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# *Studying Animal Feelings*

## *Integrating Sentience Research and Welfare Science*



***Abstract:*** *The goal of this article is to bring together two fields of research — animal sentience research and animal welfare science — with the aim of advancing our understanding of animal emotions, especially their subjectively experienced or 'felt' component (feelings). While these two research areas share a common interest in animal feelings, they have had surprisingly little interaction. In this paper, we make a call for the integration of these fields and outline some of the ways in which work done in each of these areas can inform and benefit the other, such as strengthening the theoretical and conceptual bases of both fields, and sharing methods used by each, advocating further future collaboration for the benefit of both disciplines.*

**Keywords:** sentience; consciousness; animal welfare science; animal emotions; animal affect; feelings.

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## 1. Introduction

Animal sentience research and animal welfare science are two distinct research programmes, and yet they have a lot of overlap in subject matter, especially when it comes to recent developments in both fields. Specifically, both disciplines are primarily interested in investigating the *felt experiences* of animals: animal sentience research focusing primarily on the presence of sentience (is there something that it is like to be that animal?) and welfare science aiming to find out about its contents (what it feels like to be that animal). Unfortunately, these fields have had far less interaction than one might expect from fields of research with such a large degree of overlap. While philosophers have long speculated about the subjective experiences of other animals (e.g. Nagel, 1974), we argue that collaboration between animal sentience research and animal welfare science, through exchanging concepts, methods, and data, is the best way to move towards an understanding of these 'other minds'.

Whereas consciousness science was originally a field dedicated almost exclusively to human consciousness, a trend that has unfortunately largely continued, the last decade has seen the emergence of a dedicated and multidisciplinary field of animal consciousness research (Browning and Birch, 2022). This is an important development, because human consciousness is arguably quite idiosyncratic and a focus on this alone provides a narrow and limited lens through which to study the phenomenon of consciousness more broadly. Consciousness plausibly has more ancient evolutionary origins than the hominin lineage alone and is likely to be shared with many animals that currently exist around us. The anthropocentric idea that we could wait to establish a completed theory of human consciousness and then simply apply it to other animals is misguided, because consciousness is very unlikely to take the same shape in different species (see Veit, 2022c). Because we cannot assume that animals have human-like consciousness, there is a need for a distinct scientific field dedicated to their subjective experience. This makes animal sentience research an important resource for determining which animals are capable of subjective experience, as well as the features, mechanisms, and functions of that experience.

While animal sentience research originally tried almost exclusively to address the question of which animals are sentient and which aren't, there is now increasing emphasis on studying the actual contents of animal experiences (see e.g. Birch, Schnell and Clayton, 2020, and

Dung and Newen, 2023, on dimensional approaches to animal consciousness). For the most part, this research has more narrowly focused on perceptual forms of consciousness, rather than valenced affective or evaluative experiences. As we shall argue, this makes animal welfare science an ideal collaborative partner, since much current research in that field studies the feelings of a vast range of different animals.

Though early iterations of animal welfare science treated welfare as health or physiological functioning, the majority of animal welfare scientists now consider welfare to consist — either in whole or in part — in the subjective feelings of animals (Duncan, 2002; Mellor *et al.*, 2020; Veasey, 2017; Browning, 2020). This is why there has been a shift in focus for the field towards studying animal emotions, or 'affects', but with an important focus on the felt components of these processes, often simply referred to as feelings.[4] However, while animal welfare science uses a range of indicators purported to track the subjective experience of animals, it still struggles with how to validate these indicators (Browning, 2023b), as well as other issues such as how to make welfare comparisons between species (Browning, 2023a); problems that a strong theoretical grounding in the science of animal sentience can help make progress on. Despite this, instead of integrating or establishing important connections, animal welfare science and animal sentience research have to date remained quite distinct and largely separate.

Given the parallel developments in both fields, one might have expected plenty of exchanges in recent years, but while there has been some collaboration, this has been far less than what is needed to properly explore how an integration of these fields will help us to progress our understanding of animal emotions, particularly their subjectively experienced or 'felt' component. Due to the shared history, and overlap in subject matter, we believe that there are large potential benefits in such collaboration. In this paper, we will make the case for the advantages of greater cooperation between these fields, outlining what they have to offer one another, both conceptually and methodologically. Our main intended target audience is thus the vast number of animal sentience researchers and animal

[4] These terms are not precisely defined and, while often used coextensively, may also refer to subtly different forms of animal experience or responses (Adolphs, 2017; Paul *et al.*, 2020).

welfare scientists that still know little of each other's fields and who could benefit from a more integrated or collaborative approach to the study of animal feelings. Nevertheless, the discussion here will also be of interest to anyone who is interested in the question of how we can scientifically study the sentience and welfare of animals.

As there is no agreed-upon shared terminology between these fields, let us begin by offering some clarificatory remarks regarding key terms that we use in this article. Here we will use the terms 'sentience' and 'consciousness' interchangeably. We take both to refer to what is sometimes called phenomenal consciousness — i.e. as Nagel (1974) would put it, the 'what-it-is-like'-ness of experience; its subjective feel (see also Browning and Birch, 2022). However, our focus here will be on experiences with an evaluatively positive or negative character, or 'valence'. Of most relevance to the project we describe here is such 'affective' sentience, the type of conscious experience characterized by affects or emotions — most commonly referred to as 'pleasures' and 'pains', but also including a range of experiences such as hunger, boredom, curiosity, fear, and comfort. While the usage of terms like 'valence', 'affect', and 'emotions' is often ambiguous between consciously experienced or unconsciously processed states, we are here only interested in the former, thus our use of the word 'feelings' to pick out these states. As we shall discuss, distinguishing between the two may be the most difficult challenge facing both fields, and one that they can work together to address. The target of this paper will thus be to assess how animal sentience research and animal welfare science can usefully interact to study the felt experiences of animals, with both the epistemic aim of gaining greater insight into the emotional experience of other animals, as well as the ethical aims of determining which animals require protection and finding out how to better improve their welfare.

The article is structured as follows. In Section 2, we will discuss current animal sentience research, and the historical scepticism that has delayed its progress. In Section 3, we will introduce the field of animal welfare science and its history. In Section 4, we will look at the conceptual and methodological links that can be found between the two fields, before moving on in Section 5 to conclude the discussion and outline future research directions.

