Phylogenetic Context," in K Andrews and J Beck (eds.) *The Routledge Handbook of Philosophy of Animal Minds* London: Routledge pp. 216-226.

[15] Powell R and Mikhalevich I (2020) Affective sentience and moral protection. *Animal Sentience* 29(35).
[16] Allen C and Trestman M "Animal Consciousness", *The Stanford Encyclopedia of Philosophy* (Winter 2020 Edition), Edward N. Zalta (ed.)

consciousness are, however, complicated by the private and, philosophers argue, subjective nature of consciousness, and the absence of narrative language in animals which would allow them to communicate their experiences. The lack of direct access to the interior lives of animals presents an epistemic challenge, known as the 'problem of other minds', for humans seeking to interpret and establish evidence for the forms of consciousness, if any, experienced by animals.

7. Early philosophical conceptions of consciousness, driven by beliefs of human exceptionalism and speciesism, posit a discontinuity between humans and other animal species.[17] Such anthropocentric approaches focus on the differences between humans and animals, measuring animals against human values, and claim that consciousness is unique to humans. Animals are thus denied intentional states and perceived as irrational, reflex-driven automata, with their behaviour understood solely through mechanistic explanations.[18]

8. More recent philosophical accounts argue similarly for the human-uniqueness of consciousness based on other assumptions. Dennett's anti-realist theory posits consciousness as a 'fiction' or 'story-telling' constructed through people's narrative descriptions, which necessitates the use of language.[19] Arguments in response to the language-based criteria for consciousness posit that whilst language is an integral component of the human narrative experience in the world, basic experiences of the world do not depend on it.[20] Accounts of consciousness which require a 'theory of mind' – the ability to ascribe mental states to others – generally reserve consciousness as a property unique to humans, though novel methodologies and innovations are engaged with studying animal minds to determine whether non-human animals have a theory of mind.[21]

9. The scientific study of animal sentience and consciousness followed much later. Investigation of the private and subjective nature of consciousness was considered beyond the scope of science with its objective methods of inquiry.[22] By the 19th century, insights from evolutionary theory from naturalists such as Lamarck and Darwin posited an evolutionary and mental continuity between species.[23] Animals were considered sentient, and their feelings, such as pleasure and pain, were viewed as adaptations which evolved as part of the pressures of natural selection. In the early 20th century, however, the study of animal feelings came to be disregarded by behavioural scientists, who were influenced by a branch of psychology called 'behaviourism' in which animal feelings and other subjective terms linked to the study of the mind and consciousness were discarded. Animal behaviour was explained in terms of learning and memory and it was considered unacceptable to describe observed behaviours with terms which attributed any intentionality to animals.[24] Behavioural scientists subsequently restricted their focus to the study of observable behaviour, paying little to no attention to the subjective states of animals.[25] The approach of behaviourism influenced the discipline of

[17] Tononi G and Koch C (2015) Consciousness: here, there and everywhere? *Phil. Trans. R Soc.* B **370:** 20140167.
[18] Allen C and Trestman M "Animal Consciousness", *The Stanford Encyclopedia of Philosophy* (Winter 2020 Edition), Edward N. Zalta (ed.)
[19] Dennett DC (1995) Animal consciousness and why it matters *Social Research* 62: 691–710.
[20] Nautilus (2019) Consciousness Doesn't Depend on Language
[21] Krupenye C and Call J (2019) Theory of mind in animals: Current and future directions *Cognitive Science*. 10(6):e1503.
[22] Nagel T (1974). What is it like to be a bat? *Philosophical Review*, 83, 435–450.
[23] Le Neindre P *et al.* (2017) Animal consciousness. EFSA supporting publication 2017:EN-1196, p.28.
[24] de Waal F (2016) *Are we smart enough to know how smart animals are?* W. W. Norton & Company.
[25] Duncan JH (2006) The changing concept of animal sentience. *Applied Animal Behaviour Science* 100(1-2), 11-19.

ethology in Europe which also then limited its study to the observable behaviour of animals.[26]

10. The study of animal consciousness was reintroduced into the science of animal behaviour in the latter half of the 20th century by D.R.Griffin, through his founding of 'cognitive ethology' – an approach which infers and analyses cognitive and information processing capacities from behaviours.[27] This 'cognitive turn' away from behaviourism – also marked as the 'cognitive revolution' – encouraged ethologists and comparative psychologists to investigate and pay attention to the subjective feelings and cognitive capacities of animals and understand them in the context of evolution. Griffin argued that ethology had ignored fundamental questions related to the mental experiences and minds of animals and claimed that animal behaviours were more than complicated mechanistic responses and required an explanation of human-like mental processes.[28] He further argued that evidence of consciousness could be inferred from the behavioural flexibility and versatility observed in animals.[29]

11. Griffin highlighted the similarities between human and non-human subjective experiences, on account of the evolutionary continuity of cognitive functions and processes which control behaviours in humans and animals. He proposed that the absence of narrative language in animals could be overcome by the development of appropriate behavioural tests and comparative analysis of brain responses through neurophysiological processes.[30] Griffin's observations of animal behaviour led him to conclude that consciousness is present in animals, especially in vertebrates. His ideas offered a legitimate basis for the scientific study of consciousness, which seeks to establish the nature and origins of consciousness, its distribution among species, and phylogenetic links by drawing together insights from ethology, the cognitive sciences, and evolutionary theory.

12. The development of cognitive ethology and advances in psychology and neuroscience have enabled a greater focus on empirical studies that investigate aspects of the mental lives of animals and have implications for consciousness.[31] Whilst the metaphysical and epistemological uncertainty on consciousness persists within philosophical debates, a growing body of biological, psychological, and behavioural research on the cognitive abilities of animals and their emotions is changing our notion of animal sentience and consciousness, in both vertebrates and some invertebrates.

Changing research directions and new methodologies

13. Conceptual and methodological advances have led to a significant shift in scientific consensus on animal sentience in recent years, such that it is now widely accepted that animals experience feelings of pain and pleasure which matter to them, have a wider range of capacities than previously thought, and can possess a sophisticated capacity to control their lives. In 2012, an international group of scientists collaborated to produce the Cambridge Declaration on Consciousness, declaring that "the weight of evidence

---

[26] Duncan JH (2006) The changing concept of animal sentience. *Applied Animal Behaviour Science* 100(1-2), 11-19.
[27] See paper given by Griffin in 1975 on subjective feelings at the International Ethology Conference and a book published on the topic in 1976; and Griffin DR (2001) *Animal minds: beyond cognition to consciousness University* of Chicago Press.
[28] Le Neindre P et al (2017) Animal consciousness. EFSA supporting publication EN-1196, p.32.
[29] Griffin DR and Speck GB (2004) New evidence of animal consciousness. *Anim Cogn* **7,** 5–18. x
[30] Griffin DR (1976) *The question of animal awareness: evolutionary continuity of mental experience* New York: Rockefeller University Press.
[31] Crick F and Koch C (1990) Towards a neurobiological theory of consciousness. Semin. Neurosci. **2**, 263–275; Crick F and Koch C (1995) Why neuroscience may be able to explain consciousness. Sci. Am. **273**, 84–85.

indicates that humans are not unique in possessing the neurological substrates that generate consciousness," stating that evidence suggests that "non-human animals, including all mammals and birds, and many other creatures, including octopuses" have the neurological substrates that support conscious experience.[32] The Declaration draws attention to new techniques and strategies for research in the field of consciousness and calls for a "re-evaluation of previously held preconceptions" in this field.[33]

14. A systematic review of the scientific literature on animal sentience conducted in 2013 found that most research in preceding decades is primarily focused on the negative experiences of animals with the top keywords 'fear', 'stress', 'pain', 'anxiety', and 'depression' – all negative – appearing in most studies.[34] Whilst past research studies have primarily been designed to focus on the negative experience and emotions of animals, there is prevailing acknowledgement that current and future studies ought to be designed to explore the subjective experiences of animals and should include a wide range of both positive and negative affective states, such as pleasure and states of boredom.[35] The emergence of positive psychology and affective neuroscience demonstrates this shift in focus, beyond pain and suffering, towards other states and experiences which matter to animals, contribute to their quality of life, and offer insights into the conditions necessary for their flourishing.[36]

15. An interdisciplinary community of researchers on animal consciousness has formed in recent years from fields such as animal welfare science, behavioural science, neuroscience, evolutionary biology, comparative psychology, and philosophy to address questions more directly on animal sentience and consciousness, and develop the behavioural, cognitive, and neuronal criteria which could attribute conscious states to animals.[37] In 2016, the interdisciplinary journal *Animal Sentience* was founded as "the first academic journal to focus on nonhuman animals and their capacity for feeling, perception, and consciousness" in a scientifically rigorous way.[38]

16. Research directions have shifted away from asking "whether any nonhuman animals are conscious to questions of which animals are conscious and what form their conscious experiences take."[39] Research questions are being rethought of in terms of what it is like for an animal to lead the life it leads and an acceptance that animals are not necessarily less clever or less complex than humans, but instead are different in certain respects. As well as research investigating how animals live, conceptual changes are also taking place in how we think about and interpret animal behaviour and cognition.

17. Neurobiologists and neurophysiologists have turned their attention towards the brain to search for the neuronal correlates of consciousness and establish the minimal neuronal mechanisms which would be required for a given conscious experience.[40] Empirical investigation of these characteristics in animals through comparative psychology, cognitive ethology, and other disciplines, alongside research on features of brain

---

[32] The Cambridge Declaration on Consciousness (2012)
[33] The Cambridge Declaration on Consciousness (2012)
[34] Proctor HS *et al.* (2013). Searching for Animal Sentience: A Systematic Review of the Scientific Literature. *Animals 3*(3), 882–906.
[35] Duncan JH (2006) The changing concept of animal sentience. *Applied Animal Behaviour Science* 100(1-2), 11-19.
[36] Alexander R *et al.* (2021) The neuroscience of positive emotions and affect: Implications for cultivating happiness and wellbeing *Neuroscience & Biobehavioral Reviews* 121, 220-249.
[37] Birch J *et al.* (2020) Dimensions of animal consciousness *Trends in Cognitive Sciences* 24(10), 789-801.
[38] Animal Sentience: An interdisciplinary journal on animal feeling
[39] Birch J *et al.* (2020) Dimensions of animal consciousness *Trends in Cognitive Sciences* 24(10), 789-801.
[40] Koch C (2018) What is consciousness? Nature.

structures and higher cognitive processes linked to conscious experience, may offer indicators which lend their support for accounts and theories of consciousness.[41]

18. There is strong agreement that consciousness results from brain processes, and that the neurological or structural similarity of human and animal brains supports conscious experience in animals.[42] Mammals share the basic brain anatomy with humans and have a central nervous system and a neocortex, both linked in humans to thought, perception and feeling which strengthens the case that animals do have phenomenal mental experiences and are sentient. However, researchers argue that this does not suggest that in order for sentience or consciousness to exist across the large diversity of animal species, including invertebrates, the same behavioural, neurophysiological, or evolutionary conditions must be met as those applicable to humans, since the structures that make consciousness possible and their associated functions may vary across species.

