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How Should We Study Animal Consciousness Scientifically?

1. Introduction by Jonathan Birch

Other sculptors, other statues from the same stone! Other minds, other worlds from the same monotonous and inexpressive chaos! My world is but one in a million alike embedded, alike real to those who may abstract them. How different must be the worlds in the consciousness of ant, cuttle-fish, or crab! (William James, 1890, p. 289)

A conscious being has a subjective point of view on the world and on its own body. This idea of a 'point of view' is easiest to grasp in the case of vision. Ernst Mach, in the *Analysis of Sensations*, famously attempted to draw his own visual point of view (Figure 1). But there is far more to human subjective experience than vision. Our subjective point of view includes sounds, odours, tastes, tactile experiences — a complete sensory world. And these sensory experiences of a world

Correspondence: Email: j.birch2@lse.ac.uk outside us are integrated with bodily feelings, emotions, conscious thoughts, conscious memories, and imagination. This point of view can be contrasted with a great mass of processing that occurs unconsciously, without surfacing in experience. In humans, this mass includes the early stages of sensory processing, as well as many processes of bodily self-regulation and motor control.



Figure 1. Drawing from Ernst Mach (1886/1914), The Analysis of Sensations.

Are we alone, or do some other animals also have subjective points of view? In 2012, the 'Cambridge Declaration on Consciousness' captured an emerging consensus that 'non-human animals, including all mammals and birds, and many other creatures, including octopuses' possess neurological substrates complex enough to support conscious experiences. The declaration signalled that, rather than debating whether *any* non-human animals have subjective experiences, it is time to move on to the questions of *which* animals have them — and *what forms* their experiences take.

Ten years later, a new interdisciplinary field is emerging. Like consciousness science, it draws together many disciplines around a shared set of questions — but the mix of disciplines is somewhat different. To study animal experiences, we need expertise not only from cognitive science, neuroscience, and psychology, but also from animal welfare and veterinary science, comparative psychology, and

evolutionary biology. Philosophy also has a crucial role in placing this field on a solid conceptual and methodological footing (Figure 2).

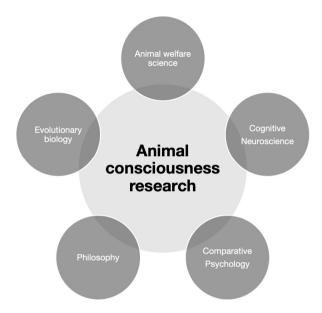


Figure 2. The emerging interdisciplinary field of animal consciousness research.

This emerging field faces foundational challenges. To study subjective experience in animals, we need methods that do not rely on animals verbally reporting how they feel. As a result, many methods from human consciousness science cannot be directly translated. But this should be a starting point for debate, not grounds for despair. It should push us harder to do something we already need to do to study consciousness in infants and in patients with disorders of consciousness—develop better ways of studying subjective experience without verbal report. We may one day look back on the idea of using verbal report to study consciousness as akin to measuring the temperature of a liquid by putting a hand in it—as our *initial* way of latching on to the phenomenon of interest, a starting point, not a measurement technique we can never transcend, or one that works for the full range of cases.

The present special issue of the *Journal of Consciousness Studies* aims to advance that foundational debate. The editors have invited authors to respond to one of the following key questions:

- How does the evolution of consciousness relate to the evolution of cognition? (Zacks, Ginsburg and Jablonka, this issue; Halina, Harrison and Klein, this issue).
- What is stronger evidence of consciousness in animals: behaviour or neural mechanisms? (Lamme, this issue; Crump and Birch, this issue).
- How can we measure the subjectively experienced side of welfare? (Broom, this issue; Browning, this issue).
- What is the ethical significance of consciousness? (Kammerer, this issue; Lee, this issue).
- *Could all life be conscious?* (Thompson, this issue).

To start the issue, I asked all the contributors and my co-editors to answer a single question in 500 words or fewer: how should we study animal consciousness scientifically? Here are their answers.

2. Donald M. Broom

Humans are animals, so the term 'conscious' means the same for humans and other species. A conscious individual is an individual which has the capability to perceive and respond to sensory stimuli. Conscious thus means not unconscious and the methods of study involve identifying the functioning of the brain and the associated behaviour that gives information that the individual is conscious rather than unconscious (Weiskrantz, 1997; Broom, 2003). It is better to use 'aware' than 'conscious' when there is complex experience and associated brain analysis, so the measures of consciousness do not necessarily include complex function evaluation.