## 2. Animal Sentience Research — History and Scepticism

Research on animal sentience and consciousness has exploded over the last three decades. As Proctor (2012) showed, in a meta-analysis of published research that mentions animal sentience, there was an increase of almost tenfold over the 20 years from 1990 to 2011. This is a trend which seems to have only continued, particularly with the founding in 2015 of the dedicated journal *Animal Sentience* (see Harnad, 2016). Nevertheless, the emerging science of animal consciousness, like many emerging sciences, has of yet no dedicated societies or professorships. It is an interdisciplinary field with researchers from different backgrounds looking at the question of animal sentience from a variety of perspectives. Its researchers are located in cognitive science, neuroscience, animal behaviour, ecology and evolution, as well as philosophy, although admittedly few have specialized in animal consciousness alone. Rather than a research programme with a common method, it is an interdisciplinary research area linked by a common explanatory target — the presence, features, and dimensions of animal consciousness, as well as its mechanisms and evolutionary function. Animal sentience researchers investigate by which mechanisms sentience operates, how it evolved, and through which parts of the animal kingdom (or beyond) it extends. However, most important for this paper is the attempts by animal sentience researchers to uncover the details of the subjective experiences of other animals, addressing questions such as whether, say, a fish is capable of negative moods, excitement, and the like.

Perhaps unsurprisingly, the field still faces a lot of scepticism. While even today there are still plenty of people sceptical about the possibility of a science of animal consciousness, their number is significantly reduced compared to those during the historical heights of behaviourism in the mid-twentieth century. This was a tradition in which consciousness (in both humans and non-human animals) was seen as subjective, inaccessible, and private — and thus beyond the scope of scientific enquiry. With the demise of behaviourism and a rapidly increasing interest in animal welfare, the scepticism against the very possibility of such a scientific investigation has made way for a less categorical scepticism that instead highlights the difficulty of studying the experiences of animals.

It is undeniable that the study of animal consciousness is far from easy, as it relates to subjective mental experiences and cannot (yet) be

directly related to particular anatomical or physiological markers (Browning and Veit, 2020). Even with developments in neuroscience linking brain activity to specific emotions, we are still far from assessing the mental states of others. In particular, as we cannot communicate directly with animals through speech, we are entirely reliant on indirect indicators of sentience, rather than the supposed 'gold standard' of verbal self-report. It is for this reason that some scientists, while appreciating the scientific interest in animal consciousness, deem it to be inherently speculative. Some authors, such as LeDoux (2019), take the strong position that we could explain all animal behaviour without appeal to consciousness and associate experience only with rich human-like levels of cognition — a position that, as we will discuss in Section 3, also raises concerns about the appropriate targets and methods of animal welfare science. However, here we raise it merely to illustrate the point that animal sentience research is still a developing science that is subject to strong scepticism in some quarters.

However, there has also been push-back against this sort of scepticism, arguing that no area of science operates with absolute certainty, and informed speculation grounded in empirical observations combined with best available theory is common in many areas. Bekoff (2012), for instance, has argued the lack of certainty in the discipline does not mean it is a useless scientific endeavour. Very few scientific disciplines deal in certainty, and many, including human psychology, have similarly inaccessible 'hidden' targets. Through careful observation and experimentation, we may still hope to gain some understanding, even if we can't be entirely sure. Proctor, Carder and Cornish (2013) similarly point out that 'whilst other areas of science will often make do with imperfect data, animal sentience is required to buck the trend and provide unequivocal proof' (p. 883). It is unreasonable to reject the findings of a science, especially an emerging one, simply because it has not yet removed all causes for doubt. These should instead be seen as opportunities for the growth and development of the field.

Though it was once common for sceptics to deny sentience to all non-human animals, that is no longer the case. The Cambridge Declaration on Consciousness (Low *et al.*, 2012) was a milestone in this regard, reflecting a commitment within the scientific community to taking many animals to possess consciousness, and shifting the challenge to figuring out how to identify and measure it. This may now shift the burden of proof back on to the remaining sceptics,

asking them to provide proof of lack of sentience, given the weight of anatomical and behavioural evidence that would otherwise suggest conscious emotional experience; as suggested by Bekoff (2012).

Indeed, the presence of sentience seems to be a background assumption in much modern research. In their meta-analysis of sentience research, Proctor, Carder and Cornish (2013) found that very few of the studies were done with the primary purpose of exploring sentience. Instead, almost all assumed the presence of the key trait or emotion relevant to the study, showing that an acceptance of sentience is actually quite widespread. Studies using animals as test subjects for drugs such as analgesics or antidepressants necessarily rely on their sentience. It is notable that the assumption of negative affect was far more common than positive, with a focus on fear, stress, pain, anxiety, and depression. This is likely due to the more obvious and intense outward expression and communication of such states, and reflects a similar trend in animal welfare science that has, up until recently, largely overlooked positive welfare experience (Yeates and Main, 2008; Boissy *et al.*, 2007).

It is understandable that fear of anthropomorphism can make people wary of too quickly attributing emotional states to animals. This is not entirely misguided, as we must be careful to read what the evidence is telling us relative to the animal under study, and not over-interpret based on our own experiences, assumptions, or ethical preferences. However, given the shared evolutionary history and analogous anatomy and physiology, there is reason to think that (some) animals are capable of similar feelings to our own, and this should not be ruled out without reason. The growing field of animal sentience research provides ways of investigating these claims and making them more rigorous. Though animal sentience research has so far primarily focused on the perceptual side of conscious experience, as we will discuss in Section 4, drawing on some of the methods of animal welfare science will help sentience researchers grow their programme into investigation into the nature and distribution of valenced experiences, or emotions.

## 3. Animal Welfare Science

Turning to animal welfare science, in some ways it could be viewed as the normative branch of animal sentience research, examining the experience of animals from the perspective of what makes their lives go well or poorly. While animal sentience research will provide

grounds for taking it to be the case that there is 'something that it is like' to be a particular species (and thus that these animals are subjects of moral concern), there is then an implicit call for animal welfare science to investigate what is good or bad for them and how their lives can be improved. As we will discuss in Section 4, as well as providing the 'targets' for research in animal welfare science, animal sentience research can also help provide empirical and theoretical grounding for the practice of animal welfare science.

Since experience can have positive or negative valence, there is normative force in acting to reduce the occurrence of negative states and increase the occurrence of positive states, and animal welfare science is guided by this ethical commitment. While animal sentience research is also partially guided by the goal of determining which animals are capable of suffering, the history of the field is marked by attempts to steer clear from ethics and animal welfare issues, precisely because scientific work in the twentieth century that was influenced by moral concerns was seen as biased and less objective (Animal Ethics, 2020).[5]

Animal welfare science is similar to other sciences such as conservation biology or welfare economics, that also involve a normative component and an advisory role in social decision-making and policy contexts. However, the science is still primarily aimed at *naturalizing* animal welfare, i.e. to make the notions of animal suffering, interests, preferences, pleasure, pain, wants, etc. scientifically respectable and measurable in order to scientifically assess and improve the welfare of non-human animals. Like animal sentience research, welfare science is also an emerging field, having only really arisen since early work in the 1970s (Broom, 2014). A 2014 meta-analysis of animal welfare publications over the previous 20 years found an increase of around 10–15% per year, with over half having been released in the last four years of the study (Walker, Diez-Leon and Mason, 2014). Again, this is a trend which appears to only have continued, with publications in animal welfare science exploding rapidly.