19. Sentience can be inferred from the presence of cognitive (information processing) capacities in animals through cognition research studies in comparative psychology.[43] Cognitive capacities relevant for sentience include mental processes, such as perception, memory, and learning, such that sentient beings have an awareness of others and the environment, the ability to evaluate their actions and the actions of others in relation to themselves, the ability to recall past events and actions and relate these to consequences, and plan for the future.[44] These capacities depend on brain function and are likely to have evolved to enable animals to deal with the external world.[45] Evidence of cognition is usually indirectly observed through the behavioural and physiological responses of animals, and neuroscientists are also now turning to direct measures of brain activity.[46] There remains the challenge of distinguishing between cognition and simpler learning processes or physiological processes like reflex action on the basis of behavioural studies alone, since the same behaviour may be observed for these different processes.[47] However, the focus on cognition has received criticism from those who hold that animal feelings (the ability to experience positive and negative affective states) are what matter morally for animal suffering, not the cognitive sophistication or intelligence of animals.[48]

The link between cognition, emotion, and consciousness

20. Whilst aspects of sentience, such as feelings, depend on certain cognitive processes and a level of cognitive sophistication,[49] emotional experiences can also impact the cognitive abilities of animals and alter their evaluative processes and judgement biases.[50] Proponents of affective sentience argue that the affective component (i.e. the

---

[41] LeDoux JE *et al.* (2020) A little history goes a long way toward understanding why we study consciousness the way we do today Proceedings of the National Academy of Sciences 117 (13) 6976-6984.
[42] Le Neindre P *et al.* (2017) Animal consciousness. EFSA supporting publication 2017:EN-1196, p.33.
[43] Powell R and Mikhalevich I (2020) Affective sentience and moral protection. *Animal Sentience* 29(35).
[44] Broom DM (2019) Sentience. In: Choe, JC (ed.), Encyclopedia of Animal Behavior, (2nd ed.). vol. 1 pp. 131-133.
[45] Fraser D and Duncan IJH (1998) 'Pleasures', 'pains' and animal welfare: toward a natural history of affect. *Animal Welfare* 7(4), 383-396.
[46] Wasermann EA and Zentall TR (2012) Introduction in: The Oxford handbook of comparative cognition (2 ed.)
[47] Wasermann EA and Zentall TR (2012) Introduction in: The Oxford handbook of comparative cognition (2 ed.)
[48] Mellor DJ (2016) Updating animal welfare thinking: Moving beyond the "Five Freedoms" towards "A life worth living". *Animals* 6: 21 and Browning H (2019) What should we do about sheep? The role of intelligence in welfare considerations. *Animal Sentience* 25(23).
[49] Broom DM (2019) Sentience In: Choe, JC (ed.), Encyclopedia of Animal Behavior, (2nd ed.). vol. 1 pp. 131-133.
[50] Mendl M and Paul ES (2004) Consciousness, emotion and animal welfare: Insights from cognitive science. *Animal Welfare* 13, S17-25.

capacity for experiencing states of pleasure and displeasure)[51] must be present for the cognitive capacities of animals to have any moral relevance, and that cognitive capacities alone without the affective dimension are insufficient for moral standing and welfare related concerns.[52] Others argue further that proof of emotion in animals is insufficient for determining whether animals are conscious of their emotional states.[53] Conscious experience of emotion in animals can be supported with evidence of states such as empathy, emotional contagion, and state matching, through which social animals are seen to perceive and share the emotional states of their conspecifics.

21. Establishing the link between cognition and consciousness requires answering questions about how these processes are related, whether they are distinct and independent or whether one is required for the other.[54] Cognitive theories of consciousness propose ways of understanding and interpreting empirical data which account for and explain the relation between cognitive processes and consciousness, and further determine whether a particular system has conscious experiences and the conditions within which conscious experience arises within a given system.[55]

22. The two main cognitive theories of consciousness are global workspace theory and integrated information theory. The former, also known as global neuronal workspace (GNW), posits that consciousness is a result of sensory information being 'broadcast' across the brain so that many different parts of the brain – most importantly the telencephalic cortex – have access to and process the information for conscious experience. According to the integrated information theory (IIT), consciousness is a causal property built into the structure of a complex system, so that with greater complexity, more diverse types of information can be integrated to provide conscious experience. In both theories, consciousness depends on higher cognitive processes and the interactions between nervous structures.[56]

23. New approaches towards understanding animal consciousness include the development of multi-dimensional scales or "distinctive profile scales" of consciousness instead of a unidimensional sliding scale for different species which relies on levels of consciousness.[57] Jonathan Birch and his colleagues argue that it is less helpful to ask whether one animal is "more conscious" or "less conscious" than another, since species may score variably on different aspects of consciousness. To capture the variation, five separate elements or dimensions of variation are specified in the proposed multidimensional framework of consciousness:

- *Perceptual richness (p-richness)* – a measure of how well animals consciously perceive aspects of their environment through their senses. This can be tested through experiments involving trace conditioning, discrimination learning, reversal learning, and induced blindsight.
- *Evaluative richness (e-richness)* – a measure of how consciously animals experience emotions and have affective experiences which feel good or bad, or

[51] Powell R and Mikhalevich I (2020) Affective sentience and moral protection. *Animal Sentience* 29(35)
[52] DeGrazia D and Beauchamp TL (2020) Principles of animal research ethics. In T. L. Beauchamp and D. DeGrazia (eds.), *Principles of Animal Research Ethics* (New York: Oxford University Press).
[53] Le Neindre P *et al.* (2017) Animal consciousness. EFSA supporting publication 2017:EN-1196, p.76.
[54] Gulick RV (2012) Consciousness and cognition in The Oxford Handbook of Philosophy of Cognitive Science
[55] Nature (9 May 2018) What is consciousness?
[56] LeDoux JE *et al.* (Mar 2020) A little history goes a long way toward understanding why we study consciousness the way we do today *Proceedings of the National Academy of Sciences* 117 (13) 6976-6984.
[57] Birch J *et al.* (2020) Dimensions of animal consciousness Trends in Cognitive Sciences 24(10), 789-801.

have positive or negative valence, and how the richness of these valenced experiences varies across the range of animals. This can be tested through experiments on motivational trade-offs, cognitive bias, outcome devaluation and revaluation, and emotional contagion.

- *Integration at a time* – the measure of a single-unified perspective resulting from the integration of information from an animal's sensory organs. This can be tested through experiments designed to investigate meta-control, visuo-spatial bias, multitasking, and cross-modal integration.
- *Integration across time* (also referred to as 'temporality') – whether an animal has a continuous stream of experience that flows from one moment to the next such that past experiences can be consciously recalled influencing the present and feeding into future experiences. This can be tested through experiments designed for episodic-like memory, source memory, memory integration, and future planning.
- *Self-consciousness (selfhood)* – whether an animal is consciously aware of itself. This can be tested through experiments such as the mirror-mark, and others testing body awareness and experience projection.

The five dimensions of variation are intended to allow for comparisons within and between species, though challenges remain for measuring and quantifying the variations and testing for conscious affects and perspectives to construct evidence-based consciousness profiles.[58]

24. Neuroscientists are using new imaging techniques, automatic behaviour monitors and other neurotechnologies combined with artificial intelligence, machine learning, and new mathematical tools to study brain networks and neural activation patterns that could represent internal brain states and offer greater insights into animal behaviour and conscious states. These advances can allow scientists, for example, to monitor electrical activity in the brain, and generate terabytes of data recording activity in hundreds of neurons across different brain areas on millisecond timescales to find patterns that could represent internal brain states.[59]

25. Neuroscientists are noticing that much more goes on beneath the surface in neural circuits preceding, during, and after different animal behaviours. They are seeing that activity in groups of neurons forming these internal states persists and outlasts the original stimulus that triggers them and can be generalised so that different stimuli prompt the same state. For example, in an experiment in which a rat was placed close to mice for a few seconds, the mice defensively hugged a wall for several minutes and a group of neurons in the hypothalamus became activated for the whole time beyond the stimulus being present.[60] When those neurons were later reactivated using light, the mice exhibited the wall-hugging behaviour even in the absence of a rat. In an experiment with zebrafish larvae, different groups of neurons were activated when the larvae hunted locally or went exploring in unfamiliar water for new food sources.[61]

26. More attention is being directed at exploring how the entire brain coordinates internal states, the ways in which internal brain states can represent emotions or motivations,

---

[58] Birch J *et al.* (2020) Dimensions of animal consciousness Trends in Cognitive Sciences 24(10), 789-801.
[59] Abbott A (2020) Inside the mind of an animal *Nature* **584**, 182-185.
[60] Kennedy A *et al.* (2020) Stimulus-specific hypothalamic encoding of a persistent defensive state *Nature* 586, 730–734.
[61] Marques JC *et al.* (2020) Internal state dynamics shape brainwide activity and foraging behaviour *Nature 577*(7789), 239–243.

and the properties of internal states that drive specific behaviours.[62] Such methods are also being employed to study pain in rodent models. Traditionally, observation tests have been used to record when the rat lifts its paw from a hot plate, a movement which indicates "the protective aspects of pain, but not necessarily the actual perception of pain." A programme has been launched in an attempt to gain insights into the internal states of pain perception by reading brain signals directly.[63]

27. Greater emphasis is now being placed on understanding animal minds on their own terms, as individuals with personalities, with a move away from anthropocentrism and group stereotypes when approaching questions of sentience and consciousness in animals.[64] Anthropocentric views assign humans as the measure of all things and measure animals against human values, which has often led to the dismissal of animal emotions and feelings.[65] Discussion and research on sentience is shifting from a vertical conception with humans at the top to a more horizontal qualitative, ecological, and non-anthropocentric conception that is sensitive to the fact that animals have evolved according to their particular niche.[66]

28. The task of interpreting empirical research findings on sentience and consciousness requires caution both against anthropomorphism, which can falsely attribute human properties to nonhuman animals, and also against anthropodenial, the failure to attribute (what are known as) human properties to nonhuman animals.[67] A proposal for avoiding some of these errors is to avoid drawing boundary lines between what are considered sentient and non-sentient beings through a set pre-determined criteria derived from human experiences and perceptions of sentience, and embrace the view that sentience comes in many different kinds and may not appear the same in all creatures. An example of anthropomorphism in the design of experiments is when tests focus only on faces when determining whether animals can discriminate between conspecifics.[68] More research is now focusing on investigating what it feels like to be a particular animal and how a given species may consciously experience the world according to different dimensions of consciousness.[69]

Research findings and case studies

29. The empirical search for animal sentience and consciousness is characterised by two main methodological approaches: physiological and behavioural. Behavioural and physiological criteria alongside evolutionary considerations offer a basis for deciding whether an animal is considered sentient and the forms of conscious experience it can access.