Measures indicating that an individual is conscious include: identifying voluntary behaviour, carrying out tests of behavioural responsiveness to stimuli, measuring electrical responses in the brain evoked by stimuli, and analysing the electroencephalogram (EEG) (Gregory, 2007; Gibson *et al.*, 2009). The EEG is the overall electrical activity in an area of the brain and contributes to useful measurement because the electroencephalographic patterns of conscious individuals can be accurately distinguished from the patterns in unconscious individuals.

Measurement of awareness involves studying behaviour, physiology, or brain function in an individual of any animal species and should not be limited to those with a particular brain anatomy. Much of the research is associated with investigations of cognitive ability, sentience, and welfare. A range of sophisticated tests indicating behavioural and brain function show that individuals must have certain kinds of awareness.

There is no single ability, or performance in a particular test, that must be used in order to demonstrate that an individual is aware or that the members of a species can be aware. For example, the finding that an individual can use information from a mirror provides evidence of awareness, but is only one of many ways of showing what awareness exists in the individual, so it is not logical to conclude that only individuals that can use a mirror are aware (Broom, 2014).

Welfare is not confined to individuals that are sentient, since those that do not have the capacity to have feelings still have coping mechanisms (*ibid.*). Hence the welfare of all animals should be considered, but protection should take account of what function is possible, for example pain relief is needed only by animals that can feel pain. Because of the important role of feelings and emotions as coping mechanisms affecting welfare, and the role of awareness in feelings, many measures of welfare provide information about awareness (Broom and Johnson, 2019; Mendl and Paul, 2020; Broom, 2022).

3. Heather Browning

We should study animal consciousness not by looking for its presence or absence, but by seeking to explore the features of the conscious experience of different animals. In many cases there may be no such features to explore, but approaching the question in this way leaves more space to identify animals that may have a more limited range or intensity of experiences.

In particular, we should be focusing on the valenced mental states — the feelings, or affects — that an animal can experience. Rather than identifying the presence or absence of consciousness, we would instead look for which affects an animal experiences, and to what degree. For example, we may find some organisms with only mild pressure sensations, or others with primarily hunger experiences.

This approach is supported by an increasing recent emphasis on affect as the fundamental conscious process (e.g. Panksepp, 2005;

Mellor, 2019; Solms, 2021). And as well as giving more flexibility in the type of research conducted, it can provide the answers that will help guide ethics and policy around our treatment of animals.

This approach would require a divergence from current methods relying on perceptual and cognitive indicators derived from studies on humans. Use of these indicators relies on possibly problematic background assumptions about the shared functions of consciousness between humans and other animals (Browning and Veit, 2020) and can't tell us about the type of experience an animal has — the *what it is like* for that animal.

Instead of human-developed indicators, we may prefer those constructed from a more bottom-up approach — attempting to identify the evolutionary functions and mechanisms by which affects operate, and then searching for those markers which track these abilities. We can look for clusters of markers, supported by our best theoretical frameworks regarding our understanding of the mechanisms and functions of conscious experiencing.

Some of the current work on animal consciousness has followed this model, in looking for pain experience. This work looks not for a single marker of conscious experience but uses clusters of features and abilities to establish the presence of pain. When attempting to determine whether a particular animal can experience pain, a range of indicators are used, including physiological (such as neural structures and neurochemical pathways) and behavioural (such as learning and trade-off behaviour) (e.g. criteria outlined in Smith and Boyd, 1991). These indicators have been developed across multiple domains using different background biological theory regarding the mechanism, and proximate and ultimate functions of the experience.

I see a future research programme for animal consciousness as extending this approach across a range of affects — exploring not just their presence or absence, but also the degree of feeling and the contexts in which they operate. This would allow us to ask questions regarding the features of consciousness of different animals — their extent and qualities; something like the 'consciousness profiles' advocated by Birch, Schnell and Clayton (2020), but focused on affective range. From the full set of possible affects, many animals may have only some subset, and will have these to different degrees and across different circumstances. Understanding this will allow us to understand what it is like to be these animals, as well as to help us in achieving some of the social and ethical aims attendant with the study

of animal consciousness, such as appropriate understanding of and attention to their interests.

4. Andrew Crump

No 'golden marker' proves that a candidate animal species is conscious, but we can collect various lines of evidence to convince all but the fiercest critic.