Animal welfare is typically taken as something like the sum of positive and negative experiences (Browning, 2020). Many researchers now consider sentience to be sufficient for welfare, while some

5 Though there is still scepticism towards animal sentience research, coming from people like LeDoux (2019), who assert that researchers are too heavily influenced by their desire to help animals.

require additional factors, such as health, but almost universally sentience is considered necessary. Because sentience has become such a crucial factor in animal welfare sciences, with many denying that the notion of welfare can even be applied in cases of non-conscious organisms such as plants (*ibid.*), it should be immediately obvious that animal welfare science will directly depend on animal sentience research. Whichever animals are determined to possess sentience are to be investigated by animal welfare scientists, and an understanding of animal sentience will necessarily underpin the practice of animal welfare science.

While the field originally focused primarily on health indicators and measures of stress, primarily because they were highly operationalizable and immune to the behaviourist criticisms of the last century, the moral concern for animal suffering — led in large part by Marian Dawkins (1980) — shifted the science to a focus on animal feelings. Animal welfare science is concerned with our ability to measure when these positive and negative experiences are occurring. It develops, assesses, and uses a range of behavioural and physiological indicators that correlate with welfare experience — such as behaviour, blood hormones, and brain function — and identifies under which conditions good or poor welfare occurs. While sentience research may investigate the nature of these felt states, welfare science is mostly interested in finding out under which conditions they occur and developing recommendations on housing and husbandry. Understanding the biology and needs of different animals provides a basis for investigating and understanding their welfare.

Animal welfare science faces perhaps even greater scepticism than sentience research, due to its normative aspect, and focus on feelings and emotions. While consciousness research that focuses on perceptual states has at least some degree of respectability, research into the more evaluative capacities and moods, personality, emotions, motivations, and feelings — of both humans and animals — raises greater suspicion. One example of the sceptical trend is Dawkins, who argued early on that animal welfare science ought to include animals' subjective experiences as the key to their welfare, but has later shifted her view. In a target article in *Behavioral and Brain Sciences*, Dawkins (1990) began with the ambitious words: 'Let us not mince words: Animal welfare involves the subjective feelings of animals' (p. 1). She expanded this view in her later book, *Through Our Eyes Only? The Search for Animal Consciousness* (Dawkins, 1998b), in which she called for a science of animal consciousness as Donald Griffin had

envisioned, dedicating the book to him. Yet, following the subsequent explosion of work on the hard problem of consciousness, Dawkins was led to believe that animal welfare science was 'at risk of looking vague, unscientific and unable to agree on its own core concept' if it included animal consciousness in its definition of animal welfare (2021, p. 6). As a result, she now considers her earlier stance a mistake and shifted to a view that was largely focused on health and behavioural preferences instead of animal feelings as the target phenomenon of animal welfare (see Dawkins, 2017).

This is potentially a strong challenge to the very foundation of a science of animal welfare. While Dawkins maintains that a welfare science should be based on animal health and preferences, others have argued that the concept of welfare requires consciousness to retain its normative force (Birch, 2022). This would mean that if non-human animals lack positively and negatively valenced experiences, then there would not be any need for animal welfare science as animals would no longer be subjects of moral concern.

It is true that welfare, as understood as subjective experience, raises the same questions about measurability that are seen in sentience research. We cannot directly access subjective states and so only ever have indirect evidence about what an animal is feeling (or if it is even feeling at all). However, as we have discussed, few sciences trade in proof, and great progress has been made using a variety of indirect indicators in behaviour and physiology, and arguments from relevant analogy to humans. Behavioural tests such as motivation and preference tests, as well as observing interaction with the environment (approach and avoidance) and communication, when interpreted correctly can tell us a lot about what an animal is thinking and feeling. Additionally, even where there is scepticism about the links between observed behaviour and conscious experience, this does not require a deeper denial that animals have felt experience. At best, it should serve to emphasize how tentative our understanding of animal sentience is. For precautionary reasons there would still be a moral and political need for animal welfare protection even in the face of a strong sceptical viewpoint.

While both animal welfare science and animal sentience research face challenges in subject matter and methods, we argue these challenges are surmountable when these fields work together to strengthen their conceptual and methodological foundations. As we hope the discussion of these two fields has illustrated, both disciplines study closely connected phenomena and integration of the fields will

help us to better understand these phenomena as well as to overcome some of the limitations in each research programme. This will involve the sharing of concepts, methods, and data, as well as greater collaboration in research.

## 4. Bringing Both Fields Together

Given our brief introductions to both fields, it should be obvious that there is great overlap between animal sentience research and animal welfare science. Both share the target phenomenon of animal minds, with welfare science placing a special emphasis on the affective/emotional experiences of animals. Both were hindered by the lingering behaviourist tradition and only managed to emerge over the past 30–40 years, though these struggles were largely independent from one another. The historical links between consciousness and welfare as well as the overlap in subject matter give reason to think sentience research and animal welfare science have useful things to offer one another, both conceptually and methodologically. Yet, researchers in these fields have remained largely insular, with separation of research programmes and methods, despite there being plenty of opportunities for useful integration.

In the remainder of this paper, we will detail the ways that work done in each of these areas can inform and benefit the other. In particular, we will highlight three primary areas, related to some of the challenges and weaknesses in each field that we have discussed above. These are: (i) answering the question of which animals are sentient and thus targets of welfare concern, (ii) providing the conceptual frameworks of the evolution and functioning of consciousness that underpin the assumptions used in welfare science, and (iii) developing methods for investigating and understanding the valenced experiences of animals.

### *4.1. Finding out which animals are sentient*

The most basic, and perhaps most important, way these two areas depend on each other is in identifying which animals should be the targets of welfare concern. This is an area in which we see both fields contributing to answer a question that is important to both — for sentience research in answering one of its central research questions and for welfare science in setting its appropriate subjects for study. When welfare is understood as the subjective experience of animals, it therefore follows that only those animals capable of such experience

— those animals which are sentient — will be the appropriate targets of concern for welfare. Animal sentience research thus gives animal welfare science its targets: once there is sufficient evidence that an animal is sentient, and thus has welfare, welfare science will then work to investigate the emotional experiences of these animals and under what conditions their lives will be improved or worsened. Yet, despite this obvious connection, animal welfare scientists have so far remained largely disengaged from debates about the boundaries of sentience. This is unfortunate, given that the identification of sentience in previously unstudied groups of animals, such as insects, could give rise to an entirely new subject area within animal welfare science (e.g. developing indicators for and investigating the conditions that impact insect welfare). Animal welfare scientists should pay attention to these debates precisely because they will determine the scope of their own field.