30. By investigating the neural mechanisms that give rise to experience, scientists seek to identify the neuronal correlates of consciousness to establish a scientific theory that can establish the necessary and sufficient conditions through which a physical system has

---

[62] See MIT Department of Brain and Cognitive Sciences for information about the laboratory researching how neural circuits generate sustained behavioural states.
[63] See F.M. Kirby Neurobiology Center for information about research programmes in neuroscience, led by Clifford Woolf.
[64] Sevillano V (2020) Group stereotypes: Human and nonhuman. *Animal Sentience* 27(15).
[65] Proctor HS *et al.* (2013). Searching for Animal Sentience: A Systematic Review of the Scientific Literature. *Animals 3*(3), 882–906.
[66] Chase JM and Leibold MA (2003) *Ecological niches: Linking classical and contemporary approaches*. Chicago: Univ. of Chicago Press; Pyron RA et al (2015) Phylogenetic niche conservatism and the evolutionary basis of ecological speciation. *Biol Rev Camb Philos Soc* 90(4):1248-62. DOI: 10.1111/brv.12154.
[67] Kristin Andrews (2020) *How to Study Animal Minds*
[68] Brodbeck DR *et al.* (2019) Domestication and cognitive complexity. *Animal Sentience* 25(32)
[69] Veit W and Huebner B (2020) Drawing the boundaries of animal sentience. *Animal Sentience* 29(13)

conscious experiences. Brain structures and neural processes between human and animal minds are compared on the assumption that conscious experience or consciousness requires a particular architecture of the nervous system, namely the presence of a cerebral cortex (or a functional equivalent) and specific neural networks and processes. In particular, 'the synchronous coupling of oscillatory electrical signals and broadcasting feedback signals between different brain areas' are neural mechanisms that support the emergence of consciousness.[70] The brain structures of mammals are very similar to human brains. However, avian and fish brains lack a cerebral cortex. Though this could lead to the conclusion that avian, fish and other non-mammalian species lack consciousness on account of their differing neural architecture, researchers caution against searching for the same neural architecture across different species to establish sentience and consciousness in non-mammalian species. Instead, attention is directed beyond anatomy to brain function when determining whether a system has the neuronal correlates to support consciousness.[71]

31. Investigating the experience of pain in animals involves demonstrating that pain has both a sensory and an emotional component.[72] Physiological evidence for sentience (experience of pain as a conscious negative affective state) is found in the presence of nociceptors which detect noxious stimuli and protect body tissue from damage, and in the production of analgesic chemical substances in animals to which reduce pain and suffering. Nociceptors alone do not provide proof that animals experience pain. In addition to nociceptors, integrative brain regions (involving the cortex) where different sensory information is gathered, and pathways connecting nociceptors to these regions are features that indicate the presence of pain in animals.[73] However, there is evidence to suggest that the lack of cortical areas in other (non-human/non-mammalian) species does not mean that they do not have the conscious experience of pain.[74] Other behaviours that provide evidence for pain include motivational trade-offs, withdrawal from and avoidance of noxious stimuli, responses to analgesics and local anaesthetics including the self-administration of analgesia, protective behaviours such as rubbing or wound tending after an injury, and associative learning through which animals learn to avoid noxious stimuli, which can be tested through conditioned place aversion.[75]

32. There is a lacuna in research literature on the neuroscience of positive emotions since most research efforts have focused primarily on exploring the neural correlates of negative emotions. Recent research is starting to identify the neurobiological mechanisms and neurophysiological processes associated with positive emotions, including neurochemicals, neurotransmitters, neuropeptides, and hormones to identify the neural correlates of positive emotions.[76] Flexible or neuroplastic brains, and

---

[70] Le Neindre P et al (2017) Animal consciousness. EFSA supporting publication 2017:EN-1196, p.5.
[71] Broom DM (2019) Sentience. In: Choe, JC (ed.), Encyclopedia of Animal Behavior, (2nd ed.). vol. 1 pp. 131-133.
[72] Walters ET (2018) Defining pain and painful sentience in animals *Animal Sentience* 21(14).
[73] Sneddon LU (2004) "Evolution of nociception in vertebrates: Comparative analysis of lower vertebrates", *Brain Research Reviews*, 46, pp. 123-130.
[74] Shriver AJ (2016) Cortex necessary for pain — but not in sense that matters. *Animal Sentience* 3(27) DOI: 10.51291/2377-7478.1051 and see Damasio A et al. (2013) Persistence of feelings and sentience after bilateral damage of the insula. *Cerebral Cortex,* 23(4), 833-846 for research findings which show that patients report experiencing pain even in cases where there is extensive bilateral damage to the insula cortex.
[75] Parliament UK (July 2021) Written evidence submitted by Jonathan Birth and colleagues (AWB0026) in response to the Sentience Bill consultation citing Andrews *et al.* (2013) The identification and management of pain, suffering and distress in cephalopods, including anaesthesia, analgesia and human killing. Journal of Experimental Marine Biology & Ecology, 447, 46–64; Clark RE & Squire LR (1998) Classical conditioning and brain systems: the role of awareness. *Science* 280(5360), 77-81.
[76] Alexander R *et al*. (2021) The neuroscience of positive emotions and affect: Implications for cultivating happiness and wellbeing *Neuroscience & Biobehavioral Reviews* 121: 220-249.

developmental, social, and environmental factors play a role in positive emotion.[77] Evidence for positive emotions in animals is found in play behaviour and interactions with conspecifics, and environmental enrichment is shown to positively impact brain development, especially related to neuroplasticity and neurogenesis.

33. Comparative behavioural studies seek similarities between human and animal behaviour through cognitive processes and observed behaviours.[78] This approach explores the question of animal consciousness through the level of cognitive sophistication that different species of animal are capable of and by seeking to establish their range of cognitive capacities, including whether they have metacognition – a cognitive awareness of how they experience the world. Recent and ongoing scientific research into the cognitive capacities of animals of different species, including birds and fish, has continued to deliver insights suggesting that they are capable of more complex thought, feeling, and social behaviours than previously recognised. Properties of animal consciousness have been analysed along five key domains: emotions, metacognition, processing of past and future (episodic memory), social behaviour, and human-animal relationships.[79] Methods such as preference testing, motivational testing, and experiments designed to understand animal communication offer indirect ways of investigating animal feelings and how positive or negatively valenced these feelings are for animals as they experience different situations. Sentient animals may be aware of pain, distress, and have pleasurable feelings without higher-order self-consciousness.[80]

34. Establishing whether animals have episodic or 'episodic-like' memory – the facility for mental time travel, such that they can consciously remember their past and use this knowledge to plan for their future – can contribute to understandings of whether animals are not only sentient, but also self-conscious. It is argued that this higher level of consciousness and capacity for mental time travel affords a being greater moral consideration than if they were merely sentient, because it can 'make an individual's life go better or worse than it could otherwise.'[81] Beings who are self-conscious can be benefited or harmed in ways that merely sentient beings cannot, since the former have desires, and can look into the future to anticipate pleasant and unpleasant experiences, and can, therefore, have greater degrees of pleasure or suffering.[82]

35. Episodic-like memory in animals can be empirically tested through behavioural and cognitive tests establishing whether animals can identify what (the context), where (the place), and when (the time) of the events they experience.[83] This capacity for remembering is differentiated from the capacity for instinctive or learned knowledge. Neural investigations on the neurobiological mechanisms for this capacity show that the hippocampus plays a key functional role in episodic memory, as well as the prefrontal and parietal regions.[84] The Bischof-Köhler (B-K) hypothesis places a behavioural condition on concluding whether an animal is demonstrating evidence of episodic-like memory: "the future planning should be independent of the animal's current motivational

---

[77] Alexander R *et al*. (2021) The neuroscience of positive emotions and affect: Implications for cultivating happiness and wellbeing *Neuroscience & Biobehavioral Reviews* 121: 220-249.
[78] Zentall T (2018) The value of research in comparative cognition *International Journal of Comparative Psychology* 31: 1-17.
[79] Le Neindre P *et al.* (2017) Animal consciousness. Summary of the multidisciplinary assessment. 8 p. hal-01736385.
[80] Parliament UK (January 2018) Written evidence submitted by the RSPCA (AWB0006) to the EFRA Committee; and Vallortigara G (2017) Sentience does not require "higher" cognition *Animal Sentience* 17(6).
[81] Varner GE (2012) *Personhood, ethics, and animal cognition situating animals in Hare's two level utilitarianism* New York: Oxford University Press.
[82] Le Neindre P et al (2017) Animal consciousness. EFSA supporting publication 2017:EN-1196, p.146.
[83] Templer VL & Hampton RR (2013) Episodic memory in nonhuman animals *Current biology 23*(17), R801–R806
[84] Crystal JD (2009) Elements of episodic-like memory in animal models *Behavioural Processes* 80(3): 269-277.

state."[85] Evidence of episodic-like memory is being found in mammals, birds, and insects, and has become apparent through cases of animals gathering or hiding their food for future retrieval.[86]

36. There are limited studies which have been conducted to investigate sentience in livestock. Research from studies on animals such as chickens, cows, goats, pigs, sheep, fish, and some invertebrates are presented below. The findings demonstrate behavioural, physiological, and neuroanatomical evidence for sentience across different species of animals.

