

C

Consciousness



Rocco J. Gennaro
University of Southern Indiana, Evansville,
IN, USA

This chapter will address the extent to which nonhuman animals are conscious. Most important perhaps is what criteria should be used in making such a determination. We have certainly come a long way from the Cartesian view that animals are mere “automata” and do not even have conscious experience. In addition to the obvious and significant behavioral similarities between humans and many animals, much more is known today about our neurophysiological and genetic similarities. Still, there are some grey areas and genuine difficulties in interpreting some experimental results pertaining to animal cognition and in analyzing the comparative neuroanatomy.

The more general “problem of other minds,” including the so-called argument by analogy, is introduced in the section “[Animals and the Problem of Other Minds](#)”. In the section “[Lloyd Morgan’s Canon and Parsimony](#),” “Morgan’s Canon” and the related principle of simplicity is addressed especially as they pertain to attributions of animal consciousness. The section “[More on Some Hard Cases and Brain Structure](#)” focuses on some of the harder cases, such as fish and insects, where it is

necessary to delve more deeply into some comparative neurophysiology. Finally, in the section “[Animal Consciousness and Higher-Order Thought Theory](#),” the charge that one prominent philosophical theory of consciousness (the higher-order thought theory) is inconsistent with animal consciousness is explored. Here the focus is on the possibility of self-awareness and metacognition in animals.

Philosophical and scientific work on animal minds and consciousness has surged in recent years with the publication of several major studies and reviews, such as Tye (2016), Andrews and Beck (2018), Allen-Hermanson (2018), as well as the recently launched on-line journal *Animal Sentience* (see, e.g., Harnad 2016, Klein and Barron 2016; see also Allen and Trestman 2016, Andrews 2016). Much of this work takes on the challenge of the most difficult borderline cases, such as reptiles, crabs, insects, and fish, as well as further examination of the evolution of consciousness.

Perhaps the most commonly used notion of “conscious” is captured by Thomas Nagel’s “what it is like” sense (Nagel 1974). When I am in a conscious mental state, there is “something it is like” for me to be in *that state* from the first-person point of view. When I smell a rose or have a conscious visual experience, there is something it “seems like” from my perspective. This is primarily the sense of “conscious state” that I use

throughout this chapter. Ideally, we would like to know which, and to what extent, animals are capable of having conscious subjective experiences such as pains, perceptions, and emotions. As Nagel famously asked, “What is it like to be a bat?”

Animals and the Problem of Other Minds

It is clear that we have come a long way from the Cartesian view that animals are mere “automata” and that animals do not even have conscious experience. Other major figures in the early modern period, such as Leibniz, also struggled with the question of animal (or “brute” or “beast”) consciousness (Gennaro 1999). There has indeed been a long history of philosophical opinion and argument about animal consciousness (see, e.g., Allen and Trestman 2016; Allen-Hermanson 2018). In addition to some clear behavioral similarities between humans and many animals, much more is known today about other physiological similarities such as brain and DNA structures. To be sure, there are also important differences and some genuinely difficult grey areas where one might have legitimate doubts about a given animal and consciousness. Nonetheless, it seems fair to say that most philosophers today agree that a significant portion of the animal kingdom is capable of having conscious mental states. Of course, this is not to say that animals can have *all* of the same kinds of sophisticated conscious states enjoyed by human beings, such as reflecting on philosophical and mathematical problems, enjoying artworks, or thinking about the vast universe or the distant past. However, it still seems reasonable to believe that animals can have at least some conscious states ranging from rudimentary pains and emotions to various perceptual states (visual, olfactory, tactile, etc.) and episodic memory.

One traditional way to approach this topic is via the “problem of other minds,” that is, how we can know that others have conscious mental states especially given the more indirect access we have to them as compared to our own minds. Although there is no generally accepted solution to this

problem, most people in practice simply take it for granted that other *human beings* have mental states similar to theirs. However, knowledge of animal minds does present some particular difficulties. Nonhuman animals cannot describe their mental states using language even though they can most certainly communicate with each other (and even to us) in various other ways. Although there have been attempts to teach human-like languages to members of other species, none can do so in a way that would easily solve this problem. Instead, it would seem that despite the similarities between our behavior and those of other animals, any such knowledge of their minds would have to be less certain than what seems to be much more immediate knowledge of our own minds. Nonetheless, a strong inductive rationale for animal consciousness seems sufficient to establish a reasonable belief that most animals have conscious mental states. Sometimes this takes the form of an “argument by analogy” such that, for example, we know how we feel when we exhibit the behavior of someone in fear or in pain and so it seems reasonable to think that the same conscious states are present when a dog or chicken displays the same behavior. This is presumably because we think of such behaviour as *caused by* the relevant conscious state. It is unlikely that we always make such conscious inferences when we observe animal behavior; rather, we probably often simply take it for granted. But this analogical strategy can be found in well-known philosophers throughout history (e.g., Locke, Hume, Mill, and Russell.) One worry about this type of argument is that it seems to generalize from my own single case, which would indeed be a rather weak instance of induction. However, we might instead suppose that it is an argument from *my species* to most individuals of another species (see Perrett 1997). Of course, the details can vary greatly from species to species.

A related line of argument is the so-called inference to the best explanation (IBE) which does not necessarily depend on self-observation. This is because it relies more on the fact that a successful empirical theory sometimes posits the existence of things that are not directly observed (such as electrons) but rather known indirectly by

way of their observable effects. In a similar fashion, positing conscious states can be the best explanation of what causes an animal's observable behavior (Pargetter 1984). IBE (sometimes called "abduction") is a version of "hypothesis testing" which might be formulated via a "likelihood" principle according to which one hypothesis is favored over another if it alone predicts an observation that would otherwise be unexpected (Sober 2001; see also Allen-Hermanson 2018; Melnyk 1994.)

In any case, what evidence might be used to infer the presence of consciousness in animals? Although many different criteria have been proposed (e.g., Baars 2005; Seth et al. 2005; Edelman et al. 2005), most fall under one or more of the following general headings:

1. Nonverbal or non-vocal behavioral evidence.
2. Ability to use language and/or to communicate.
3. Ability to learn, solve problems, and be creative.
4. Similarity of brain structure to humans.

So, for example, rocks and tables display none of the above criteria and thus we do not think they are conscious. Trees and plants are alive but also do not meet any of the above criteria, for example, they do not jump away or scream when approached with a chainsaw or lawnmower. At the other extreme, humans normally seem to meet all four criteria. However, when we look at the animal kingdom we find that the evidence is often mixed, at least to some extent. Some animals may only meet two or three criteria whereas others might only meet one. What should we make of these cases? At the least, we might suppose that the more criteria met the more likely an animal is conscious even if none of the above criteria is conclusively necessary or sufficient for having conscious states. Of course, it may also depend upon the *degree* to which a given animal can meet a particular criterion.