However, animal welfare science can also be usefully drawn on to provide novel resources to help sentience researchers answer the question of which animals are sentient. Where welfare measures appear to be used successfully on an animal previously not considered sentient, or unsuccessfully on an animal previously considered to be sentient, this would give us reason to revisit our assessment of sentience and perhaps revise methods accordingly, a possibility that has been left under-explored, despite a few excellent examples. For instance, one potential case we would like to highlight is the success of the use of cognitive bias tests in bees. Cognitive judgment bias tests train animals to associate one stimulus with a reward and another with a punishment, and then test to see how the animal responds to an 'ambiguous' stimulus. Responding as though in anticipation of a reward is taken as an optimistic response, and as though in anticipation of a punishment as a pessimistic response, where work in humans shows that the former is indicative of positive mood and the latter of negative mood (Mendl *et al.*, 2009). The fact that honeybees have demonstrated pessimistic biases after a negative experience (Bateson *et al.*, 2011), while not definitive evidence, may count as a reason to consider them sentient. This can then be further investigated — in the case of bees, for instance, the judgment is strengthened by recent work from Lars Chittka's bee lab that has shown that bees are able to calculate motivational trade-offs (Gibbons *et al.*, 2022), an ability often taken to be a core function of sentience. Because of this, we think that animal sentience researchers should pay greater attention to work going on within animal welfare science, since there are new

methods and much empirical data coming out of this field that could be highly relevant to their own research.

The current debates on the boundaries of sentience throughout the animal kingdom show how important the use of strong established indicators is for both disciplines. Since a large part of the work in animal sentience is in attempting to identify which animals are sentient — generally which are capable of experiencing pain, as the avoidance of pain is one of the most basic welfare requirements — research is constantly changing the boundaries of where we think sentience lies. As we have mentioned, it is now widely accepted that many animals are sentient, as per the Cambridge Declaration on Consciousness in 2012 which stated that 'the weight of evidence indicates that humans are not unique in possessing the neurological substrates that generate consciousness. Non-human animals, including all mammals and birds, and many other creatures, including octopuses, also possess these neurological substrates' (Low *et al.*, 2012, p. 2). The focus has now shifted to determining which other animals may also fit into this group.

Most sentience research has been focused on vertebrates, and the majority of researchers now accept that evidence supports the conclusion that all vertebrates are sentient, due to similarities in the nervous system and brain structure, as well as behavioural responses. More recent work has suggested that several groups of invertebrates — cephalopod molluscs and decapod crustaceans — are also likely to be sentient (Birch *et al.*, 2021; Crump *et al.*, 2022). As currently only a small fraction of extant species and even taxonomic groups have been studied to determine sentience, the boundaries are still unclear, and work is still ongoing. However, the use of indicators and methods of measurement developed in both animal sentience research and welfare science can further help to make progress. And as we will discuss shortly, use of the methods developed in animal welfare science can aid sentience research in investigating the evaluative, valenced side of conscious experience, those states that are central to why we care about attributions of sentience in the context of animal welfare protection.

### *4.2. Conceptual foundations of animal welfare science*

As we have discussed, it is important for the practice of animal welfare science to have strong conceptual foundations relevant to the measurement of subjectively experienced affects or emotions. This is

where sentience research can arguably contribute the most to welfare science, by providing the background theory regarding the evolution and mechanisms of consciousness that can help with issues such as the selection and validation of welfare indicators, and identification of appropriate welfare interventions.

### *4.2.1. Evolution*

One key research area in animal sentience is aimed at understanding its evolution. That is, looking into when consciousness evolved, and under what conditions. The answers to these questions will give us information about the adaptive role of consciousness, which can then be used to ground research methods aimed at investigating animal feelings. It can also tell us about which interventions are likely to increase or decrease animal welfare. If we understand the evolutionary role sentience plays, we will be able to better predict what is good for animals based on their evolved life histories and ecological environments (Veit, 2022a).

There is currently a fairly consistent set of hypotheses about the evolution of sentience, which argues that the presence of affective states was beneficial for learning and motivation (Cabanac, Cabanac and Parent, 2009; Dawkins, 1998a; Fraser and Duncan, 1998; Ginsburg and Jablonka, 2019; Veit, 2022c). While there are differences between extant proposals, they nevertheless bear striking similarities to each other. In particular, the role of pain in facilitating learning and avoidance of harmful situations is often emphasized and discussed: 'feeling pain, as opposed to just nociception, would be a selective advantage for animals, as it would help facilitate meaningful learning' (Proctor, 2012, p. 633). Similar arguments are made for a range of positive and negative affects. Fraser and Duncan (1998) argue that negative feelings, such as pain, fear, and hunger, have evolved to address 'needs' situations, 'where there is an immediate threat to fitness from not performing a certain behaviour' (p. 16), while positive feelings create motivation for 'opportunity situations' which may be beneficial only after all needs are taken care of, but are low cost and provide pleasure. Other arguments for the evolution of consciousness focus on functioning within complex environments (e.g. Broom, 2007).

However, it is important that hypotheses such as these are tested and supported with the best currently available evidence. While it is plausible that the presence of pain experience both provides motivation to avoid painful stimuli, and allows for learned behaviours of this

type, this idea requires further investigation. Among animal welfare scientists, there appears to be at least something of a soft consensus that this is the functional role of sentience and the reason it evolved (Dawkins, 1998a; Fraser and Duncan, 1998; Mellor, 2019). This consensus, of course, should not be overstated, since there is plenty of disagreement about what kinds of evaluations are felt and which are mere unconscious processes. Disentangling conscious from unconscious affect will have to be a priority for future work, but an evolutionary perspective will likely prove to be useful here.

Notably, while there are many hypotheses about the evolutionary origins of consciousness, these should not necessarily be seen as explanations of hedonic valence, i.e. the positive and negative states of experience. While some see this capacity as an inherent part of consciousness (e.g. Ginsburg and Jablonka, 2019), others do not and allow for the possibility of perceptual consciousness without attending pleasure or suffering (e.g. Godfrey-Smith, 2020). Whereas the former view would tie animal consciousness research and animal welfare research incredibly close together, the latter may allow for at least a partial gap between the fields. What we are thus in need of is further research into the adaptive value of consciousness and sentience alike.