Birds - chicken

37. Research studies demonstrating functional similarities in avian and mammalian brains are bringing into question longstanding assumptions about the simple and primitive nature of avian brains.[87] Neuroanatomical research on bird brains is challenging the notion that a layered cerebral cortex – as found in human and mammalian brains – is required for consciousness and complex cognition.[88] Research on avian brain structures identifying the function of neuronal groups supports the view that the avian pallium, a portion of the avian forebrain, can be compared to the 6-layered cortex in mammals and presents an alternative neural architecture supporting consciousness.[89] The pallium region of the avian brain consists of neurons arranged in groups representing a cortical-like structure, with the pallium containing functional columns of neurons similar to those found in the mammalian neocortex. A further discovery about the neuroarchitecture of the avian brain, which suggests a cortex-like structural similarity between avian and mammalian brains, is "an iteratively repeated, column-like neuronal circuitry" with the circuits connected to the columns and to other parts of the brain through layer-like connections like those found in the mammalian cerebral cortex.[90] These discoveries about the avian brain provide evidence for the possibility of similar cognitive capacities in mammals and birds.[91]

38. In a study investigating the neural correlates of sensory consciousness in corvid birds through behavioural research, carrion crows are trained to report whether a stimulus is present or absent in a rule-based delayed detection task.[92] As the crows perform the tasks, a two-stage process of awareness is observed in the neuronal activity: the initial activity corresponds to the physical stimulus intensity, and subsequent activity predicts the crows' perceptual reports. The study shows that as the bird performs a visual detection task a neuronal response in the endbrain area linked to complex cognition, the nidopallium caudolaterale (NCL), correlates with its perception of a stimulus. Researchers interpret this neuronal activity as containing information about the crows' subjective experience throughout the task and conclude that this may offer empirical evidence of avian consciousness. The implications of these findings for the phylogenetic origins of consciousness suggest the possibility of the last common ancestor to birds and

---

[85] Eacott MJ and Easton A (2012) Remembering the past and thinking about the future: Is it really about time? *Learning and Motivation* 43(4): 200-208.
[86] Shettleworth SJ (2007) Animal behaviour - Planning for breakfast *Nature* 445(7130): 825-826.
[87] Marino L (2017) The inconvenient truth about thinking chickens. *Animal Sentience* 17(1).
[88] Herculano-Houzel S (2020) Birds do have a brain cortex-and think *Science* 369(6511): 1567–1568.
[89] Kuenzel W (2014) Research advances made in the avian brain and their relevance to poultry scientists *Poultry science, 93 12*, 2945-52.
[90] Stacho M *et al*. (2020) A cortex-like canonical circuit in the avian forebrain *Science* 369(6511), eabc5534.
[91] Lori M (2017) Thinking chickens: a review of cognition, emotion, and behavior in the domestic chicken *Anim Cogn* 20: 127-147; Jarvis ED et al (2005) Avian brains and a new understanding of vertebrate brain evolution *Nat Rev Neurosci* 6:151-159.
[92] Nieder A *et al.* (2020) A neural correlate of sensory consciousness in a corvid bird *Science* 369(6511), 1626–1629.

mammals having had some form of consciousness which was inherited by both, or alternatively, consciousness having emerged independently at a later stage in birds.

39. Despite their relatively small size, bird brains, specifically those of corvids and parrots, have been found to contain very large numbers of neurons primarily located in the forebrain, with far greater neuronal densities than those in mammal brains.[93] The number of neurons offers an explanation for the higher information-processing and cognitive power of avian brains. Other species of bird, like pigeons and chicken, have lower neuronal densities with a smaller number of neurons than parrots or corvids with similar sized brains. However, even in birds like the chicken the neuronal density matches that found in the primate pallium.[94]

40. The neuroanatomy of chickens can be affected by the environment in which they are reared. Environmental conditions can impact hippocampal volume and contribute to an increase or attrition in volume in situations where chickens are deprived of experiences.[95] Laying hens reared in environmentally complex housing conditions benefit from an increase in hippocampal cell soma size, whilst those reared in barren environments suffer long-term deficits in spatial cognition and working memory.[96] Thus, environmental conditions can play an important role in restricting or promoting cognitive development in chicken.

41. Chickens are mostly precluded from studies on complex cognitive processes and have largely been the subject of studies exploring simple cognitive processes and basic associative processes.[97] However, behavioural studies on domestic chickens reveal that, contrary to prevailing beliefs and attitudes, they are cognitively complex and intelligent animals, with sophisticated emotional and social capacities comparable to those found in many mammals.[98] Chickens have well developed visual and spatial capacities, and can recognise partly occluded objects through a process called amodal completion. This capacity is demonstrated by both adult hens and newly hatched chicks. Furthermore, chickens have knowledge and understanding that an object exists even if it is out of sight, demonstrating their ability for object permanence. They can also distinguish between biological and nonbiological movement. In an experiment which exposed chicks to images made from moving light dots, they were seen to prefer images of a walking hen over a nonbiological motion stimulus. This ability of biological motion perception requires complex processing in the brain with the integration of multiple sensory inputs.[99]

42. Chickens have basic arithmetic capacities and can differentiate between a smaller and larger set of objects, and demonstrate evidence of ordinality, through their ability to order quantities numerically. Chickens advance towards a screen hiding the larger number of balls after a series of balls are added or taken away from behind two screens in an experiment testing their numerical abilities and mental account of a changing number of

[93] Olkowicz S *et al.* (2016) Birds have primate-like numbers of neurons in the forebrain *PNAS* 113 (26) 7255-7260.
[94] Olkowicz S *et al.* (2016) Birds have primate-like numbers of neurons in the forebrain *PNAS* 113 (26) 7255-7260.
[95] Tahamtani Fernanda M *et al*. (2016) Does Early Environmental Complexity Influence Tyrosine Hydroxylase in the Chicken Hippocampus and "Prefrontal" Caudolateral Nidopallium? *Front Vet Sci* **3:** 8.
[96] Tahamtani FM *et al.* (2015) Early life in a barren environment adversely affects spatial cognition in laying hens (*Gallus gallus domesticus*) *Front Vet Sci* **2**: 3.
[97] Lori M (2017) Thinking chickens: a review of cognition, emotion, and behavior in the domestic chicken *Anim Cogn* 20: 127-147.
[98] Nicol CJ (2015) *The behavioural biology of chickens*.
[99] Regolin L *et al.* (2000) Visual perception of biological motion in newly hatched chicks as revealed by an imprinting procedure *Anim Cogn* (2000) 3: 53–60.

objects.[100] Chicks use geometrical cues to find food hidden at the centre of different shapes.[101] Other birds, like the Clarke's nutcracker, use complex geometrical concepts and form cognitive spatial maps to locate and retrieve food which they have hidden, days or sometimes months later.[102] Western scrub jays demonstrate evidence of episodic memory through their ability to remember details about their food-caching and retrieving at a later date.

43. Chickens demonstrate a sense of time perception and can anticipate positive and negative future events.[103] The rely on a range of different sounds and visual signals to engage in referential communication and have distinctive calls to signal the approach of a predator to other chickens depending on whether the predator is on the ground or overhead.[104] These calls are made only in the presence of other chickens as a warning, and when the calls are recorded and played back to chickens in a laboratory setting they respond appropriately based on whether the call is to signal a predator overhead or on the ground. Chickens thus demonstrate intentionality, cognitive complexity, mental representation, and perspective-taking through their communication.[105]

44. Other capacities which chickens are seen to demonstrate include self-control (to optimise future outcomes by refraining from eating or waiting longer to eat if they are given longer access to food or given better food after a delay),[106] and the ability for logical inference and self-awareness of their status in a social hierarchy (through observing the interactions of other chickens).[107] Chickens engage in social learning and learn especially from dominant individuals in the social hierarchy by paying greater attention to them.[108]

45. There is evidence to suggest that chickens experience a range of complex emotions and express different emotional responses in anticipation of positive or negative events.[109] For example, states of fear in chickens are accompanied by physiological and behavioural stress responses. Hens demonstrate empathy and emotional contagion, through their ability to be affected by and share the emotional states of other members of their group. In an experiment that exposed chicks to an air puff, hens responded with distress displaying physiological and behavioural changes when their chicks were subjected to the air puff.[110] The hens' responses were cognitively informed since they relied on their knowledge of the aversive nature of the air puff and reflected the level of distress their chicks experienced. This experiment demonstrates that chickens can feel

---

[100] Rugani R *et al.* (2007) Rudimental numerical competence in 5-day-old domestic chicks (Gallus gallus): identification of ordinal position *Journal of experimental psychology Animal behavior processes 33*(1): 21–31.
[101] Tommasi L *et al.* (1997) Young chickens learn to localize the centre of a spatial environment *J Comp Physiol A* **180:** 567–572.
[102] Kaplan G and Rogers LJ (2005) Bird brain? It may be a compliment *Dana Foundation*
[103] Lori M (2017) Thinking chickens: a review of cognition, emotion, and behavior in the domestic chicken *Anim Cogn* 20: 127-147, citing Zimmerman PH *et al.* (2011) Behaviour of domestic fowl in anticipation of positive and negative stimuli *Anim Behav* 81: 569-577.
[104] Marler P and Evans C (1996) Bird calls: just emotional displays or something more? *Ibis* 138: 26-33 and Evans CS (2002) Cracking the code: communication and cognition in birds. In: Bekoff M *et al.* (eds) *The cognitive animal: empirical and theoretical perspectives on animal cognition.* MIT Press.
[105] Lori M (2017) Thinking chickens: a review of cognition, emotion, and behavior in the domestic chicken *Anim Cogn* 20: 127-147.
[106] Abeyesinghe SM *et al.* (2005) Can domestic fowl, *Gallus gallus domesticus*, show self-control? *Anim Behav* 70:1–11.
[107] Gottier RF (1968) The Dominance-Submission Hierarchy in the Social Behavior of the Domestic Chicken *The Journal of Genetic Psychology* 112:2, 205-226.
[108] Nicol CJ and Pope SJ (1999) The effects of demonstrator social status and prior foraging success on social learning in laying hens *Animal Behaviour* 57: 163-171.
[109] Zimmerman PH *et al.* (2011) Behaviour of domestic fowl in anticipation of positive and negative stimuli *Anim Behav* 81(3): 569-577.
[110] Edgar JL *et al.* (2013) Protective mother hens: cognitive influences on the avian maternal response *Anim Behav* 86(2): 223-229.

the emotional states of others in their social group, and further that their empathic responses are driven by a cognitive component too.

Cows - cattle

46. Physiological and neuroanatomical similarities between human and cattle brains, alongside behavioural evidence suggest that cattle are sentient, and have pleasant and unpleasant conscious experiences. During episodes of injury in cattle or exposure to noxious stimuli, nociceptors in the skin send signals through neural pathways to the central nervous system and from there to the thalamus and then to the parieto-insular cortex. This response matches findings from functional magnetic resonance studies which show increased activation of the cortex in humans when they report subjective states of pain, and a functional change in this part of the brain when analgesics are administered to reduce feelings of pain. As a result, it is inferred that cattle feel the pain from an injury or noxious stimulus and the necessary motor response to reduce, move away from, or avoid the pain is activated. Cattle in pain make distressed calls, have reduced appetite, are less social, and have an inflammatory immune response as well as the release of cortisol.[111] Although there are some differences in the human and cattle brain architecture, some researchers argue that these differences are not significant enough and do not provide sufficient evidence to indicate that cattle do not feel pain.