Generally speaking, with regard to criterion (1), we can point to an animal's behavioral reaction to stimuli or a given bodily movement. If a dog moves in a way similar to me when someone

steps on my leg, this seems to be some evidence that the dog is conscious. If mental states cause bodily movements, then it seems reasonable to infer that the mental state (pain, suffering) is present when the typical bodily effect is observed.

With regard to criterion (2), the ability to use language and/or to communicate, we obviously communicate with each other via a common language and thus we take for granted that there is conscious thought behind linguistic utterances. Unlike most philosophers, however, Dennett (1991, 1995) seems supportive of the idea that consciousness requires language in the sense of "story telling" and thus perhaps only humans are conscious. The conscious "self" is really only a kind of narrative that we tell ourselves. But even though many animals cannot linguistically communicate *with us*, it is clear that they communicate *with each other*, such as in fairly sophisticated whale, chimp, and bird vocalizations. Treating the use of human-like language as a necessary condition for consciousness seems to be an unnecessarily high bar to clear.

With regard to criterion (3), the ability to learn, solve problems, and be creative, the fact that a human student or an animal can learn from a teacher or trainer provides some evidence that they have conscious minds. Conscious working memory and thought seem necessary for at least some kinds of learning. Further, if an animal is able to solve a somewhat novel practical problem, then it seems that at least some primitive conscious thinking is required. Many animals are able to "figure out" what to do when confronted with a challenging or unexpected situation, such as having to make a tool to acquire some food. In some cases, there can even be what appears to be a creative solution to a problem. Humans are clearly also able to be creative in a number of ways. Rocks and trees, on the other extreme, do not learn or solve problems.

Along the same lines, some use "behavioral versatility" or "stimulus independence" as good overall evidence in support of animal consciousness (Griffin and Speck 2004; Newen and Bartels 2007). If, for example, an animal adjusts its behavior appropriately in response to unpredictable challenges, it seems more likely that it is

consciously thinking about its situation than when it responds uniformly. Fixed and rigid responses to stimuli seem to indicate a lack of conceptual representation whereas behavioral versatility indicates an ability to think about a given stimulus and act in a much more context-dependent fashion. This sort of capacity seems also to indicate an ability to *learn* from prior experience and to solve problems.

With regard to criterion (4), similarity of brain structure, we might use comparative neurophysiological evidence to help us to determine animal consciousness. A variety of theoretical and empirical arguments have been put forward for the conclusion that consciousness is shared across all mammals. For example, Seth et al. (2005) argue that widespread reentrant activity in the thalamo-cortical complex involve anatomical systems that are at minimum shared among all mammals and some non-mammals. In addition, many animals share with us some rather primitive areas of the brain, such as the amygdala in the limbic system, responsible for emotions such as fear. This is how discovering specific neural correlates of consciousness in humans might in turn shed light on animal consciousness, especially given our common evolutionary history. To the extent that animals lack some of the brain structures responsible for more sophisticated mental capacities in us (such as the prefrontal cortex), it seems reasonable to suppose that they are not capable of having these kinds of mental states. However, it may also be that some mental capacities are realized in different brain areas in other species (I will return to this line of argument in the section “[More on Some Hard Cases and Brain Structure.](#)”).

Of course, for *each* of our four criteria, there always appear to be counterexamples which suggest that the criterion is not *by itself sufficient* for consciousness. Present day robots and machines, just to make this point, are capable of some communication and language use (as well as some appropriate behavioral responses to stimuli). But it is unclear that either suffices for robot consciousness, perhaps partly because there is no common biological history or similarity. Bees, for example, are well-known to communicate to other bees about where honey can be found

through a series of rather complicated “dances.” Perhaps bees are conscious but it is at least not as obvious as some other animals. The case is perhaps even weaker for various insects, such as ants, which nonetheless display “avoidance behavior” and some intra-species communication that allow them to survive. Weaker still would be the behavior of bacteria and single-celled organisms where the behavior in question tends to be rigidly fixed. There is also nothing remotely like a “brain” in bacteria and not much of one in some tiny insects. What about creativity? Defining creativity is difficult but someone might suppose that spiders creatively make their rather sophisticated webs even though spider consciousness is at least not that clear. Also, we can program computers to solve chess and mathematical problems but again this hardly seems to be enough for consciousness.

It may also be that each of the four criteria is not *necessary* for consciousness, depending on unusual circumstances or one’s metaphysical views. For example, someone who is paralyzed and cannot behave or communicate may of course still be conscious. And perhaps some primitive organisms can be conscious without being able to solve problems or be creative at all.

Nonetheless, it seems that one can reach a reasonable inductive inference in favor of consciousness the more criteria that are met (e.g., in higher mammals) and a reasonable inductive inference against consciousness when, say, less than two criteria are met. It is also very important to emphasize that satisfying each criterion can come in very different degrees, for example, compare the behavior of an ape with the behavior of a lizard. Further, the matter can become very complex even within a single type of organism, such as fish (Allen 2013).

In some instances, of course, it may even be difficult to know whether *another human* is conscious, such as in coma cases and in persistent vegetative states (PVS), both of which also raise significant ethical questions (Farah 2008; Braddock 2017). However, the existence of some truly borderline cases does not rule out many other clearer cases of the presence or absence of consciousness.

Lloyd Morgan's Canon and Parsimony

Before delving further into some details and specific species, let us pause first to consider an important methodological issue. Much has been made recently over how considerations of “parsimony” or “simplicity” in mental state attributions to animals should be understood. We should of course be careful not to anthropomorphize, on the one hand, but also not to underestimate animal minds, on the other hand. The often quoted Morgan's Canon says that “in no case may we interpret an action as the outcome of the exercise of a higher psychological faculty, if it can be interpreted as the outcome of the exercise of one which stands lower in the psychological scale” (Morgan 1894, p. 53). On the surface, the canon seems to favor less-sophisticated mental state attributions or even explanations which only reference the body and behavior of animals under various conditions.

However, many authors have noted serious problems with this notion as well as significant ambiguity in the canon itself (Browne 2004; Allen-Hermanson 2005; Fitzpatrick 2008; Sober 2009, 2012). It is unclear how to interpret Morgan's Canon and how it relates to the associated notions of “parsimony” or “simplicity.” For example, Browne (2004) explains that Morgan's Canon is thus not quite the same as following a law of parsimony. He recognizes that “it is parsimonious to explain similar, complex, stimulus-response patterns by similar psychological mechanisms” (Browne 2004, p. 648). So when various animals perform in ways similar to humans on a given task, “it is unparsimonious to adopt one kind of lower-level explanation for the animal's response on one task and a different kind of lower-level explanation for the animal's response on [another] task” (Browne 2004, pp. 643–644). Browne thus also seems to have in mind what was discussed in the section “[Animals and the Problem of Other Minds](#),” that is, some kind of reasonable analogical or explanatory notion of simplicity. We ought to attribute mental states to animals (and thus explain their behavior) when they behave similarly to humans under similar conditions.