Once we better understand when and why consciousness evolved, we will be better able to look for its taxonomic distribution, as well as understand how it works. For example, if the learning role is confirmed, then this validates one important type of evidence for consciousness — the ability to learn quickly, or to perform specific types of complex learning such as trace conditioning (Birch, 2020) or unlimited associative learning (Ginsburg and Jablonka, 2019). Understanding the evolution of consciousness also allows us to start exploring the implications for the types of subjective experiences different animals may undergo. Knowing the function(s) of conscious experience helps to ground investigations into how animals feel, the range of affects they may experience, and the conditions under which they might experience them — all important areas for animal welfare science.

#### *4.2.2. Mechanism*

Another focus of sentience research is the mechanisms by which consciousness functions. Research here can focus on which brain structures and processes give rise to different types of conscious experiences, and the inbound and outgoing pathways, both from stimuli to affect, and back from affect to physiological and

behavioural responses. Understanding these will give us a better understanding of how to look for the presence of consciousness and to identify and understand its more qualitative components. For example, it was once thought that size or structure of the brain was related to consciousness, but there has been no evidence found that brain size or presence of a cerebral cortex can be correlated with consciousness (Proctor, 2012). Instead, complexity of brain function, rather than size or structure, may be a better candidate for understanding consciousness and welfare. Understanding brain complexity will then be a result of brain function rather than anatomy, as comparative studies have found that the brains of different animals function differently, and different abilities might be multiply realizable (Broom, 2016).

Work in affective neuroscience is also likely to play a large role here and has unsurprisingly been drawn on by animal sentience researchers and animal welfare scientists alike. The work of its founder, Jaak Panksepp (1991; 1998), was particularly important in this regard. His emphasis on the importance of studying animal feeling even earned him the Baily Endowed Chair of Animal Well-Being Science. While his hypotheses regarding evolutionarily ancient primary affective systems, such as the FEAR and SEEKING system, are now sometimes seen as too simplistic and perhaps even naïve (LeDoux, 2019), they were an important step in moving us towards a neuroscientific study of animal feelings. As we better understand the neural correlates of different affects (the 'neural correlates of affective consciousness'; Paul *et al.*, 2020), we can look for them directly, and better understand how the brain achieves general sentience and particular emotions, in the felt sense of that term. The neural structures that are thought to underlie particular affective states in humans are also found in many other animals (Berridge and Kringelbach, 2013) and, alongside considerations of evolutionary continuity, can provide increased confidence in attributions of similarity in affective experience when these brain areas are active. It is far more likely a difference in degree than a difference in kind. This does not mean that animal emotions must have the same qualitative character as those in humans, but they may still serve the same function, and still have the same positive and negative pull.

Of particular interest here is distinguishing and identifying the mechanisms related to the conscious processing of emotions or affects, as opposed to unconscious neuronal activity and reflex behaviours (LeDoux, 2019). Indeed, distinguishing conscious from unconscious processes may be the most pressing problem facing both

animal sentience research and animal welfare science, though for different reasons. For animal sentience research, it is central in understanding the mechanisms and functions of conscious experience. For animal welfare science, it is important for determining which experiences will matter from the point of view of the animal, and which we should therefore be paying attention to when wanting to improve welfare.

Take the example of pain. Pain processing occurs in two stages. The first is detection of noxious stimuli through activation of nociceptors, which trigger an automatic CNS response — think of the automatic removal response you might have when you accidentally place your hand on hotplate; the action comes before the sensation. As this signal moves up to the brain, at some point the affective state of felt pain is created. Distinguishing the former from the latter process is a necessary part of understanding conscious emotional experience, and, as we will discuss shortly, research in both sentience and welfare has a role to play in helping to pull apart these different processes to identify both their physiological and behavioural markers.

One established method for differentiating between conscious and unconscious perceptual processing is trace conditioning, a form of operant conditioning in which the stimuli are presented across a time gap — shown in humans to only be successful when the stimuli are consciously experienced and therefore a paradigm that some have argued could also be applied in animal sentience research (Browning and Birch, 2022). However, equivalent methods are needed (but currently lacking) for examining the similar distinction between conscious and unconscious emotions. The problem of disentangling conscious from non-conscious evaluative processes will thus be a core future challenge for animal welfare science and animal sentience research alike, and we are optimistic that joining forces will help make greater progress in this area. This is related, but not identical, to the problem of determining which animals are conscious as, even for animals we take to be conscious, there is an additional task in identifying which specific affects they consciously experience to understand what the animals actually feel. Understanding the mechanisms by which conscious affect operates will help make progress on this problem, as well as helping animal welfare scientists investigate the welfare experiences of different animals under different conditions.

### *4.2.3. Applications in welfare science*

The answers to the questions of the evolution and mechanisms of sentience form an important part of the background knowledge and assumptions required for the practice of animal welfare science. Many areas of welfare science, such as validation of the behavioural and physiological indicators used in measurement, making comparisons of the welfare of different animals, and comparing and integrating measures of positive and negative welfare, all rely on understanding in these areas.

Theories of the evolution of consciousness can be used as the basis for developing new indicators of animal welfare. For instance, the proposal by Ginsburg and Jablonka (2019) that it is the neurological structures underpinning unlimited associative learning that enable consciousness suggest that we could focus on various tests to try to measure the complexity of different species' ability to engage in associative learning. Such tests are very uncommon within animal welfare science but could provide an excellent case for integration. Similarly, Veit's (2022a; 2023) suggestion that consciousness evolved to deal with the life history complexity of animals could orient animal welfare scientists towards paying greater attention to the evolutionary history and ecological environments their species have evolved in to make better assessments of whether they are capable of suffering and which interventions could best improve their well-being.

Theory and evidence from sentience research can also be used for validation of indicators of welfare. As mentioned, animal welfare science works by using various behavioural and physiological indicators to measure changes in welfare. For example, looking at the frequency and tone of vocalization can tell us something about whether an animal is happy or worried, and measures of blood hormones can indicate stress. However, these indicators are only useful if they are valid. That is, we must have some way of determining that they are actually measuring what we are wanting them to measure — in this case, the felt experiences of animals that constitute welfare.

Part of the process of validating indicators involves embedding within the best available theory (Browning, 2020; 2023b), which is where animal sentience research offers a means to improve validation. Without established theory, this is based primarily off the intuitions and experience of the scientists. However, if we understand the mechanisms working between welfare experience and the measured

indicators, we have more reason to think that our measurements are mapping onto the right state of the world. So, for example, if we take the vocalizations made by goats, we will have more confidence that these are mapping onto welfare experience if we can understand that goats are social animals that communicate their distress to conspecifics. When taking measures of blood hormones to indicate stress, we will be more confident of their reliability if we understand the hormonal cascade that creates changes in hormone levels and under what conditions it is triggered. We will also have reason to think we have made the right choice of conditions from which to test indicators. For example, understanding the evolutionary history of a stoat will help us to think that provision of water is a relevant positive stimulus, while for a tamarin the presence of an aerial predator is a negative one.