47. Behavioural studies show that cows are cognitively and socially complex, have rich mental lives, experience emotional states, have conscious desires and preferences, and that, individually, cows demonstrate unique personality traits.[112] Cows demonstrate rapid learning abilities and spatial memory and can retain information about the location of a feeder for up to six weeks after the test, and retain the memory of an association between a visual cue and a food reward for up to a year.[113] Salt-deficient calves have shown the ability to learn how to dispense sodium solution by pressing a panel.[114] Most studies on cows are conducted in applied settings, in relation to the role of cows as food commodities. Further research is required to investigate cows as individuals on their own terms, with a greater focus on their psychological characteristics, and other cognitive abilities such as object permanence, time perception, and numerosity.

48. Cattle can discriminate (even in the form of 2D images such as photographs) between familiar and unfamiliar conspecifics (thus displaying an understanding of “sameness” in relation to their own species). Cattle and calves can also discriminate between friendly and unfriendly humans, and express fear responses when they come into contact with humans who have previously treated them badly.[115] In experiments testing the ability of cattle to engage in tasks of learning, cattle are seen to express emotion and self-awareness, and display signs of pleasure when they learn a task quickly.[116] Reflecting on these experiments, it is suggested that in comparing their performance and expressing emotional reactions to their learning, cattle have a conscious memory and

---

[111] Comstock G (2018) Concerning Cattle: Behavioral and Neuroscientific Evidence for Pain, Desire, and Self-Consciousness in Barnhill A *et al.* (eds) *The Oxford handbook of food ethics* Oxford Handbooks Online.
[112] Marino L & Allen K (2017) The psychology of cows *Animal Behavior and Cognition* 4(4): 474-498.
[113] Hirata M & Takeno N (2014) Do cattle (Bos taurus) retain an association of a visual cue with a food reward for a year? *Animal Science Journal* 85, 729 – 734.
[114] Sly J & Bell FR (1979) Experimental analysis of the seeking behaviour observed in ruminants when they are sodium deficient *Physiology and Behaviour* 22: 499 – 505.
[115] Coulon M *et al.* (2011) Cattle discriminate between familiar and unfamiliar conspecifics by using only head visual cues *Animal cognition* 14(2): 279–290; de Passillé, AM *et al.* (1996) Dairy calves' discrimination of people based on previous handling *Journal of animal science* 74(5): 969–974.
[116] Hagen K and Broom DM (2004) Emotional reactions to learning in cattle *Appl Anim Behav Sci* 85(3–4): 203-213.

awareness of their recent performance (a few minutes into the past) and can also be aware of how long it takes them to complete a task.[117]

49. Positive and negative emotional states in cows are expressed through behavioural and physiological changes and can also affect the cognitive function of animals leading to cognitive bias. Fear responses in cows can be tested through the Open-Field Test, in which cows are seen to defecate, increase their vocalisations and attempt to escape in states of fear. Changes in eye white percentage are also used as indicators for emotional valence, with greater eye white percentage indicating fear and frustration (such as when cow mothers are separated from their calves), and less eye white a sign of a positive emotional state (as seen when cows are reunited with their calves).[118]

50. Play behaviour in calves releases endorphins and is a sign of positive engagement with conspecifics and with the environment and is associated with positive welfare. A calf that is kept in solitary conditions and deprived of social stimulation shows less behavioural flexibility and lacks skills for play with other calves. The prefrontal cortex of calves that are deprived of such social experiences shows less development of cortical connections than are seen in animals raised in social environments.[119] This points to the differences in social learning abilities that arise in calves that are housed individually as compared with calves that are housed in social conditions.

51. Cows show a propensity for emotional contagion. In the presence of conspecifics that are stressed, they too exhibit signs of stress. However, due to social buffering and the importance of the social group, their stress levels are lowered in group settings, especially in the presence of other non-stressed conspecifics.[120] In this respect, social housing for cows can act as a form of long-term social buffering and contributes to healthy psychological and cognitive development.[121] Cows feel distress when isolated, and cow-calf separation practices are a source of grief and emotional distress for cow mothers when they are separated from their calves.[122] Young calves recognise the call of their mothers,[123] and calves that are kept with their mothers show greater resilience and lower physiological stress levels when placed in new and challenging situations, as compared with calves that are separated from their mothers.[124]

Goats

52. Results from experiments found that goats make complex foraging choices that depend on social interaction and factors such as position in the dominance hierarchy relative to

---

[117] Comstock G (2018) Concerning Cattle: Behavioral and Neuroscientific Evidence for Pain, Desire, and Self-Consciousness in Barnhill A *et al.* (eds) *The Oxford handbook of food ethics* Oxford Handbooks Online.
[118] Sandem A and Braastad BO (2005) Effects of cow–calf separation on visible eye white and behaviour in dairy cows—A brief report *Appl Anim Behav Sci* 95(3–4): 233-239.
[119] Gaillard C *et al.* (2014) Social housing improves dairy calves' performance in two cognitive tests *PloS one* 9(2), e90205.
[120] Shin D *et al.* (2017). Social relationships enhance the time spent eating and intake of a novel diet in pregnant Hanwoo (Bos taurus coreanae) heifers *PeerJ* 5: e3329; Ishiwata T *et al.* (2007) Choice of attractive conditions by beef cattle in a Y-maze just after release from restraint *Journal of Animal Science* 85: 1080-1085.
[121] Marino L & Allen K (2017) The psychology of cows *Animal Behavior and Cognition* 4(4): 474-498.
[122] Ventura BA *et al.* (2013) Views on contentious practices in dairy farming: The case of early cow-calf separation *J Dairy Sci* 96: 6105-6116.
[123] Barfield CH *et al.* (1994) Domestic Calves (*Bos taurus*) Recognize their Own Mothers by Auditory Cues Ethology 97: 257-264.
[124] Wagner K *et al.* (2013) Mother rearing of dairy calves: Reactions to isolation and to confrontation with an unfamiliar conspecific in a new environment *Appl Anim Behav Sci* 147: 43 – 54; Weary DM and Chua B (2000) Effects of early separation on the dairy cow and calf: 1. Separation at 6 h, 1 day and 4 days after birth *Appl Anim Behav Sci* 69(3): 177-188.

conspecifics and the visual gaze of a competitor.[125] Goats have been found to follow the directional gaze cues from other species (in this case, humans) in order to find hidden food.[126] They also show human-directed visual orienting behaviour in ways that are similar to the referential and intentional communication by domestic companion animals.[127]

53. Goats show signs of being able to distinguish between positively and negatively valenced vocalisations. In a study investigating emotion perception, goats were exposed to positively and negatively associated calls from conspecifics. Behavioural and physiological measures used to track their responses on hearing the differently valenced calls played back to them. Evidence from the experiment suggests that goats can differentiate between calls to perceive emotion and that the behaviour and physiological responses of goats correspond to the type of call they hear, suggesting that goats may be likely to detect emotion in conspecifics.[128]

Pigs

54. Pigs are cognitively complex and highly social animals with a capacity for complex object discrimination and long-term memory.[129] During foraging, they rely on their memory, as well as their visual and olfactory senses,[130] and demonstrate spatial learning and memory through their foraging strategies, an ability which relies upon mental representations in their short and long-term memory.[131] Their preference for food sites that contain a larger quantity of food indicates that they may have some skills for numerical discrimination.[132] Pigs demonstrate time perception through their ability to differentiate between different time intervals, and can learn to estimate time intervals of days.[133]

55. A combination of different behavioural and physiological measures such as vocalisation patterns, bodily movement, and changes in heart rates can be used to indicate the strength of both positive and negative emotional valence in pigs by exposing them to repeated aversive and rewarding events.[134] High frequency calls in pigs often indicate negative situations. Pigs can anticipate when they may be faced with positive or negative situations. In a study in which pigs were made to wait before entering a room with a positive situation or a negative situation, they reacted with high-frequency vocalisations

---

[125] Kaminski J *et al.* (2006) Goats' behaviour in a competitive food paradigm: Evidence for perspective taking? *Behaviour* 143(11): 1341-1356.
[126] Kaminski J *et al.* (2005) Domestic goats, Capra hircus, follow gaze direction and use social cues in an object choice task *Animal Behaviour* 69: 11-18.
[127] Nawroth C *et al.* (2016) Goats display audience-dependent human-directed gazing behaviour in a problem-solving task *Biology letters* 12(7), 20160283.
[128] Baciadonna L *et al.* (2019) Goats distinguish between positive and negative emotion-linked vocalisations *Front Zool* **16:** 25.
[129] Marino L and Colvin CM (2015) Thinking pigs: A comparative review of cognition, emotion and personality in Sus domesticus *International Journal of Comparative Psychology* 28.
[130] Croney CC *et al.* (2003) A note on visual, olfactory and spatial cue use in foraging behaviour of pigs: indirectly assessing cognitive abilities *Appl Anim Behav Sci* 83: 303–308.
[131] van der Staay FJ *et al.* (2012) The appetitively motivated “cognitive” holeboard: A family of complex spatial discrimination tasks for assessing learning and memory Neuroscience and Biobehavioural Reviews 36: 379-403; Gieling ET *et al.* (2011) Assessing learning and memory in pigs *Anim Cogn* **14:** 151–173.
[132] Held S *et al.* (2005) Foraging behaviour in domestic pigs (Sus scrofa): Remembering and prioritizing food sites of different value *Animal Cognition* 8: 114-121.
[133] Ferguson SA *et al.* (2009) Female mini-pig performance of temporal response differentiation, incremental repeated acquisition, and progressive ration operant tasks *Behavioural Processes* 80: 28-34; Spinka M *et al.* (1998) Do domestic pigs prefer short-term to medium-term confinement? *Applied Animal Behaviour Science* 58(3-4): 221-232; Fuhrer N and Gygax L (2017) From minutes to days—The ability of sows (Sus scrofa) to estimate time intervals *Behavioural Processes* 142: 146-155.
[134] Leliveld LM *et al.* (2016) Behavioural and physiological measures indicate subtle variations in the emotional valence of young pigs *Physiology & behavior* 157: 116–124; Karin A *et al.* (2021) Vocalisations in farm animals: A step towards positive welfare assessment *Applied Animal Behaviour Science* 236: 105264.

and were more resistant to entering the room when they anticipated entering the negative room due to the associated signal tones as they waited to enter.[135] Other experiments have shown that expectations of food and situations of play lead to states of increased arousal.

56. Pigs are playful animals and engage in complex forms of social and object play.[136] Opportunities for play are key for the healthy socio-cognitive and emotional development of pigs. The availability of toys and straw can contribute to pigs experiencing more positive affective states, whilst conditions such as lack of space, exposure to noise, and repeated exposure to pain affect mood changes and lead to negative affective states.[137] Pigs find opportunities for play and exploration pleasurable and rewarding and are more optimistic because of these experiences.[138] Behavioural abnormalities are observed in pigs which are reared in farrowing crates because they are deprived of the opportunities and environments for play and exploration.[139]

57. Pigs can discriminate between conspecifics and between familiar and unfamiliar humans. They engage in strategic behaviour especially when foraging, by following their conspecifics who have knowledge of where food is hidden, and successfully use mirrors to locate hidden food.[140] Pigs also demonstrate emotional contagion in social situations and adopt and exhibit the same behaviours and physiological responses as those in other pigs who are experiencing or anticipating a positive or negative situation. These behaviours are interpreted in pigs as indicative of their having some form of empathy and perspective-taking.