Michael Tye echoes much of the above sentiment and relies on a kind of argument by analogy

as well as the principle of simplicity (Tye 2016, Chapter 5). Citing Newton and Reid, he approvingly borrows the slogan that “similar effects proceed from the same or similar causes.” Indeed, to assign other causes would be to introduce “superfluous causes” and run afoul of something like a principle of simplicity. With respect to animal pain, for example, Tye comments that he is “entitled to infer that the feeling of pain causes [a] behaviour in [animals] too unless I have a *defeater* to that inference, that is, a reason to believe that a causal story is operative in those animals that cannot be reconciled with the causal story that adverts to pain” (2016, p. 75). As we shall see, one potential defeater might be a difference in neuroanatomy, but Tye ultimately rejects the notion that the lack of neocortex by itself defeats the inference to pain attribution to many animals.

More on Some Hard Cases and Brain Structure

Aside from the obvious academic interest, there is also the very practical matter of the morality of animal experimentation and eating animals (Singer 1990; Jamieson 2018). At the very least, whether or not an animal can suffer and feel pain should be taken into account with regard to how they ought to be treated. Billions of animals are killed every year for food and used in research. Many of them are subjected to rather cruel conditions. Of course, some think that even if animals are conscious in some basic sense, they still do not deserve moral consideration especially as compared to humans. Few, if any, researchers and meat-eaters doubt that virtually all of these animals can experience pain. Pain, it would seem, is also a fairly primitive conscious state by comparison to most other kinds of mental states (Allen 2004; Shriver 2006, 2018). Still, the function of pain is not merely to avoid bodily damage; it can also have an emotional or motivational element. Thus, there has been significant focus on basic animal sentience in recent years, especially with respect to some of the harder cases, such as fish, crabs, birds, reptiles, cephalopods, and various insects (Tye 2016). Significant discussion

of animal neuroanatomy seems particularly relevant to some of the literature, although behavioral responses to stimuli are inevitably also relied upon.

Neurological studies of animal pain often start with the distinction between “nociception” and pain. Nociception is the capacity to sense potentially damaging noxious stimuli and is one of the most primitive sensory capacities. Nocioceptors are linked to nerve endings in the skin, some of which are associated with initially brief and localized sharp pain and others of which result in longer-lasting pain. Neurons functionally specialized for nociception can even be found in invertebrates such as the medical leech and snails. Since nociceptors are found in such a wide range of species and are even functionally effective in spinally transected animals, their presence in a species provides little justification in inferring conscious pain experiences. Tye explains that in humans “the painfulness of pain in humans is based on activity in two different neural regions: the somatosensory cortex and the ACC [anterior cingulate cortex]” (Tye 2016, p. 79). The ACC is more closely related to the “felt badness” or “unpleasantness” of pain. It seems that when the somatosensory cortex is damaged, what results is still an unpleasant sensation but it is not really described as “pain” as such. We should keep in mind, however, there are abnormal human cases of developmental neuroplasticity (e.g., in hydrocephaly where there is no neocortex) such that conscious states seem to be realized in different than normal neural structures from a very young age. These are indeed abnormal cases of neural plasticity in humans, but they do show that there may be reasons to think that in some animals “the absence of a neocortex does not in and of itself entail that cells homologous to those found in the neocortex are missing too” (Tye 2016, p. 84). Although a lack of neocortex must be taken into account when examining a given creature’s ability to have pains and other conscious states, Tye does not think that it defeats the inference to the presence of felt pain depending upon the extent of behavioral similarity. Interpretation of various experimental results is a matter of ongoing debate with part of the problem having to do with knowing the

extent of “neural plasticity” or “multiple realizability” of a given cortical function.

Let us look more closely at some of the harder cases:

Evidence from lesions and brain imaging seems to indicate a key role in human pain for certain cortical structures, especially the anterior cingulate, somatosensory, and insular cortices (Craig 2009). Neuroanatomical factors as well as physiological changes strongly indicate conscious pain in mammals (Shriver 2006) and birds (Calabrese and Woolley 2015). Lesion studies of mammals and birds strongly suggest serious deficits in pain experience (Allen et al. 2005). Even though there is no neocortex in birds, there are still certain sorts of constituent and ancient neuron cell types found in birds that are found in our neocortex (Tye 2016, pp. 122–125). In addition, behavioral indicators of pain as seen, for example, in farm animals include vocalizations, abnormal postures and limping, and reductions in activity (Prunier et al. 2013). Chicken most certainly actively seek pain relief when forced to live in overcrowded pens and cages. For example, under certain crippling conditions, they choose feed laced with a pain reliever far more often than a feed without it. Under these circumstances, it would seem that avoiding pain suggests that a creature can *feel* pain and thus is capable of at least some conscious states.

There is a very lively debate over fish consciousness and especially about whether fish can experience pain, stress, and suffering (see Rose 2002 and Sneddon et al. 2003 for opposing views). This is particularly relevant in the very practical context of welfare regulation in commercial and sport-fishing. The term “fish” is itself rather ambiguous and does not really correspond to any clear taxonomic group of creatures. There is an incredible diversity and number of fish groups or species, and so it is particularly difficult to make generalizations about fish consciousness (see Braithwaite 2010; Allen 2013; Brown 2015; Tye 2016, Chapter 6, for reviews and extensive treatment). Tuna fish are, for example, closer to us in many ways than they are to sharks, and not all fish are “cold-blooded.”

Nonetheless, a key issue for fish (and reptiles and other animals, for that matter) is the absence

of a neocortex (Rose 2002; cf. Rose et al. 2014). Rose (2002) argues that because fish lack the anterior cingulate cortex (ACC), they may not be bothered by pain or merely have (unconscious) nociception. Sneddon et al. (2003) disagree and argue that there is adequate behavioral and physiological evidence for pain in fish (see also Chandroo et al. 2004; Sneddon 2011; Balcombe 2016). Trout, for example, have nociceptors but also respond favorably to painkillers when treated with noxious stimuli and fish react to morphine much as we do. There are numerous articles on fish consciousness in the on-line journal *Animal Sentience*, including Key (2015, 2016) who argues that fish lack the necessary neurocytoarchitecture, microcircuitry, and structural connectivity for the neural processing required for feeling pain. Numerous commentators, such as Broom (2016), Seth (2016), Shriver (2016), and Striedter (2016), reply to Key. Woodruff (2017) reviews neuroanatomical, neurophysiological, and behavioral studies which leads him to the conclusion that fish do have neurobiological correlates and behavioral flexibility of sufficient complexity to support the hypothesis that they are capable of phenomenal consciousness.