In humans, consciousness facilitates a cluster of cognitive functions, so evidence of this cluster would suggest consciousness in our candidate species (Birch, 2020; Shea, 2012). Take trace conditioning: associative learning with a time interval between the conditioned and unconditioned stimulus. When a sound tone predicts a post-interval air-puff in the eye, humans only learn to blink after the tone if they are consciously aware of the stimuli and interval (Clark and Squire, 1998; 1999). Conversely, delay conditioning — where the tone and air-puff overlap — seems to be possible unconsciously (Clark and Squire, 1998; 1999). Trace conditioning is, therefore, evidence for consciousness; delay conditioning is not.

Or consider visual illusions linked to conscious perception. For example, the Ponzo illusion, where equal-width parallel lines look wider when they are closer to the intersection of converging perpendicular lines. Humans only perceive this illusion consciously — subliminal stimuli eliminate it (Chen *et al.*, 2018). In the Ebbinghaus illusion, meanwhile, circles surrounded by small, close circles appear bigger than circles surrounded by larger, farther circles. Subliminal stimuli still induce this size illusion (*ibid.*). The Ponzo illusion, but not the Ebbinghaus illusion, thus signals consciousness.

However, even if human consciousness facilitates a cluster of cognitive functions which our candidate species displays, a critic could argue that the underlying mechanism might differ. Why implicate consciousness? To address this, we could demonstrate that subliminal stimuli switch off the cluster in our candidate species, as in humans (Birch, 2020). We might compare consciousness-linked cognition with similar unconscious cognition. Do subliminal stimuli eliminate trace conditioning but not delay conditioning? The Ponzo illusion but not the Ebbinghaus illusion? Such findings would indicate distinct conscious and unconscious processing within our candidate species.

Even so, says the critic, how did we validate subliminal and supraliminal stimuli? This could be achieved if our candidate species reported stimulus presence/absence (e.g. by touching a screen), but exceeded chance in tasks with stimuli reported absent (Cowey and Stoerig, 1995). Such results distinguish an objective response threshold (what the animal knows) from a subjective threshold (what it thinks it knows). Subliminal stimuli fall between these two thresholds — they influence behaviour without our conscious knowledge — whilst supraliminal stimuli exceed both thresholds. Dissociating subjective and objective thresholds would, therefore, validate our subliminal stimuli.

We would then have interlocking lines of evidence that the candidate species is conscious. First, a cluster of cognitive functions which consciousness facilitates in humans. Second, subliminal stimuli switching off these functions collectively. And, third, distinct subjective and objective thresholds validating the subliminal stimuli. Such a strong case does not yet exist, especially for more controversial species, but this research programme is fundamentally possible. It would reduce a critic to inventing an unconscious explanation, which looks and acts like human consciousness. The best explanation would surely be conscious experience — empirical evidence of animal consciousness.

5. Marta Halina, David Harrison, and Colin Klein

The scientific study of animal consciousness has gone from a niche, even taboo, topic to one commanding significant theoretical analysis and resources. Yet there remains little consensus on how the scientific study of consciousness should be extended to non-human minds. One increasingly popular approach looks for an *evolutionary transition marker* of the emergence of consciousness. Transition markers are explicitly epistemic: one identifies a set of capacities and behaviours that reliably indicates consciousness, without taking a stance on what *makes* an organism conscious.

Emblematic of this approach is work by Ginsburg and Jablonka (2019), and more recently in Birch, Ginsburg and Jablonka (2020), who identify the evolution of unlimited associative learning (UAL) as such a marker. Briefly, UAL is an organism's ability to learn about itself and its environment in an open-ended manner via a 'natural cluster' of learning capacities (such as trace and second-order conditioning; Ginsburg and Jablonka, 2021). UAL, they claim, is reliably correlated with consciousness, and thus a valuable tool for studying

both the evolution and current extent of non-human subjective experience.

In our piece (Halina, Harrison and Klein, this issue), we acknowledge the pragmatic benefit of evolutionary transition markers, but contend that the study of animal consciousness will require positive theoretical and metaphysical commitments. We take issue in particular with the proposed cluster of features that is meant to be a marker of conscious experience. Cluster-based approaches provide poor epistemic criteria because they do not distinguish between true clusters and mere 'clutters' of heterogeneous, contingently cooccurring features (Mameli, 2008). The distinction between the two depends in part on which can support real explanations — for, as is well known, prediction and explanation are distinct notions with different demands. We use this to suggest several problems that naturally arise for merely epistemic criteria and argue (contra Birch, Ginsburg and Jablonka, 2020) that they cannot be overcome without some sense of the computational mechanisms and neural architectures that support and enable consciousness.