Sheep

58. Sheep demonstrate individuality through differences in their personalities. Their personality traits include shyness-boldness, gregariousness, calmness-anxiety, reactivity, and activity levels. Their personality influences group behaviour, including distribution and the movement of the group, with sheep preferring to forage within their social groups. Sheep demonstrate different forms of predictive intelligence concerning their social interactions and predators. They also show flexibility of intelligence through learning rules which connect stimuli and rewards and subsequently responding to these rules as they change.[141]

59. Sheep, like many other domesticated animals, are cognitively complex and perform well on discrimination tasks.[142] They demonstrate excellent memory skills and can remember and recognise fifty other sheep after two years,[143] and they have spatial memory which

---

[135] Imfeld-Mueller S *et al.* (2011) Do pigs distinguish between situations of different emotional valences during anticipation? *Applied Animal Behaviour Science* 131: 86-93.
[136] Horback K (2014) Nosing around: Play in pigs *Animal Behavior and Cognition* 1(2): 186-196.
[137] Leliveld LM *et al.* (2016) Behavioural and physiological measures indicate subtle variations in the emotional valence of young pigs *Physiology & behavior* 157: 116–124.
[138] Douglas C *et al.* (2012) Environmental enrichment induces optimistic cognitive biases in pigs *Appl Anim Behav Sci* 139, 65-73.
[139] Pedersen LJ *et al.* (2014) How much is enough? The amount of straw necessary to satisfy pigs' need to perform exploratory behaviour *Appl Anim Behav Sci* 160: 46-55.
[140] Broom D (2010) Cognitive ability and awareness in domestic animals and decisions about obligations to animals *Appl Anim Behav Sci* 126: 1-11.
[141] Morton AJ & Avanzo L (2011) Executive decision-making in the domestic sheep *PLoS ONE* 6(1), e15752; Gamez D (2019) The intelligence of sheep *Animal Sentience* 25(27).
[142] Marino L and Merskin D (2019) Intelligence, complexity, and individuality in sheep *Animal Sentience* 25(1).
[143] Kenrick KM *et al.* (2001) Sheep don't forget a face *Nature* 414(6860): 165-166.

allows them to remember and perform well in maze navigation tasks.[144] They can recognise faces from two-dimensional images,[145] and prefer the faces conspecifics, especially familiar over unfamiliar sheep. Social buffering is seen when the stress levels of distressed and isolated sheep are reduced if they are shown a picture of a familiar conspecific.[146] Emotional contagion in sheep is demonstrated through contagious yawning,[147] and ewes show empathy to their lambs if they are seen to be in pain.[148] When lambs are separated from their mothers at a young age, signs of distress are apparent through their vocalisations and pacing.[149]

60. Behavioural and physiological changes such as heart rate, temperature, and ear posture in sheep indicate that they experience a range of internal subjective states and emotions, including fear, anger, boredom, disgust, and happiness.[150] Sheep also experience cognitive bias, and showed greater pessimism and had learning deficits after being exposed to more stressful situations.[151] They also form expectations and show disappointment and frustration if their expectations for rewards are not met.[152] Positive emotional states in sheep occur when they are engaged in play and lambs display more play behaviours when they are in an enriched play arena with ear postures and salivary cortisol providing measures of their positive affective states.[153]

Fish

61. Despite lacking a neocortex, the brain of the fish shares a number of characteristics with the mammalian brain.[154] Research into the structure and function of the teleost brain, for example, suggests that the optic tectum, a midbrain structure that is thought to correspond to the mammalian superior colliculus, may play an important role in the generation of sentience. With its complex extrinsic and intrinsic connections, the optic tectum has been proposed to allow for sensorimotor integration and is thought to be the centre of multi-sensory conscious perception in both fish and amphibians.[155] In fact, the tectum receives sensory input of different modalities (e.g. retinal input) as well as from mesencephalic and hindbrain nuclei, diencephalic and telencephalic regions, including the pallium, and sends its outputs to premotor brainstem nuclei that control motor behaviour. After receiving sensory input, the tectum generates isomorphic neural representations of the visual space, which are subjectively experienced by the fish as mental images.[156] Evidence of the involvement of the fish tectum in sensory conscious

---

[144] Lee C *et al.* (2006) Development of a maze test and its application to assess spatial learning and memory in Merino sheep. *Appl Anim Behav Sci* 96(1-2): 43-51.
[145] Knolle F *et al.* (2017) Sheep recognize familiar and unfamiliar human faces from two-dimensional images *R. Soc. open sci.* 4: 171228.
[146] da Costa AP *et al.* (2004) Face pictures reduce behavioural, autonomic, endocrine and neural indices of stress and fear in sheep *Proceedings. Biological Sciences* 271(1552), 2077-2084.
[147] Marino L and Merskin D (2019) Intelligence, complexity, and individuality in sheep *Animal Sentience* 25(1).
[148] Hild S *et al.* (2011) Ewes are more attentive to their offspring experiencing pain but not stress *Appl Anim Behav Sci* 132: 3-4: 114-120.
[149] Freitas-de-Melo A *et al.* (2017) Low pasture allowance until late gestation in ewes: behavioural and physiological changes in ewes and lambs from lambing to weaning *Animal* 11(2), 285–294.
[150] Marino L and Merskin D (2019) Intelligence, complexity, and individuality in sheep *Animal Sentience* 25(1); Veissier I *et al.* (2009) Animals' emotions: Studies in sheep using appraisal theories. Animal Welfare, 18(4), 347-354.
[151] Destrez A *et al.* (2013) Long-term exposure to unpredictable and uncontrollable aversive events alters fearfulness in sheep *Animal* 7(3): 476-484.
[152] Reefman N *et al.* (2009) Physiological expression of emotional reactions in sheep *Physiology & Behaviour* 98(1-2), 235-241.
[153] Chapagain D (2014) Investigating the motivation to play in lambs *Appl Anim Behav Sci* 160, 64-74; Chapagain D *et al.* (2014) Investigating the motivation to play in lambs *Applied Animal Behaviour Science* 160: 64-74.
[154] Braithwate V (2010) *Do fish feel pain?* OUP Oxford.
[155] Feinberg TE and Mallatt J (2013) The evolutionary and genetic origins of consciousness in the Cambrian Period over 500 million years ago Published online: 4 October 2013.
[156] Woodruff ML (2017) Consciousness in teleosts: There is something it feels like to be a fish *Animal Sentience* 13(1).

perception is challenging the assumption that a layered neocortex is required for minimal animal sentience.

62. Another brain area that is thought to play an important role in the generation of sentience in fish is the pallium. This is a neuroanatomically complex telencephalic structure that has reciprocal connections with subpallial areas. These connections have been proposed to support a number of functions in fish, including the conscious experience of environmental stimuli and the modulation of emotional reactions.[157] There are similarities between the fish pallium and mammalian brain structures. Researchers have examined the dorsolateral pallium of the knifefish and found a layered and columnar organisation very similar to that of the mammalian cortex.[158] The medial pallium is considered to be the homologous with the human amygdala which, in mammals, plays a key role in processing and responding to fearful and threatening stimuli.[159] The lateral pallium is considered to be the homologous with the mammalian hippocampus, which is involved in declarative memory, the conscious recollection of events, and spatial memory. The pallium has connections with the tectum, preglomerular complex (PgC) and other subpallial structures which can influence motor programmes, thereby allowing emotions and memories to influence the motor behaviour of the fish.[160]

63. Molecular, physiological and behavioural studies indicate that fish can feel pain. Goldfish tend to avoid areas where they had previously received an electric shock, even though they know that they will find food in those areas. Even when deprived of food, they have been found to resist for up to three days before accessing the feeding/shock areas.[161] In a study investigating the effects of lesions in the medial pallium, goldfish were placed in a shuffle-box and were taught to swim from a compartment of the shuffle-box to another in response to a coloured light in order to avoid an electric shock. Researchers found that fish can learn to avoid the electric shock, but such ability is significantly impaired in subjects with lesioned medial pallium.[162] These findings provide further evidence of the importance of the medial pallium processing and responding to threats and fearful events. When in pain, fish respond by decreasing their activity.[163] Such response, however, can be ameliorated by administrating analgesics and pain relief drugs and when given a choice, a fish will take action to relieve its pain.[164]

64. A growing body of evidence shows that fish have complex perceptual, social and cognitive abilities and is challenging the assumption that fish behaviours are simply a result of reflex responses, implicit learning, and procedural memories. Fish possess sophisticated spatial learning, memory and navigation skills and can use landmarks, magnetic fields, sun compass and even cognitive maps to navigate the environment.[165]

---

157 Woodruff ML (2017) Consciousness in teleosts: There is something it feels like to be a fish *Animal Sentience* 13(1).
158 Trinh AT, Harvey-Girard E, Teixeira F, and Maler L (2016) Cryptic laminar and columnar organization in the dorsolateral pallium of a weakly electric fish *Journal of Comparative Neurology* 524(2): 408-28.
159 Calder A, Lawrence A, and Young A (2001) Neuropsychology of fear and loathing. *Nature Review Neuroscience* 2**:** 352– 63
160 Woodruff ML (2017) Consciousness in teleosts: There is something it feels like to be a fish *Animal Sentience* 13(1).
161 Millsopp S and Laming P (2008) Trade-offs between feeding and shock avoidance in goldfish (Carassius auratus) *Applied Animal Behaviour Science* 113(1-3): 247-54
162 Portavella M, Torres B, and Salas C (2004) Avoidance response in goldfish: emotional and temporal involvement of medial and lateral telencephalic pallium. Journal of Neuroscience 24(9): 2335-42.
163 Sneddon LU, Lopez-Luna J, Wolfenden DC, *et al.* (2018) Fish sentience denial: Muddying the waters *Animal Sentience* 21(3).
164 Lopez-Luna J, Al Jubouri Q, Al-Nuaimy W, and Sneddon LU (2017) Reduction in activity by noxious chemical stimulation is ameliorated by immersion in analgesic drugs in zebrafish *Journal of Experimental Biology* 220(8): 1451-8; Sneddon LU, Lopez-Luna J, Wolfenden DC, *et al.* (2018) Fish sentience denial: Muddying the waters *Animal Sentience* 21(3).
165 Bshary R and Brown C (2014) Fish cognition *Current Biology* 24(19): 947-50.