Tye (2016, Chapter 6) also argues that fish can feel pain and have other conscious states. He argues at great length that a lack of neocortex is not by itself a defeater for consciousness in various animals. The overall behavior of fish, such as struggling to get away when caught on a hook, is very similar to the way we would behave in such circumstances. And since nociceptors transmit signals that generate pain in humans and other mammals, it seems plausible to suppose that fish feel pain too. Behavioral indications of fear and anxiety in many fish also seem to abound and much the same seems true of basic perceptual consciousness including smell, vision, hearing, and visual discrimination (Tye 2016, pp. 107–113). Once again, the best and simplest explanation of the extensive behavioral similarities between humans and fish, according to Tye, is that fish undergo the same experiences that we do.

A neocortex is also not present in lizards and reptiles, but Cabanac et al. (2009) present some evidence that there is felt pleasure and pain in iguanas. They argue that consciousness is shared

by all *amniotes* which include all descendants of the common ancestor of living birds and mammals, such as lizards, snakes, and turtles. Some interesting behavioral indicators of consciousness are also discussed, such as “trade-off” behavior (where, e.g., fish decrease feeding attempts as electric shocks are increased until food deprivation increases), navigational detouring (which requires an animal to pursue a series of non-rewarding intermediate goals in order to obtain an ultimate reward), expression of emotion, expression of sensory pleasure, and emotional fever (an increase in body temperature in response to a stressful situation). It does indeed often seem rather difficult to explain these behaviors entirely without also attributing consciousness. Reptiles also show spatial cognitive abilities similar to those of rats and exhibit learning or behavioral flexibility in their pursuit of food. Even though reptiles lack a hippocampus as well as a neocortex, there is some reason to suppose that the medial cortex in reptiles operates in a similar way to the hippocampus in mammals (Tye 2016, pp. 131–133).

One intriguing group of invertebrate animals that has received significant attention with respect to consciousness is cephalopods, e.g., octopuses, squids, and cuttlefish. These are clever and large-brained animals who are well-known for incredible abilities to camouflage themselves and for flexible hunting strategies. Mather (2008) argues that cephalopods exhibit many behavioral indicators of consciousness, including complex learning and spatial memory. The octopus is especially interesting. They are highly intelligent, very adept at learning, and display a variety of complex cognitive abilities (Godfrey-Smith 2013). The octopus can even escape from a jar by unscrewing it from the inside. Once again, we must be careful however. Cephalopod neuroanatomy is so very different from mammalian architecture that it may be difficult to be entirely confident in attributions of consciousness. For one thing, over two-thirds of their neurons are located in their tentacles.

Another group of animals garnering significant attention is arthropods, which includes insects, crustaceans, spiders, and many other less familiar animals (Tye 2016, Chapter 8). This is an ancient

and diverse group of creatures and so, again, any generalizations should be made with caution. It is interesting, however, to note that arthropods were among the earliest animals to evolve complex active bodies and brains capable of controlling them (Trestman 2013). So, if one function of consciousness is to solve problems which arise due to controlling complex bodies (Merker 2005), consciousness may have evolved very early on among arthropods. The case for insect sentience is sometimes also made on the basis of neuroanatomical similarity to the mammalian midbrain (Klein and Barron 2016). Klein and Barron argue that basic subjective experience is supported by the integrated midbrain and basal ganglia structures which are among the oldest and most highly conserved brain systems in vertebrates. They argue that the insect brain supports functions analogous to those of the vertebrate midbrain and hence that insects may also have a capacity for subjective experience. (Replies to Klein and Barron can be found in the same 2016 issue of *Animal Sentience*.)

The fact that honeybees recognize faces even from unfamiliar perspectives might be suggestive of mental rotation and visual imagery (Dyer et al. 2005). Jackson and Wilcox (1993) document a variety of impressive behaviors in jumping spiders, including detouring and other forms of apparent planning, as well as flexible, context-sensitive adjustment of predatory behavior to prey behavior. There are numerous studies on bees and, for example, pattern recognition, navigation, communication, visual working memory (Srinivasan 2010), and mood and emotions (Mendl et al. 2011).

Nociceptors are missing in virtually all insects, but they still do respond to and learn to avoid a range of noxious stimuli, including honeybees. Still, it does seem that a stronger behavioral case can be made against insect consciousness since, for example, they do not move to protect injured body parts in the way that mammals do. Perhaps, however, some of these behaviors can be explained away as attempts to survive in spite of the pain. In the case of bees, there are at least some important physiological similarities and further evidence of intelligence and working

memory (Tye 2016, pp. 148–156). As was briefly mentioned in the section “[Animals and the Problem of Other Minds](#),” bees are also well-known for their very sophisticated navigational abilities and intra-species communication via “waggle dances” with respect to the location of food.

Crabs are crustaceans with a highly developed sense of smell but poor vision. Elwood and Appel (2009) seem to show that hermit crabs can remember an aversive event (an electric shock) and can use that memory in later context-sensitive decision-making (see also Elwood et al. 2009). This seems to be evidence of remembering a painful experience. Crabs also react to analgesics in the same way that honeybees do. If crabs feel pain, then surely bees also do since bees have ten times more neurons than crabs have. Indeed, bee brain *density* is ten times greater than a mammalian cerebral cortex (Tye 2016, pp. 156–158).

In some of the above cases, there are clearly some potential “defeaters” (as Tye calls them) to the conclusion that there really are conscious states in some species. It may indeed even be impossible to infer with any sense of confidence, especially with respect to some insects and crustaceans. Still, as we have seen, there may also be cases where a potential defeater might itself be defeated, such as in some instances where a creature lacks a neocortex. In addition, many kinds of creatures, such as fish and insects, come with an incredible variety of species and so there may be some exceptions which make generalizations difficult to justify.

Feinberg and Mallatt (2016) take a more explicitly evolutionary approach to animal consciousness although some of the same issues raised above are front and center (see also Godfrey-Smith 2018). When did consciousness first appear on Earth and how did it evolve? What constitutes consciousness and which animals are sentient? Using their own list of the neurobiological features that seem responsible for consciousness, Feinberg and Mallatt argue that consciousness appeared much earlier in evolutionary history than is commonly assumed. About 520–560 million years ago, they explain, the great “Cambrian explosion” of animal diversity produced the first complex brains, which were

accompanied by the first appearance of consciousness. Simple reflexive behaviors evolved into a unified inner world of subjective experiences. From this they deduce that all vertebrates are and have always been conscious, including fish, reptiles, amphibians, and birds. Considering invertebrates, they find that arthropods (including insects and probably crustaceans) and cephalopods (including the octopus) also meet many of the criteria for consciousness. Part of this still controversial issue is whether or not consciousness evolved as an adaptive function and then remained as a benefit for organisms (Maley and Piccinini 2018). For example, consciousness may allow organisms to construct an internal model of the world, learn in certain ways, or perform voluntary actions. If this is so, then consciousness confers an adaptive advantage to organisms that have it.