Animal sentience research can assist through providing improved understanding of these mechanisms, both in their operation and their evolution, and thus can help welfare science with the right choice of indicators. Using information from sentience research can help provide the necessary background theory through which to validate welfare indicators. This will necessarily be an ongoing and iterative process, where work in animal sentience and welfare science can inform and improve one another. What counts as the best available theory in any field is subject to revision, and a young research programme like animal sentience research is highly likely to see such changes. However, success in validating indicators for welfare science can also serve as evidence that the current theories from animal sentience research are on the right track (or, conversely, that they may need to be re-examined). Just as in other sciences, we can be confident that the integration and cross-validation of methods and theories can move us closer to capturing the correct mechanisms. The absence of certainty should not be taken to suggest that any theory is equally useful, as evidence from both sciences can help show which have more or less support.

Another area where a strong theory of animal sentience can help the practice of animal welfare science is when making comparisons of welfare across different species. There are many situations in which we might want to make welfare comparisons, such as when making decisions about distribution of resources intended to help animals, where we want to know which animals would benefit more from investment of resources (e.g. is it more important to improve the lives of intensively farmed pigs, or chickens?). Making these comparisons

can often be difficult, as they rely on us knowing something about how similar the minds of the animals of interest are — for instance, whether they have the same 'capacity' for welfare (i.e. same level of 'highs' and 'lows') and whether they express their welfare to the same degree in their measured responses.

Browning (2023a) discusses the similarity assumptions required for making comparisons of welfare between different animals. The justifications for these assumptions were based in appeal to evolutionary history and analogous anatomy and physiology. This then requires the theory and data from sentience research. Understanding where sentience in general (or the particular types of affect or indicators in use) evolved will help us to know whether there were similar enough forces acting on the different individuals to create the same responses. Of course, while it is a common assumption among animal sentience researchers that sentience serves the same function for different species, this could still be realized by different mechanisms, and thus also understanding the mechanisms by which consciousness operates, and how different affects and responses are created, will allow us to see whether these pathways are relevantly similar between individuals. This can help us determine which animals are similar enough for the comparisons we want to make (e.g. whether it only be animals of the same species, or perhaps related species). Further integration with one of the core goals of animal sentience research may help animal welfare scientists to make decisions about which animals to prioritize without having to rely on unreliable intuitions about features such as the animal's size or perceived similarity to humans.

One other area of concern in measurement of animal welfare is making comparisons between positive and negative experiences, or combining them into a total welfare experience, with the potential use of an hedonic common currency (Cabanac, Cabanac and Parent, 2009; Cabanac, 1992). After all, animal welfare is made up of a mix of many types of affect, some positive, some negative, which are then taken to sum together to form an holistic welfare experience with an overall positive or negative character. Nevertheless, it could be contested whether a group of heterogeneous experiences of this type can be commensurable in this way — whether there is some sort of 'common currency' by which we could compare and combine them. The ability to find such a common scale will rely on understanding of the neurological underpinnings of the different affects and the evolutionary conditions through which they evolved, as well as those for consciousness as a whole. Similarity of evolutionary conditions, such as all

negative affects being used for aversive learning, would give us reason to think there is a common currency. Similarly, seeing that animals are able to use the inputs of different emotions to perform motivational trade-offs between different needs is a line of evidence in support of their representation through a common currency.

Finding relevant commonalities in the evolution and mechanisms of different affects, both positive and negative, would then support the comparing of different types of experience on a common scale in terms of their contribution to overall welfare. More research will have to be undertaken to confirm the idea of a common currency, but the case is slowly being made (Veit, 2022b). While we can accept that the mechanisms underlying sentience are probably multiply realizable, their core evolutionary function has likely remained the same in order for affective states to remain comparable by the organism and be able to be traded off against each other. Thus, behavioural evidence may be more important for animal welfare evaluations than neurological evidence, which has often been overemphasized in consciousness research due to the need to distinguish conscious and unconscious processes underlying cognition and behaviour. Yet, by thinking about the function of sentience, we will be in a better position to evaluate different animal welfare tests with regard to their implications for the affective feelings of the species under consideration.



### *4.3. Improving methods for measuring valenced experience*

We have highlighted that one of the current shortcomings in animal sentience research is its focus on perceptual conscious states, with too little attention paid to the valenced affective states relevant to welfare. Whereas consciousness science (particularly for humans) has largely focused on the sensory side of consciousness (the ability to consciously perceive stimuli), animal welfare science has understandably driven a much larger focus on the evaluative side of consciousness in animals (the positively and negatively valenced affects, or emotions). As we will discuss, we are optimistic that the methods developed within animal welfare science will aid animal consciousness research (and for that matter, human consciousness science) by paying more attention to the subjective experience of positive and negative feelings. These states might be harder to scientifically assess than sensory experiences, but their moral relevance makes them a particularly important research target.

Despite decades of work in animal sentience and welfare, there are still no conclusive markers in use in either field. Attributions of sentience still largely rely on collections of markers aimed at raising the evidential probability of the presence of sentience, rather than specific positive indicators (e.g. Sneddon *et al.*, 2014; Birch *et al.*, 2021; Crump *et al.*, 2022). Collecting multiple independent lines of evidence helps us strengthen our confidence in the result. Not all animals will show the same behavioural responses to pain (e.g. prey animals tend to hide it, social animals tend to vocalize), but an understanding of the ecology and evolutionary history of the species will help to put this into context. Different responses should not necessarily be taken as indicative of different experience.

Current work in this area rests on a range of background assumptions about the evolution, function, and mechanisms of sentience, some of which can be tested or justified through developments in animal welfare science to build understanding of affective experience. Sentience researchers can also look to welfare science for their well-validated indicators of different feelings, or of overall welfare experience. Animal welfare science has over the years developed sound methodologies for measuring welfare. Particularly, they have identified and validated a range of behavioural, cognitive, and physiological indicators that can be used to measure welfare, and therefore tell us something about consciousness. The large amount of work done in welfare science to identify and validate these indicators for welfare gives animal sentience research a good pool of measures to draw from.

There is thus an application in research into the function of sentience, particularly its affective dimension. Looking into which indicators are used by animal welfare scientists, and why they work, could help develop understanding of consciousness and how it functions. Looking into the welfare literature will help identify possible indicators for use in consciousness research, to measure and identify consciousness where it occurs. Taking from welfare science the well-validated behavioural and physiological indicators, these form a good starting point for investigation into the mechanisms by which affective states can produce the effects, which helps then to answer some of the questions we have raised.

Animal welfare research on preference and motivation testing, for instance, may offer support for the idea that the evolutionary function of sentience constitutes something like a proximate ‘common currency’ to trade different pleasures and pains off against each other.