Fish can also effectively use geometrical information to guide their movements.[166] Importantly, the spatial learning abilities of fish can be enhanced if the complexity of their rearing environment is increased, indicating the importance of environmental conditions in fish cognitive development.[167]

65. Behavioural experiments reveal good long-term memory capacities in teleost fish. Fish can retain spatial information for more than eighteen days, they can remember the location of a tide pool for about forty days and can recognise individual conspecifics thirty days after being exposed to them. Some fish can even remember landmark cues after six months. [168] When food is hidden before their eyes, horses can remember the food's location for around six seconds while fish would remember the hidden food for more than three minutes. In a behavioural experiment, snapper fish were fed with dead sardines, some of which had been dyed red. Initially, the colour of the sardines made no differences to the fish. However, when the experimenters made the red sardines unpalatable by sewing stinging medusa tentacles into their mouths, the snappers started avoiding all the red sardines and kept avoiding them for the following two weeks.[169]

66. Fish may even perform better than mammals in tasks requiring memory and learning skills. In a study, cleaner fish, chimpanzees, orangutans and capuchin monkeys were presented with two plates, one red and one blue, containing the same amount of food. However, while the red plates were soon removed, the blue ones were not. Only adult fish and two out of four chimpanzees learned to eat first from the red plates before eating from the permanent blue ones in less than 100 trials in order to maximise food resources. [170] This shows that fish can anticipate the consequences of their own actions.

67. Fish communicate with conspecifics in different ways, for example by grinding their teeth, rubbing bones together and vibrating their swim bladders.[171] Some species, such as the knife fish and the elephant nose fish, use an electric organ located at the end of their tails to generate electrical signals to communicate with other fish. These special organs can also be used to identify other fish. In fact, researchers have found that different frequencies of the electrical impulses can serve as unique identifiers for different individuals.[172]

68. Fish can experience a range of feelings, including fear, pleasure and pain. This is shown by a number of behavioural and physiological studies, which have revealed the presence of dopaminergic, GABAergic, serotonergic and other neurotransmitter systems known for modulating a range of affective and motivational states in mammals.[173] When feeling afraid, a fish would react as other animals would, for example by breathing faster, releasing alarm pheromones and freezing or by trying to flee or to look bigger. Behavioural studies also provide evidence of play behaviour in fish. For instance, cichlids

---

[166] Brown AA, Spetch ML, and Hurd PL (2007) Growing in circles: Rearing environment alters spatial navigation in fish *Psychological Science* 18(7): 569-73.
[167] Bshary R and Brown C (2014) Fish cognition *Current Biology* 24(19): 947-50.
[168] Bshary R, Wickler W, and Fricke H (2002) Fish cognition: a primate's eye view *Animal cognition* 5(1): 1-13.
[169] Reighard J (1908) An experimental field study of warning coloration in coral reef fishes, in *Papers from the Tortugas Laboratory of the Carnegie Institution of Washington*, *vol. II* (Washington, D.C.: Carnegie Institution), pp. 257-325.
[170] Salwiczek LH, Prétôt L, Demarta L, *et al.* (2012) Adult cleaner wrasse outperform capuchin monkeys, chimpanzees and orang-utans in a complex foraging task derived from cleaner–client reef fish cooperation *PLoS One* Published online: 21 November 2012.
[171] Balcombe, J. (2016). In praise of fishes: Précis of What a fish knows (Balcombe 2016). Animal Sentience 8(1).
[172] Braithwate V (2010) *Do fish feel pain?* OUP Oxford.
[173] Woodruff ML (2017) Consciousness in teleosts: There is something it feels like to be a fish *Animal Sentience* 13(1).

can be observed playing with a submersible thermometer, especially when alone and unstressed.[174]

Invertebrates: cephalopods and decapods

69. Very few species of cephalopods and decapods have been studied in relation to sentience. Broadly speaking, the nervous system of octopods, squid and other cephalopods can be divided into a sub- and a supra-oesophageal masses, and an optic lobe.[175] Of great interest for researchers investigating sentience in cephalopods is the vertical lobe, an area located in the supra-oesophageal mass that receives inputs from other parts of the body, including the mantle, eyes and arms, and that is thought to contribute to multi-sensory integration.[176] In decapods, this integrative function may be performed by the central complex, the hemiellipsoid, depending on the species.[177]

70. Despite a long-standing assumption that small invertebrate brains cannot support cognition, a growing body of evidence reveals sophisticated cognitive skills in decapod, cephalopods and in other invertebrates.[178] Cephalopods have generally good spatial navigation, problem-solving, communication, learning and memory skills. Cuttlefish, for example, would search for prey depending on what they have eaten and where and how long ago they ate.[179] Some of these invertebrates can even learn to make use of rudimentary tools. For example, octopuses can learn to assemble coconut shell halves to create a shelter. Once they have learned how to use them, some octopuses would even carry the coconut shells with them for future use.[180] Researchers believe the cephalopod vertical lobe to be the analogous to the mammalian hippocampus and to be responsible for learning and memory skills.[181] Crabs can learn to associate a threatening stimulus with a specific context. Neuroanatomical and immunohistochemical evidence suggests that the hemiellipsoid may be responsible for learning and memory in crabs.[182]

71. Octopuses are curious and playful animals and, when given objects, they may use these as toys with which to play.[183] They have been observed playing with a range of tools, including Lego objects.[184] Octopuses have also been seen playing with a plastic bottle

---

[174] Balcombe, J. (2016). In praise of fishes: Précis of What a fish knows (Balcombe 2016). Animal Sentience 8(1).

[175] Shigeno S, Andrews PL, Ponte G, and Fiorito G (2018) Cephalopod brains: an overview of current knowledge to facilitate comparison with vertebrates *Frontiers in Physiology* Published online: 20 July 2018

[176] Birch J, Burn C, Schnell A, Browning H, and Crump A (2021) *Review of the Evidence of Sentience in Cephalopod Molluscs and Decapod Crustaceans* LSE Consulting.

[177] Sandeman DC, Kenning M, and Harzsch S (2014) Adaptive trends in malacostracan brain form and function related to behavior in Derby C and Thiel M (Eds.) Crustacean nervous system and their control of behaviour (pp. 11- 48) New York Oxford University Press.

[178] Mikhalevich I and Powell R (2020) Minds without spines: Evolutionarily inclusive animal ethics *Animal Sentience* 29(1)

[179] Jozet-Alves C, Bertin M, and Clayton NS (2013) Evidence of episodic-like memory in cuttlefish *Current Biology* 23(23): 1033-5.

[180] Finn JK, Tregenza T, and Norman MD (2009) Defensive tool use in a coconut-carrying octopus *Current biology 19*(23): 1069-70.

[181] Shigeno S, Andrews PL, Ponte G, and Fiorito G (2018) Cephalopod brains: an overview of current knowledge to facilitate comparison with vertebrates *Frontiers in Physiology* Published online: 20 July 2018

[182] Maza FJ, Sztarker J, Shkedy A, Peszano VN, Locatelli FF, and Delorenzi A (2016) Context-dependent memory traces in the crab's mushroom bodies: Functional support for a common origin of high-order memory centers *Proceedings of the National Academy of Sciences 113*(49).

[183] Mather JA and Anderson RC (1999) Exploration, play and habituation in octopuses (Octopus dofleini) *Journal of Comparative Psychology* 113(3): 333-8; Birch J, Schnell AK, and Clayton NS (2020) Dimensions of animal consciousness *Trends in cognitive sciences* 24(10): 789-801.

[184]Kuba M, Meisel DV, Byrne RA, Griebel U, and Mather JA (2003) Looking at play in Octopus vulgaris *Berliner Paläontologische Abhandlungen* 3:163-169; Kuba MJ, Byrne RA, Meisel DV, and Mather JA (2006) When do octopuses play? Effects of repeated testing, object type, age, and food deprivation on object play in Octopus vulgaris *Journal of comparative psychology* 120(3): 184-90.

by hitting it with water jets and repeating the behaviour when the current brings the bottles back.[185]

72. A growing body of neurophysiological and behavioural evidence suggests that both cephalopods and decapods can feel pain and that they possess nociceptors sensible to noxious stimulation.[186] After suffering an injury, squid assume a defensive posture. Likewise, manually declawed crabs use the remaining claw to shield the wounded area.[187] An octopus whose arm had been injured will exhibit a wound grooming behaviour and they would tend to protect their arm by keeping it close to the body or by wrapping the other arms around the injured one.[188]

73. Administrating analgesic and anaesthetic substances can relieve pain in both decapods and cephalopods. For example, opioids reduce defensive and escape responses to electric shocks in crabs.[189] A recent experiment reveals that, after receiving a painful injection of acetic acid in the arm, octopuses start avoiding the location where they have received the injection, they groom the injured arm and, crucially, they learn to prefer locations where they can access lidocaine, a local anaesthetic. As shown by electrophysiological recordings, ongoing activity in the brachial connectives which is linked to pain, can also be silenced by the administration of lidocaine. [190] This shows that these animals would take action to relieve pain, if given the opportunity.

Limitations of studies and further research considerations

74. Historically, studies have primarily focused on investigating the negative experiences of animals. This has led to a greater understanding of negative emotions as compared to the positive ones. This is now being challenged in the context of disciplines such as 'positive psychology' and 'affective neuroscience' which promote the study of positive dimensions of animal wellbeing. Further research on a wider range of positive emotions is necessary for advancing more holistic understandings of animal minds and experiences that matter, and to identify and explore the conditions necessary for improving welfare and for the flourishing for animals.[191]

75. A systematic review of the scientific literature on animal sentience over two decades found that most studies had been conducted in laboratory settings (78%), with far fewer

---

[185] Birch J, Schnell AK, and Clayton NS (2020) Dimensions of animal consciousness *Trends in cognitive sciences* 24(10): 789-801.
[186] Crook RJ, Hanlon RT, and Walters ET (2013) Squid have nociceptors that display widespread long-term sensitization and spontaneous activity after bodily injury *Journal of Neuroscience* 33(24); Birch J, Burn C, Schnell A, Browning H, and Crump A (2021) *Review of the Evidence of Sentience in Cephalopod Molluscs and Decapod Crustaceans* LSE Consulting.
[187] Birch J, Burn C, Schnell A, Browning H, and Crump A (2021) *Review of the Evidence of Sentience in Cephalopod Molluscs and Decapod Crustaceans* LSE Consulting.
[188] Alupay JS, Hadjisolomou SP, and Crook RJ (2014) Arm injury produces long-term behavioral and neural hypersensitivity in octopus *Neuroscience Letters 558*: 137- 42.
[189] Lozada M, Romano A, and Maldonad H (1988) Effect of morphine and naloxone on a defensive response of the crab Chasmagnathus granulatus *Pharmacology Biochemistry and Behavior* 30(3): 635 – 40; Maldonado H, Romano A, and Lozada M (1989) Opioid action on response level to a danger stimulus in the crab (Chasmagnathus granulatus) *Behavioral Neuroscience 103*(5): 1139 – 43.
[190] Crook RJ (2021) Behavioral and neurophysiological evidence suggests affective pain experience in octopus *iScience* 24(3) Published online: 19 March 2021
[191] Nussbaum M (2006) *Frontiers of justice;* de Vere AJ and Kuczaj II (2016) Where are we in the study of animal emotions? *Wiley Interdisciplinary Reviews* 7(5): 354-362.