Animal Consciousness and Higher-Order Thought Theory

It is sometimes alleged that one prominent philosophical theory of consciousness, the higher-order thought (HOT) theory, is inconsistent with animal consciousness (Seager 2004). Indeed, one higher-order theorist has even embraced the normally unwelcome conclusion that most animals do not have conscious states (Carruthers 2000, 2005). Others have responded by defending HOT theory as consistent with most animal consciousness (Gennaro 2009, 2012, Chapter 8).

Let us back up: HOT theory is an example of a so-called representational theory of consciousness which attempt to reduce consciousness to “mental representations” rather than directly to neural states. The notion of “reduction” at work is to explain conscious states by means of non-conscious mental states and thus without reference to consciousness (thereby also avoiding the charge of circularity). Other representational theories include first-order representationalism (FOR) which aim to explain conscious experience primarily in terms of world-directed (or first-order) intentional states (Tye 2000). Higher-order representationalism (HOR) holds that what

makes a mental state M conscious is that it is the object of some kind of higher-order mental state directed at M (Lycan 2001; Rosenthal 2005; Gennaro 2012). There are various kinds of HOR theory with the most common division between higher-order thought (HOT) theories and higher-order perception (HOP) theories. HOT theorists, such as Rosenthal (1997, 2004, 2005) and Gennaro (1996, 2012), think it is better to understand the HOR as a thought containing concepts. HOTs are treated as cognitive states involving some kind of conceptual component. A HOT is a “meta-psychological” or “metacognitive” state, that is, a mental state directed at another mental state (“I am in mental state M”). HOP theorists urge that the HOR is a perceptual state which does not require the conceptual content invoked by HOT theorists (Lycan 1996, 2004).

So HOR theories attempt to reduce consciousness in *mentalistic* terms, such as “thoughts” and “awareness,” rather than directly in neurophysiological terms. Thus, the idea is to reduce consciousness to mental representations. The notion of a “representation” is of course very general and can be applied to pictures and various natural objects, such as the rings inside a tree. Much of what goes on in the brain might also be understood in a representational way. For example, mental events represent outer objects partly because they are caused by such objects in cases of veridical visual perception. Philosophers often call such mental states “intentional states” which have representational content, that is, mental states are “directed at” something such as a thought about a horse or a perception of a tree.

Any theory of consciousness should seek to answer the question: What makes a mental state a *conscious* mental state? The HOT theorist will point out that conscious states, as opposed to unconscious ones, are intuitively mental states that I am “aware of” being in. This overall idea is sometimes referred to as the Transitivity Principle (TP): A conscious state is a state whose subject is, in some way, aware of being in it.

Conversely, the idea that I could be having a conscious state while totally *unaware* of being in that state seems like a contradiction. A mental state of which the subject is completely unaware

is clearly an *unconscious* state. For example, I would not be aware of having a subliminal perception and so it is unconscious.

It might seem that HOT theory results in circularity by defining consciousness in terms of HOTs (since HOTs can be thought of as a kind of higher-order “awareness” of mental states, as in TP). It also might seem that an infinite regress results because a conscious mental state must be accompanied by a HOT, which, in turn, must be accompanied by another HOT ad infinitum. However, the widely accepted reply is that when a conscious mental state is a first-order world-directed conscious state, the higher-order thought (HOT) is *not* itself conscious. But when the HOT is itself conscious, there is a yet higher-order (or third-order) thought directed at the second-order state. In this case, we have *introspection* which involves a conscious HOT directed at an inner mental state. When one introspects, one’s attention is directed back into one’s mind. For example, what makes my desire to write a good chapter a conscious first-order desire is that there is an *unconscious* HOT directed at the desire. In this case, my conscious focus is directed outward at my chapter or computer screen and so I am not consciously aware of having the HOT from the first-person point of view. When I *introspect* that desire, however, I then have a *conscious* HOT (accompanied by a yet higher, third-order, HOT) directed at the desire itself. It is thus crucial to distinguish first-order conscious states (with unconscious HOTs) from introspective states (with conscious HOTs).

In any case, it may seem unlikely that animals (and even infants) have the conceptual sophistication required for HOTs, which would then render animal (and infant) consciousness very unlikely (Seager 2004). Are cats and pigs capable of having complex higher-order thoughts such as “I am in mental state M”?

In reply, however, it may be that HOTs need not be as sophisticated as it might initially appear and, in recent years, some experiments have also strongly suggested that many animals can have metacognitive states. A number of key areas are under continuing investigation including animal memory and uncertainty monitoring. The term “I-thoughts” is also often used in the literature to

mean “thoughts about one’s own mental states or oneself.” Thus, they are very similar to HOTs and closely linked to what psychologists call “metacognition,” that is, mental states about mental states, or “cognitions” about other mental representations (Koriat 2007; Beran et al. 2012). Although some still reject the notion that most nonhuman animals have I-thoughts, the evidence seems to be growing that many animals do in fact have them and may even be able to understand the mental states of others (Terrace and Metcalfe 2005; Hurley and Nudds 2006; DeGrazia 2009).

One area of inquiry has to do with episodic memory (EM) which is an explicitly conscious kind of remembering involving “mental time travel” (Tulving 1983, 2005). It is often contrasted with *semantic* memory, which need only involve knowing that a given fact is true or what a particular object is, and *procedural* memory, whereby memory of various learned skills is retained. Some notion of “I” or self-concept seems necessary to have a genuine EM. I recognize an EM *as mine* and as representing an event in *my* past. To give an example from animal cognition research, Clayton and Dickinson and their colleagues report convincing demonstrations of memory for time in scrub jays (Clayton et al. 2003). Scrub jays are food-caching birds, and when they have food they cannot eat, they hide it and recover it later. Because some of the food is preferred but perishable (such as crickets), it must be eaten within a few days, while other food (such as nuts) is less preferred but does not perish as quickly. In cleverly designed experiments using these facts, scrub jays are shown, even days after caching, to know not only *what* kind of food was *where* but also *when* they had cached it (see also Clayton et al. 2006). Although still somewhat controversial, these experimental results at least seem to show that scrub jays have some episodic memory which involves a sense of self over time. This strongly suggests that the birds have some degree of metacognition with a self-concept (or “I-concept”) which can figure into HOTs. Further, many crows and scrub jays return alone to caches they had hidden in the presence of others and recache them in new places (Emery and Clayton 2001). This suggests that they know that *others*

know (or at least “see”) where the food is cached, and thus, to avoid having their food stolen, they recache the food. This strongly suggests that these birds can even have some mental concepts directed at other minds, which is sometimes called “mindreading.” Of course, there are many different experiments aimed at determining the metacognitive abilities of various animals so it can sometimes be difficult to generalize across species.