Thus, animal welfare science offers a wealth of empirical data to lend support to different theories of the function of sentience for animals. While some tests may be biased by the assumptions of different scientists regarding what sentience does for animals, it is unlikely that these tests would capture animal welfare well, or for that matter show robust correlations with other methods used to assess animal welfare. Importantly, such research may even move us away from anthropocentric assumptions that necessarily associate the main functions of affective consciousness in humans with those of other animals, and instead uncover its original evolutionary rationale.

Animal sentience research could similarly look to the methods of animal welfare science for research projects looking to determine the richness or 'level' of sentience in different species. As we have mentioned, animal sentience researchers are progressing towards a more dimensional view of animal consciousness, that looks to investigate its features and varieties, and where these will include valenced affects or feelings the tools of animal welfare science will be particularly useful. In turn, better understanding of the features and varieties of consciousness relevant to welfare capacity will help in making interspecies comparisons of welfare, as discussed in the previous section. One example is the use of cognitive judgment bias tests which, as discussed, are commonly used in animal welfare science and appear to reflect an animal's mood state, which is suggestive of higher emotional complexity and something like an integrated welfare experience. The ability to pass such a test could thus serve as part of the evidential picture of which dimensions of consciousness a species has, particularly as related to Birch, Schnell and Clayton's (2020) 'evaluative' dimension. As this is relevant to how we think about the moral status of different animals, understanding the different levels of valenced sentience could then help in determining the importance of different types of protections or interventions that target different species.

As animal welfare science is continually working to develop measures that track the affective or emotional experiences of animals, animal sentience researchers would benefit from paying attention to and drawing on these methods in order to expand sentience research programmes into further investigation of the affective dimension of sentience.

## 5. Conclusion

In this paper, we have argued that animal sentience and welfare are two research programmes with overlapping research objectives and whose success depends in part on work going on in the other field. Furthermore, we have outlined many of the ways that collaboration could help them strengthen one another. In particular, they are both focused on the same subject matter — the subjective feelings of animals — and face the same challenges in understanding and scientifically investigating this 'hidden' target phenomenon. For this reason, the conceptual and methodological foundations of each of these sciences have a lot in common and can productively inform one another. This is important, as considerations of sentience, welfare, and the felt experiences of animals play a large role in decisions about their moral, social, and political status, as well as about the specifics of their treatment (Birch *et al.*, 2021; Yeates, 2022; Browning and Veit, 2022).

However, while we have argued that these fields have unfortunately only interacted scarcely, we do not take our call for increased integration and collaboration to be too much of a radical position. The last few years have seen some crossing over between animal sentience research and welfare science, with a small number of researchers working in both fields (see e.g. Paul *et al.*, 2020). While collaboration is still rare, recent projects such as the Foundations of Animal Sentience project at the London School of Economics have been very successful at bringing the insights of these fields together to improve our understanding of animal minds and influence animal welfare legislation.[6] We take the success of these endeavours as evidence of the benefits of integration between the two fields, and it is in part what has motivated us to lay out many of the specific ways in which these disciplines will greatly benefit from engaging with each other. Understanding the application of animal sentience research in animal welfare science will help to guide research programmes into sentience; while following work in sentience will help welfare scientists develop new measurement indicators and identify new species for study. Drawing on the work already done in welfare science in developing indicators and methods of measuring welfare will help sentience research in work trying to identify sentient species,

6 https://www.lse.ac.uk/cpnss/research/ASENT.

as well as understanding the causes and mechanisms of sentience. We thus end this paper with a call for ongoing and increased collaboration in this area. Both disciplines can benefit from the other, and working together will help to more quickly solve some of the problems both are investigating. Finally, we are confident that this will allow for a better and more complete exploration and understanding of the consciously felt aspects of animal emotions, which can assist in our ethical decision-making regarding animals and also feed back into the study of human consciousness.

## References

Adolphs, R. (2017) How should neuroscience study emotions? By distinguishing emotion states, concepts, and experiences, *Social Cognitive and Affective Neuroscience*, **12** (1), pp. 24–31.

Animal Ethics (2020) *Establishing a Research Field in Natural Sciences: Three Case Studies*, pp. 1–62, Oakland, CA: Animal Ethics, [Online], https://www.animal-ethics.org/wp-content/uploads/Establishing_Field_Natural_Sciences.pdf [3 February 2023].

Bateson, M., Desire, S., Gartside, S.E. & Wright, G.A. (2011) Agitated honeybees exhibit pessimistic cognitive biases, *Current Biology*, **21** (12), pp. 1070–1073.

Bekoff, M. (2012) Animal emotions and animal sentience and why they matter: Blending 'Science Sense' with common sense, compassion, in Turner, J. & D'Silva, J. (eds.) *Animals, Ethics and Trade*, pp. 53–66, London: Routledge.

Berridge, K.C. & Kringelbach, M.L. (2013) Neuroscience of affect: Brain mechanisms of pleasure and displeasure, *Current Opinion in Neurobiology*, **23** (3), pp. 294–303.

Birch, J. (2020) The search for invertebrate consciousness, *Noûs*, **56** (1), pp. 133–153.

Birch, J. (2022) Should animal welfare be defined in terms of consciousness?, *Philosophy of Science*, **89** (5), pp. 1114–1123.

Birch, J., Schnell, A.K. & Clayton, N.S. (2020) Dimensions of animal consciousness, *Trends in Cognitive Sciences*, **24** (10), pp. 789–801.

Birch, J., Burn, C., Schnell, A., Browning, H. & Crump, A. (2021) Review of the evidence of sentience in cephalopod molluscs and decapod crustaceans, *LSE Consulting*, [Online], https://www.lse.ac.uk/business/consulting/assets/documents/Sentience-in-Cephalopod-Molluscs-and-Decapod-Crustaceans-Final-Report-November-2021.pdf.

Boissy, A., Manteuffel, G., Jensen, M.B., Moe, R.O., Spruijt, B., Keeling, L.J., Winckler, C., Forkman, B., Dimitrov, I., Langbein, J., Bakken, M., Veissier, I. & Aubert, A. (2007) Assessment of positive emotions in animals to improve their welfare, *Physiology & Behavior*, **92** (3), pp. 375–397.

Broom, D.M. (2007) Quality of life means welfare: How is it related to other concepts and assessed?, *Animal Welfare*, **16** (2), pp. 45–53.

Broom, D.M. (2014) *Sentience and Animal Welfare*, Wallingford: CABI.

Broom, D.M. (2016) Considering animals' feelings, *Animal Sentience*, **1** (5), art. 1.

Browning, H. (2020) *If I Could Talk to the Animals: Measuring Subjective Animal Welfare*, PhD thesis, Australian National University. doi: 10.25911/5f1572fb1b5be

Browning, H. (2023a) Welfare comparisons within and across species, *Philosophical Studies*, **180**, pp. 529–551.