studies conducted on farms (12.6%) or in the wild (4.26%).[192] Laboratory studies are useful since they allow animals, through the design of experiments, to demonstrate cognitive abilities, which may not be observed in their natural environment. However, these should complement and be used in addition to studies conducted in the field.[193]

76. Most studies conducted on animals focus on applied themes and relate to the management of animals, or study animals for human benefit. Fewer studies are designed to study animals on their own terms, investigating their minds and intelligence within their evolutionary contexts with the aim of improving knowledge about animals and animal sentience. Researchers recommend that further research studies exploring animal sentience and consciousness should be goal-directed, conducted in naturalistic environments in non-invasive and non-harmful ways, and with a wider range of species, especially including domestic livestock, on which very few studies exist.[194]

A good life: linking animal sentience and consciousness to animal welfare

77. Animal sentience and consciousness offers a basis for establishing animal interests and has relevance for assessing the mental and physical welfare implications of the human treatment of animals. Sentient beings who can suffer and feel pleasure have morally relevant interests including, for example, an interest in avoiding pain and suffering and in accessing the positive and pleasurable experiences that makes their life a life worth living.[195] Studying the mental and emotional lives of animals can tell us much about the interests of animals, their preference in relation to their treatment, and about what constitutes a good life, according to their form of life.[196]

78. In past decades, research in the field of animal welfare has been primarily focused on animals' negative welfare states and the circumstances that might cause them to experience negative feelings, including boredom, frustration, anxiety, anger, fear and loneliness.[197] Animals kept in captive and monotonous environments, for example, display behaviours that are indicative of apathy and depression in humans.[198] When moved from pasture to inescapable crates, sheep may become inactive and unresponsive after an initial period of agitation.[199] This reaction is believed to be the

---

[192] Proctor HS *et al.* (2013). Searching for Animal Sentience: A Systematic Review of the Scientific Literature. *Animals 3*(3), 882–906.

[193] Wasermann EA and Zentall TR (2012) Introduction in: The Oxford handbook of comparative cognition (2 ed.) citing Zentall TR (1993). Animal cognition: An approach to the study of animal behavior. In TR Zentall (Ed.), *Animal cognition: A tribute to Donald A. Riley* (pp. 3–15). Hillsdale, NJ: Erlbaum.

[194] Lori M (2017) Thinking chickens: a review of cognition, emotion, and behavior in the domestic chicken *Anim Cogn* 20: 127-147 and Proctor, HS *et al.* (2013). Searching for Animal Sentience: A Systematic Review of the Scientific Literature. *Animals 3*(3), 882–906; see also the companion Review of literature and publicly available data on the longitudinal effect of balanced breeding strategies in context of historical health and welfare outcomes

[195] Franks B, Webb C, Gagliano M, and Smuts B(2020) Conventional science will not do justice to nonhuman interests: A fresh approach is required *Animal Sentience* 27(17); In his paper 'What is suffering and what sorts of beings can suffer?' David DeGrazia writes 'beings who are capable of suffering in at least the broad sense have interests, and beings who have interests have moral status.'

[196] Webb LE, Veenhoven R, Harfeld JL, and Jensen MB (2019) What is animal happiness? *Annals of the New York Academy of Sciences 1438*(1): 62-76

[197] Mellor *et al.* (2020) The 2020 five domains model: including human–animal interactions in assessments of animal welfare *Animals* 10(10).

[198] Špinka M and Wemelsfelder F (2011) *Environmental challenge and animal agency* in Animal welfare Wallingford, UK: CAB International 27-44

[199] Fordham DP, Al-Gahtani S, Durotoye LA, and Rodway RG (1991) Changes in plasma cortisol and β-endorphin concentrations and behaviour in sheep subjected to a change of environment *Animal Science* 52(2): 287-96; Fureix C and

result of learned helplessness, a cognitive state associated with clinical depression in human and non-human animals. [200]

79. There is, among welfare scientists, a growing recognition that good welfare is more than just the absence of suffering. For animals to live a good life, they must be given the opportunity to access a range of rewarding and pleasurable experiences. They should, for example, be given the opportunity to play, engage in environment exploration activities, and in a range of social behaviours.[201] Pigs, for example, are very curious and find novelty pleasurable and rewarding. If given a choice, pigs that are kept in monotonous conditions such as those found in intensive farming systems will take action and initiate a change in their environment. In an experiment where piglets were given a choice between entering a two-side pens with either a novel or a familiar hidden object in it, they showed a significant preference for the pen with the novel object.[202] Novelty and exploration tended to elicit play, a reaction that is also common in human children.[203] The time that the piglets spent playing increased significantly in the period after exploring new objects, suggesting that they found the change in their environment pleasurable.

80. Physical and social challenges may be perceived as rewarding experiences by some animals and could be used to keep them stimulated and improve the environment in which they live. In a behavioural experiment, pigs were assigned an individual acoustic signal as a call to work for food. When animals heard their individual sounds coming from one of four different feeding stations, they had to localise its source and respond to a button using their nose in order to be rewarded with food. The researchers observed that the pigs were not only capable, but also willing to cope with these demands and suggested that the tasks represented a positive challenge for them and a beneficial mitigation against boredom. [204]

81. Some animals might find the ability to control some aspects of their lives rewarding and the learning process an enjoyable experience. For example, after learning how to press a panel to open a gate and access food, young calves tend to have an increased heart rate and an agitated behaviour, with frequent jumps, kicks and bucks. This has been interpreted by researchers as a sign of excitement, indicating an emotional reaction to their own learning and achievements. [205]

82. As shown by these studies, providing animals with safe and stimulus-rich environments and with opportunities to socialise with congenial others is key to achieving animal welfare. There is, however, much more that we need to know about animals' wellbeing and the conditions necessary for their flourishing. Researchers in the field of animal welfare have called for more studies into the way in which animals experience positive

---

Meagher RK (2015). What can inactivity (in its various forms) reveal about affective states in non-human animals? A review Applied Animal Behaviour Science 171 8-24.

[200] Fureix C and Meagher RK (2015). What can inactivity (in its various forms) reveal about affective states in non-human animals? A review Applied Animal Behaviour Science 171 8-24.

[201] Mellor DJ (2016) Updating animal welfare thinking: Moving beyond the “Five Freedoms” towards “a Life Worth Living” *Animals* 6(3).

[202] Wood-Gush DG M and Vestergaard K (1991) The seeking of novelty and its relation to play *Animal Behaviour* 42(4): 599-606.

[203] Hutt C (1966) Exploration and play in children *Symposia of the Zoological Society of London* (18) 61–81.

[204] Ernst K, Puppe B, Schön PC, and Manteuffel G (2005) A complex automatic feeding system for pigs aimed to induce successful behavioural coping by cognitive adaptation *Applied Animal Behaviour Science* 91(3-4): 205-18.

[205] Hagen K and Broom DM (2004) Emotional reactions to learning in cattle *Applied Animal Behaviour Science* 85(3-4): 203-13.

emotions.[206] This knowledge could help finding new ways to promote pleasurable experiences and enhance long-term positive emotional states, providing us with valuable information to inform current practices, as well as animal welfare standards and assessments. [207]

Policy developments related to animal sentience and consciousness

83. The concepts of animal sentience and animal welfare were introduced into policy discussions by the Brambell Committee in 1965. The Committee's report stated that "animals show unmistakable signs of suffering from pain, exhaustion, fright, frustration… and we accept that animals can experience emotions such as rage, fear, apprehension, frustration and pleasure".[208] Sentience was considered an integral part of animal welfare, which was understood as "a wide term that embraces both the physical and mental wellbeing of the animal." [209] The Brambell report contained legislative recommendations to protect and improve the welfare of farmed animals, and stated that scientific evidence for sentience would be drawn from anatomy and physiology, as well as ethology and the science of animal behaviour.

84. With pressure from animal welfare campaigners and interest groups, animals were recognised as sentient beings in the 1997 Treaty of Amsterdam through the addition of a Protocol on the protection and welfare of animals.[210] By 2007, the language from this Protocol was incorporated as Article 13 in the European Union Treaty of Lisbon, which states that "animals are sentient beings" and introduces a duty on EU Member States "to pay full regard to the welfare requirements of animals" when formulating policy related to the use of animals.[211] The 2012-2015 EU Animal Welfare strategy explains sentience in animals as a capacity for 'feeling pleasure and pain'.[212] This legal protection in Article 13 applied to animals in the UK whilst it was a Member State of the European Union.

85. Since its departure from the European Union, the UK Government has been reviewing EU legislation on animal sentience.[213] The EU Withdrawal Act 2018 did not contain legal continuity for Article 13 of the Lisbon Treaty.[214] An Animal Welfare (Sentience) Bill was proposed by the UK Government in 2021, to make provision for an Animal Sentience Committee which would ensure that government policies pay due regard to the welfare of animals as sentient beings.[215]

---

[206] Boissy *et al*. (2007) Assessment of positive emotions in animals to improve their welfare *Physiology & behavior*, *92*(3): 375-97.
[207]Browning H (2019) What should we do about sheep? The role of intelligence in welfare considerations *Animal Sentience* 4(25); Horback K (2019) Applied cognition research to improve sheep welfare *Animal Sentience* 25(18).
[208] Farm Animal Welfare Council (2009) Farm animal welfare in Great Britain: past, present and future.
[209] Report of the Technical Committee to enquire into the welfare of animals kept under intensive livestock husbandry systems. Chairman: Professor F. W. Rogers Brambell. Cmnd. 2836, December 3 1965. Her Majesty's Stationery Office, London.
[210] European Parliament (2 October 1997) Treaty of Amsterdam amending the Treaty on European Union, the Treaties establishing the European communities and certain related acts'.
[211] European Union Law (13 December 2007) Treaty of Lisbon amending the Treaty on European Union and the Treaty establishing the European Community, signed at Lisbon.
[212] European Commission (2012) EU Animal Welfare Strategy: 2012-2015.
[213] House of Commons Library (8 July 2019) Animal Sentience and Brexit
[214] House of Commons Library (1 September 2017) European Union (Withdrawal) Bill
[215] UK Parliament (July 2021) Parliamentary Bills: Animal Welfare (Sentience) Bill [HL]