There is also the much-discussed work on uncertainty monitoring with animals such as monkeys and dolphins (Smith et al. 2003; Smith 2005). For example, a dolphin is trained in a perceptual discrimination task, first learning to identify a particular sound at a fixed frequency (the “sample” sound). The dolphin later learns to match other sounds to the sample sound. When presented with a sound that is either the same or different in pitch as the sample sound, the dolphin has to respond in one way if it is the same pitch (such as by pressing one paddle) and another way if it is a different pitch (pressing another paddle). Eventually the dolphin is introduced into a test environment and forced to make extremely difficult discriminations. To test for the capacity to take advantage of his own uncertainty, the dolphin is presented with a third “uncertain” response, the Escape paddle, which yields a greater reward than an incorrect response but a lesser reward than a correct response. The dolphin chooses the Escape paddle with a similar response pattern to humans and rhesus monkeys which suggest that the dolphin is aware of his state of uncertainty, that is, he has some knowledge of his own mental state. This is clearly a metacognitive state: the dolphin is aware that he does not know something, namely, whether or not a sound matches (or is very close to) the sample sound. Nonetheless, some authors (Carruthers 2008, 2009) argue that these and other experiments do not *force us* to infer the presence of metacognition, but one might respond in a manner similar to the section “Lloyd Morgan’s Canon and Parsimony” above. That is, it is arguably more parsimonious in some circumstances to attribute metacognitive states to animals rather than mere first-order states or no conscious mental states at all accompanied by a far more elaborate

explanation of the animal’s behavior (see also Gennaro 2012, Chapter 8, for some discussion).

Some authors (e.g., Carruthers 2000, 2005, 2009) cite experimental work suggesting that, say, even chimps lack the ability to attribute mental states *to others* (Povinelli 2000). These experiments are designed to determine if chimps take notice of when an experimenter is looking at something (say, food) or is unable to see something (for example, due to blindfolding). Chimps were just as likely to ask for food from an experimenter with a bucket over her head as from one who could see which seems to indicate a lack of the mental concept “seeing” or “visual perception.” Carruthers further argues that animals with HOTs should also be able to have thoughts about the mental states of *other creatures*. However, it is not at all clear that having I-thoughts *requires* being able to read *other* minds and, in any case, the evidence seems to be growing that many animals can mindread. For example, Laurie Santos and colleagues show that rhesus monkeys attribute visual and auditory perceptions to others in competitive paradigms (Flombaum and Santos 2005; Santos et al. 2006). Rhesus monkeys preferentially attempt to obtain food silently only in those conditions where silence was relevant to obtaining the food undetected. While a human competitor was looking away, monkeys would take grapes from a silent container, thus apparently understanding that their human competitors would hear the noise otherwise. Subjects reliably picked the container that did not alert the experimenter that a grape was being removed. This suggests that monkeys take into account how auditory information can change the cognitive state of the experimenter. As we saw in the section “Lloyd Morgan’s Canon and Parsimony,” parsimony would seem, at least at times, to be on the side of such mental state attributions.

I lack the space here to delve further into this massive literature but for much more on the issue of mindreading and metacognition in animals and infants, see Carruthers (2009), Nichols and Stich (2003), Goldman (2006), Lurz (2011), and Gennaro (2012, Chapters 7 and 8). Goldman (2006) defends the view that self-attribution of mental states (metacognition) is prior to our

capacity to attribute mental states to others (mindreading). A more modest view, offered by Nichols and Stich (2003), is that the two capacities are independent and dissociable. Carruthers (2009) argues that mindreading is actually *prior* to metacognition. The two main much discussed views are simulation theory (ST) and theory-theory (TT). ST holds that mindreading involves the ability to imaginatively take the perspective of another. TT holds that metacognition results from one's "theory of mind" being directed at oneself. Still, many existing theories are in fact hybrids of ST and TT.

Of course, it may be that HOT theory rules out *more* animal consciousness than some other theories, but it arguably does not rule out most animal consciousness. Perhaps insects and crustaceans are *less likely* to be conscious according to HOT theory, but it may depend on some specifics. Not all birds behave in the same sophisticated way that scrub jays do but it seems reasonable to suppose that many other birds are also capable of having at least some HOTs. Other animals mentioned above, such as monkeys and dolphins, are no doubt far more sophisticated than insects. Much the same holds for dogs, lions, pigs, and other mammals. Some of the behavior of, say, bees and fish might arguably even justify the attribution of self-awareness in addition to basic conscious states.

Cross-References

- ▶ Analogical Reasoning
- ▶ Brain Size
- ▶ Cognition
- ▶ Communication
- ▶ Corvids
- ▶ Episodic Memory
- ▶ Ethics
- ▶ Farm Animal Welfare
- ▶ Inductive Reasoning
- ▶ Intelligence
- ▶ Learning
- ▶ Meta-cognition
- ▶ Meta-memory
- ▶ Mind-Reading

- ▶ Neocortex
- ▶ Problem-Solving
- ▶ Self-Awareness
- ▶ Theory of Mind

References

- Allen, C. (2004). Animal pain. *Noûs*, 38, 617–643.
- Allen, C. (2013). Fish cognition and consciousness. *Journal of Agricultural and Environmental Ethics*, 26, 25–39.
- Allen, C., & Trestman, M. "Animal Consciousness". *The stanford encyclopedia of philosophy* (Winter 2016 Edition), Edward N. Zalta (ed.). <https://plato.stanford.edu/archives/win2016/entries/consciousness-animal/>.
- Allen, C., Fuchs, P., Shriver, A., & Wilson, H. (2005). Deciphering animal pain. In M. Aydede (Ed.), *Pain: New essays on the nature of pain and the methodology of its study* (pp. 351–366). Cambridge, MA: MIT Press.
- Allen-Hermanson, S. (2005). Morgan's canon revisited. *Philosophy of Science*, 72, 608–631.
- Allen-Hermanson, S. (2018). Animal consciousness. In R. Gennaro (Ed.), *Routledge handbook of consciousness* (pp. 388–407). New York: Routledge.
- Andrews, K. "Animal Cognition". *The stanford encyclopedia of philosophy* (Summer 2016 Edition), Edward N. Zalta (ed.). <http://plato.stanford.edu/archives/sum2016/entries/cognition-animal/>.
- Andrews, K., & Beck, J. (Eds.). (2018). *The Routledge handbook of philosophy of animal minds*. New York: Routledge.
- Baars, B. (2005). Subjective experience is probably not limited to humans: The evidence from neurobiology and behavior. *Consciousness and Cognition*, 14, 7–21.
- Balcombe, J. (2016). In praise of fishes: Précis of *What a Fish Knows*. *Animal Sentience*, 8(1), 1–13.
- Beran, M., Brandl, J., Perner, J., & Proust, J. (Eds.). (2012). *The foundations of metacognition*. New York: Oxford University Press.
- Braddock, M. (2017). Should we treat vegetative and minimally conscious patients as persons? *Neuroethics*, 10, 267–280.
- Braithwaite, V. (2010). *Do fish feel pain?* Oxford: Oxford University Press.
- Broom, D. (2016). Fish brains and behaviour indicate capacity for feeling pain. *Animal Sentience*, 3(4), 1–6.
- Brown, C. (2015). Fish intelligence, sentience and ethics. *Animal Cognition*, 18, 1–17.
- Browne, D. (2004). Do dolphins know their own minds? *Biology and Philosophy*, 19, 633–653.
- Cabanac, M., Cabanac, J., & Paren, A. (2009). The emergence of consciousness in phylogeny. *Behavioural Brain Research*, 198(2), 267–272.
- Calabrese, A., & Woolley, S. (2015). Coding principles of the canonical cortical microcircuit in the avian brain. *Proceedings of the National Academy of Sciences*, 112, 3517–3522.