Browning, H. (2023b) Validating indicators of subjective animal welfare, *Philosophy of Science*, online first, pp. 1–13. doi: 10.1017/psa.2023.10

Browning, H. & Veit, W. (2020) The measurement problem of consciousness, *Philosophical Topics*, **48** (1), pp. 85–108.

Browning, H. & Birch, J. (2022) Animal sentience, *Philosophy Compass*, **17** (5), e12822.

Browning, H. & Veit, W. (2022) The sentience shift in animal research, *The New Bioethics*, **28** (4), pp. 299–314.

Cabanac, M. (1992) Pleasure: The common currency, *Journal of Theoretical Biology*, **155** (2), pp. 173–200.

Cabanac, M., Cabanac, A.J. & Parent, A. (2009) The emergence of consciousness in phylogeny, *Behavioural Brain Research*, **198** (2), pp. 267–272.

Crump, A., Browning, H., Schnell, A., Burn, C. & Birch, J. (2022) Sentience in decapod crustaceans: A general framework and review of the evidence, *Animal Sentience*, **7** (32), art. 1.

Dawkins, M.S. (1980) *Animal Suffering: The Science of Animal Welfare*, London: Chapman and Hall.

Dawkins, M.S. (1990) From an animal's point of view: Motivation, fitness, and animal welfare, *Behavioural and Brain Sciences*, **13** (1), pp. 1–9.

Dawkins, M.S. (1998a) Evolution and animal welfare, *The Quarterly Review of Biology*, **73** (3), pp. 305–328.

Dawkins, M.S. (1998b) *Through Our Eyes Only? The Search for Animal Consciousness*, Oxford: Oxford University Press.

Dawkins, M.S. (2017) Animal welfare with and without consciousness, *Journal of Zoology*, **301** (1), pp. 1–10.

Dawkins, M.S. (2021) *The Science of Animal Welfare: Understanding What Animals Want*, Oxford: Oxford University Press.

Duncan, I.J. (2002) Poultry welfare: Science or subjectivity?, *British Poultry Science*, **43** (5), pp. 643–652.

Dung, L. & Newen, A. (2023) Profiles of animal consciousness: A species-sensitive, two-tier account to quality and distribution, *Cognition*, **235**, 105409.

Fraser, D. & Duncan, I.J. (1998) 'Pleasures','pains' and animal welfare: Toward a natural history of affect, *Animal Welfare*, **7** (4), pp. 383–396.

Gibbons, M., Versace, E., Crump, A., Baran, B. & Chittka, L. (2022) Motivational trade-offs and modulation of nociception in bumblebees, *Proceedings of the National Academy of Sciences*, **119** (31), e2205821119.

Ginsburg, S. & Jablonka, E. (2019) *The Evolution of the Sensitive Soul: Learning and the Origins of Consciousness*, Cambridge, MA: MIT Press.

Godfrey-Smith, P. (2020) *Metazoa: Animal Life and the Birth of the Mind*, New York: Farrar, Strauß, and Giroux.

Harnad, S. (2016) Animal sentience: The other-minds problem, *Animal Sentience*, **1** (1).

LeDoux, J. (2019) *The Deep History of Ourselves: The Four-Billion-Year Story of How We Got Conscious Brains*, New York: Viking.

Low, P., Panksepp, J., Reiss, D., Edelman, D., van Swinderen, B. & Koch, C. (2012) *The Cambridge Declaration on Consciousness*, [Online], http://fcmconference.org/img/CambridgeDeclarationOnConsciousness.pdf.

Mellor, D.J. (2019) Welfare-aligned sentience: Enhanced capacities to experience, interact, anticipate, choose and survive, *Animals*, **9** (7), art. 440.

Mellor, D.J., Beausoleil, N.J., Littlewood, K.E., McLean, A.N., McGreevy, P.D., Jones, B. & Wilkins, C. (2020) The 2020 Five Domains model: Including human–animal interactions in assessments of animal welfare, *Animals*, **10** (10), art. 1870.

Mendl, M., Burman, O.H., Parker, R.M. & Paul, E.S. (2009) Cognitive bias as an indicator of animal emotion and welfare: Emerging evidence and underlying mechanisms, *Applied Animal Behaviour Science*, **118** (3–4), pp. 161–181.

Nagel, T. (1974) What is it like to be a bat?, *The Philosophical Review*, **83** (4), pp. 435–450.

Panksepp, J. (1991) Affective neuroscience: A conceptual framework for the neurological study of emotions, in Strongman, K. (ed.) *International Reviews of Emotion Research*, pp. 59–99, Chichester: Wiley.

Panksepp, J. (1998) *Affective Neuroscience: The Foundations of Human and Animal Emotions*, Oxford: Oxford University Press.

Paul, E.S., Sher, S., Tamietto, M., Winkielman, P. & Mendl, M.T. (2020) Towards a comparative science of emotion: Affect and consciousness in humans and animals, *Neuroscience & Biobehavioral Reviews*, **108**, pp. 749–770.

Proctor, H. (2012) Animal sentience: Where are we and where are we heading?, *Animals*, **2** (4), pp. 628–639.

Proctor, H., Carder, G. & Cornish, A. (2013) Searching for animal sentience: A systematic review of the scientific literature, *Animals*, **3** (3), pp. 882–906.

Sneddon, L.U., Elwood, R.W., Adamo, S.A. & Leach, M.C. (2014) Defining and assessing animal pain, *Animal Behaviour*, **97**, pp. 201–212.

Veasey, J.S. (2017) In pursuit of peak animal welfare: The need to prioritize the meaningful over the measurable, *Zoo Biology*, **36** (6), pp. 413–425.

Veit, W. (2022a) Towards a comparative study of animal consciousness, *Biological Theory*, **17**, pp. 292–303.

Veit, W. (2022b) Complexity and the evolution of consciousness, *Biological Theory*. doi: 10.1007/s13752-022-00407-z

Veit, W. (2022c) The origins of consciousness or the war of the five dimensions, *Biological Theory*, **17**, pp. 276–291.

Veit, W. (2023) *A Philosophy for the Science of Animal Consciousness*, London: Routledge.

Walker, M., Diez-Leon, M. & Mason, G. (2014) Animal welfare science: Recent publication trends and future research priorities, *International Journal of Comparative Psychology*, **27** (1), pp. 80–100.

Yeates, J.W. (2022) Ascribing sentience: Evidential and ethical considerations in policymaking, *Animals*, **12** (15), art. 1893.

Yeates, J.W. & Main, D. (2008) Assessment of positive welfare: A review, *The Veterinary Journal*, **175** (3), pp. 293–300.