- Carruthers, P. (2000). *Phenomenal consciousness*. Cambridge: Cambridge University Press.
- Carruthers, P. (2005). *Consciousness: Essays from a higher-order perspective*. New York: Oxford University Press.
- Carruthers, P. (2008). Meta-cognition in animals: A skeptical look. *Mind and Language*, 23, 58–89.
- Carruthers, P. (2009). How we know our own minds: The relationship between mindreading and metacognition. *Behavioral and Brain Sciences*, 32, 121–138.
- Chandroo, K., Duncan, I., & Moccia, R. (2004). Can fish suffer? Perspectives on sentience, pain, fear and stress. *Applied Animal Behaviour Science*, 86, 225–250.
- Clayton, N., Bussey, T., & Dickinson, A. (2003). Can animals recall the past and plan for the future? *Nature Reviews Neuroscience*, 4, 685–691.
- Clayton, N., Emery, N., & Dickinson, A. (2006). The rationality of animal memory: Complex caching strategies of western scrub jays. In S. Hurley & M. Nudds (Eds.), *Rational animals?* (pp. 197–216). Oxford: Oxford University Press.
- Craig, A. D. (2009). How do you feel-now? The anterior insula and human awareness. *Nature Reviews Neuroscience*, 10, 59–70.
- DeGrazia, D. (2009). Self-awareness in animals. In R. Lurz (Ed.), *The philosophy of animal minds* (pp. 201–217). New York: Cambridge University Press.
- Dennett, D. C. (1991). *Consciousness explained*. Boston: Little, Brown and Company.
- Dennett, D. C. (1995). Animal consciousness: What matters and why. *Social Research*, 62, 691–710.
- Dyer, A. G., Neumeyer, C., & Chittka, L. (2005). Honeybee (*Apis mellifera*) vision can discriminate between and recognise images of human faces. *The Journal of Experimental Biology*, 208, 4709–4714.
- Edelman, D., Baars, B., & Seth, A. (2005). Identifying hallmarks of consciousness in non-mammalian species. *Consciousness and Cognition*, 14, 169–187.
- Elwood, R., & Appel, M. (2009). Pain experience in hermit crabs? *Animal Behaviour*, 77, 1243–1246.
- Elwood, R., Barr, S., & Patterson, L. (2009). Pain and stress in crustaceans. *Applied Animal Behaviour Science*, 118, 128–136.
- Emery, N., & Clayton, N. (2001). Effects of experience and social context on prospective caching strategies in scrub jays. *Nature*, 414, 443–446.
- Farah, M. (2008). Neuroethics and the problem of other minds: Implications of neuroscience for the moral status of brain-damaged patients and nonhuman animals. *Neuroethics*, 1, 9–18.
- Feinberg, T., & Mallatt, J. (2016). *The ancient origins of consciousness: How the brain created experience*. Cambridge, MA: MIT Press.
- Fitzpatrick, S. (2008). Doing away with Morgan's canon. *Mind and Language*, 23, 224–246.
- Flombaum, J., & Santos, L. (2005). Rhesus monkeys attribute perceptions to others. *Current Biology*, 15, 447–452.
- Gennaro, R. (1996). *Consciousness and self-consciousness: A defense of the higher-order thought theory of consciousness*. Amsterdam/Philadelphia: John Benjamins.
- Gennaro, R. (1999). Leibniz on consciousness and self-consciousness. In R. Gennaro & C. Huenemann (Eds.), *New essays on the rationalists* (pp. 353–371). New York: Oxford University Press.
- Gennaro, R. (2009). Animals, consciousness, and I-thoughts. In R. Lurz (Ed.), *Philosophy of animal minds* (pp. 184–200). New York: Cambridge University Press.
- Gennaro, R. (2012). *The consciousness paradox: Consciousness, concepts, and higher-order thoughts*. Cambridge, MA: The MIT Press.
- Godfrey-Smith, P. (2013). Cephalopods and the evolution of the mind. *Pacific Conservation Biology*, 19, 4–9.
- Godfrey-Smith, P. (2018). The evolution of consciousness in phylogenetic context. In K. Andrews & J. Beck (Eds.), *The Routledge handbook of philosophy of animal minds* (pp. 216–226). New York: Routledge.
- Goldman, A. (2006). *Simulating minds*. New York: Oxford University Press.
- Griffin, D., & Speck, G. (2004). New evidence of animal consciousness. *Animal Cognition*, 7, 5–18.
- Harnad, S. (2016). Animal sentience: The other-minds problem. *Animal Sentience*, 1(1), 1–11.
- Hurley, S., & Nudds, M. (Eds.). (2006). *Rational animals?* New York: Oxford University Press.
- Jackson, R., & Wilcox, S. (1993). Observations in nature of detouring behavior by *Portia fimbriata*, a web-invading aggressive mimic jumping spider from Queensland. *Journal of Zoology*, 230, 135–139.
- Jamieson, D. (2018). Animals and ethics, agents and patients. In K. Andrews & J. Beck (Eds.), *The Routledge handbook of philosophy of animal minds* (pp. 461–468). New York: Routledge.
- Key, B. (2015). Fish do not feel pain and its implications for understanding phenomenal consciousness. *Biology and Philosophy*, 30, 149–165.
- Key, B. (2016). Why fish do not feel pain. *Animal Sentience*, 3(1), 1–34.
- Klein, C., & Barron, A. (2016). Insects have the capacity for subjective experience. *Animal Sentience*, 1(1), 1–19.
- Koriat, A. (2007). Metacognition and consciousness. In P. Zelazo, M. Moscovitch, & E. Thomson (Eds.), *The Cambridge handbook of consciousness* (pp. 289–324). Cambridge, MA: Cambridge University Press.
- Lurz, R. (Ed.). (2009). *The philosophy of animal minds*. Cambridge, MA: Cambridge University Press.
- Lurz, R. (2011). *Mindreading animals*. Cambridge, MA: MIT Press.
- Lycan, W. (1996). *Consciousness and experience*. Cambridge, MA: MIT Press.
- Lycan, W. (2001). A simple argument for a higher-order representation theory of consciousness. *Analysis*, 61, 3–4.
- Lycan, W. (2004). The superiority of HOP to HOT. In R. Gennaro (Ed.), *Higher-order theories of consciousness: An anthology* (pp. 93–113). Philadelphia/Amsterdam: John Benjamins.
- Maley, C., & Piccinini, G. (2018). The biological evolution of consciousness. In R. Gennaro (Ed.), *Routledge handbook of consciousness* (pp. 379–387). New York: Routledge.

- Mather, J. (2008). Cephalopod consciousness: Behavioural evidence. *Consciousness and Cognition*, 17, 37–48.
- Melnyk, A. (1994). Inference to the best explanation and other minds. *Australasian Journal of Philosophy*, 72, 482–491.
- Mendl, M., Paul, E., & Chittka, L. (2011). Animal behaviour: Emotion in invertebrates? *Current Biology*, 21(12), R463–R465.
- Merker, B. (2005). The liabilities of mobility: A selection pressure for the transition to consciousness in animal evolution. *Consciousness and Cognition*, 14, 89–114.
- Morgan, C. L. (1894). *An introduction to comparative psychology*. New York: Scribner.
- Nagel, T. (1974). What is it like to be a bat? *Philosophical Review*, 83, 435–456.
- Newen, A., & Bartels, A. (2007). Animal minds and the possession of concepts. *Philosophical Psychology*, 20, 283–308.
- Nichols, S., & Stich, S. (2003). *Mindreading*. New York: Oxford University Press.
- Pargetter, R. (1984). The scientific inference to other minds. *Australasian Journal of Philosophy*, 62, 158–163.
- Perrett, R. (1997). The analogical argument for animal pain. *Journal of Applied Philosophy*, 14, 49–58.
- Povinelli, D. (2000). *Folk physics for apes*. New York: Oxford University Press.
- Prunier, A., Mounier, L., Le Neindre, P., Leterrier, C., Mormède, P., Paulmier, V., Prunet, P., Terlouw, C., & Guatteo, R. (2013). Identifying and monitoring pain in farm animals: A review. *Animal*, 7, 998–1010.
- Rose, J. (2002). The neurobehavioral nature of fishes and the question of awareness and pain. *Reviews in Fisheries Science*, 10, 1–38.
- Rose, J., Arlinghaus, R., Cooke, S., Diggles, B., Sawynok, W., Stevens, E., & Wynne, C. (2014). Can fish really feel pain? *Fish and Fisheries*, 15, 97–133.
- Rosenthal, D. (1997). A theory of consciousness. In N. Block, O. Flanagan, & G. Güzeldere (Eds.), *The nature of consciousness* (pp. 729–753). Cambridge, MA: MIT Press.
- Rosenthal, D. (2004). Varieties of higher-order theory. In R. Gennaro (Ed.), *Higher-order theories of consciousness: An anthology* (pp. 17–44). Philadelphia/Amsterdam: John Benjamins.
- Rosenthal, D. (2005). *Consciousness and mind*. New York: Oxford University Press.
- Santos, L., Nissen, A., & Ferrugia, J. (2006). Rhesus monkeys, *Macaca mulatta*, know what others can and cannot hear. *Animal Behaviour*, 71, 1175–1181.
- Seager, W. (2004). A cold look at HOT theory. In R. Gennaro (Ed.), *Higher-order theories of consciousness: An anthology* (pp. 255–275). Philadelphia/Amsterdam: John Benjamins.
- Seth, A. (2016). Why fish pain cannot and should not be ruled out. *Animal Sentience*, 3(2), 1–6.
- Seth, A., Baars, B., & Edelman, D. (2005). Criteria for consciousness in humans and other mammals. *Consciousness and Cognition*, 14, 119–139.
- Shriver, A. (2006). Minding mammals. *Philosophical Psychology*, 19, 433–442.
- Shriver, A. (2016). Cortex necessary for pain – But not in sense that matters. *Animal Sentience*, 3(34), 1–6.
- Shriver, A. (2018). The unpleasantness of pain for non-human animals. In K. Andrews & J. Beck (Eds.), *The Routledge handbook of philosophy of animal minds* (pp. 176–184). New York: Routledge.
- Singer, P. (1990). *Animal liberation*. New York: Avon Books.
- Smith, J. (2005). Studies of uncertainty monitoring and metacognition in animals. In H. S. Terrace & J. Metcalfe (Eds.), *The missing link in cognition: Origins of self-reflective consciousness* (pp. 242–271). New York: Oxford University Press.
- Smith, J., Shields, W., & Washburn, D. (2003). The comparative psychology of uncertainty monitoring and metacognition. *Behavioral and Brain Sciences*, 26, 317–373.
- Sneddon, L. (2011). Pain perception in fish: Evidence and implications for the use of fish. *Journal of Consciousness Studies*, 18(9–10), 209–229.
- Sneddon, L., Braithwaite, V., & Gentle, M. (2003). Do fish have nociceptors: Evidence for the evolution of a vertebrate sensory system. *Proceedings of the Royal Society London B*, 270, 1115–1121.
- Sober, E. (2001). Venetian sea levels, British bread prices, and the principle of the common cause. *British Journal for the Philosophy of Science*, 52, 331–346.
- Sober, E. (2009). Parsimony and models of animal minds. In R. Lurz (Ed.), *The philosophy of animal minds* (pp. 237–257). Cambridge: Cambridge University Press.
- Sober, E. (2012). Anthropomorphism, parsimony, and common ancestry. *Mind and Language*, 27, 229–238.
- Srinivasan, M. (2010). Honey bees as a model for vision, perception, and cognition. *Annual Review of Entomology*, 55, 267–284.
- Striedter, G. (2016). Lack of neocortex does not imply fish cannot feel pain. *Animal Sentience*, 3(21), 1–4.
- Terrace, H., & Metcalfe, J. (Eds.). (2005). *The missing link in cognition: Origins of self-reflective consciousness*. New York: Oxford University Press.
- Trestman, M. (2013). The Cambrian explosion and the origins of embodied cognition. *Biological Theory*, 8, 80–92.
- Tulving, E. (1983). *Elements of episodic memory*. Oxford: Oxford University Press.
- Tulving, E. (2005). Episodic memory and autoeoesis: Uniquely human? In H. S. Terrace & J. Metcalfe (Eds.), *The missing link in cognition* (pp. 3–56). New York: Oxford University Press.
- Tye, M. (2000). *Consciousness, color, and content*. Cambridge, MA: MIT Press.
- Tye, M. (2016). *Tense bees and shell-shocked crabs*. Oxford: Oxford University Press.
- Woodruff, M. (2017). Consciousness in teleosts: There is something it feels like to be a fish. *Animal Sentience*, 2(1), 1–21.