Thus, we suggest that the study of animal consciousness requires the identification of capacities and behaviours associated with consciousness and linking them to, or grounding them in, architectural and mechanistic details — however provisional these might be. This could take the form, as it does in Barron and Klein (2016), of providing evidence that subcortical structures support consciousness in humans, coupling this with Merker's (2007) claims about the functional role of such structures in sustaining consciousness, and linking this with work emphasizing the importance of the central complex in insects to make a claim about invertebrate consciousness. As helpful as the use of transition markers are, then, we contend that such an approach must proceed in tandem with the further metaphysical project of identifying the appropriate enabling conditions — only then will we know if we are dealing with a clutter or a cluster of abilities associated with consciousness.

6. François Kammerer

A significant portion of research on animal consciousness focuses — explicitly or implicitly — on *phenomenal consciousness*: its aim is to learn more about animals' subjective experiences (as opposed to, say, animals' access consciousness). This sort of research is both *motivated* and *influenced* by the idea that phenomenal consciousness corres-

ponds to a real, determinate, and distinctive phenomenon (consciousness exists, and it is determinately and importantly distinct from non-conscious processes), which also happens to be normatively very significant (consciousness matters ethically — a lot).

This idea does not have primarily a scientific origin, and it pre-dates most of consciousness science. It stems mainly from the surreptitious importation of primitivist and/or dualist conceptions of consciousness, which are explicitly rejected by most consciousness researchers, but continue to operate in the background. Arguably, it lingers because these primitivist and/or dualist conceptions of consciousness are themselves somewhat supported or suggested by what introspection tells us about our own conscious states. When we turn our attention inwards, we find mental states — phenomenally conscious experiences, which *feel* a certain way — which appear to be real, determinate, distinctive, and normatively significant.

This idea not only has a dubious, unscientific origin, but is also somewhat at odds — if not contradictory — with the explicit materialistic commitments of most consciousness researchers. It could naturally end up being vindicated by science — who knows! — but in the meantime we should make sure that we explicitly bracket it at the very least, so that it does not operate in the background.

In the context of animal consciousness research, this requires at least three things. First, we should cease to focus on knowing the distribution of *consciousness* in the animal world. If we do not operate with the antecedent presupposition that phenomenal consciousness is real, determinate, and distinctive, setting the discovery of the distribution of consciousness as one of our main goals appears to be a methodological move that is relatively unjustified and could easily make us err. Determining this distribution should be the final stage of research on animal minds — an afterthought, not a guideline.

Second, we should be open to the possibility that research on animal minds will lead us to something very different from a neat two-column chart (conscious animals on the left, non-conscious ones on the right). For one, it might be that there is a sense in which no one (humans included) is phenomenally conscious (an hypothesis associated with the 'illusionist' view of phenomenal consciousness, that I am inclined to endorse). Even if consciousness is real, there is at least a decent chance that the concept of consciousness does not cut nature at its joints, so that our best classifications of mental states would have very little to say about consciousness.

Third, none of this should be seen as necessarily particularly problematic for animal ethics, given that we should not operate with the presupposition that consciousness is normatively significant.

7. Victor Lamme

When my dog is looking me in the eyes, does it *see* me? It may seem to recognize me, by getting all elated and doing three backflips in response. But is there any conscious sensation going along with that? Why is it so hard to answer this question?

This is in part because the issue is fraught with hard problems, explanatory gaps, qualia, inverted spectra, and philosophical zombies; thought constructs to show how conscious sensation can never be inferred from any kind of behaviour. And despite some pushback on these ideas (e.g. Frankish, 2016), the issue of animal consciousness is still hostage to them.

Inferring conscious sensation from behaviour alone indeed is problematic because, also in humans, behaviour can dissociate from conscious sensation. A case in point is blindsight, where patients with lesions to the primary visual cortex can localize and discriminate objects without any conscious sensation of them (Weiskrantz, 1996). What if animals go through life like that all the time?

Would neural evidence help (Lamme, 2006)? Conscious vision requires an intact pathway from V1 to the temporal lobe, and blind-sight is mediated by a bypass pathway from the retina towards the colliculus, pulvinar, and parietal lobe. These two pathways also exist in monkeys, and a lesion to the V1 pathway gives the same behavioural result: responding 'no' when asked whether they saw the stimulus, while still able to localize and discriminate (Yoshida and Isa, 2015). Can we then still maintain that the monkey does not lose conscious sensation after the lesion? Such a position would require us to possess something beyond our brains that enables consciousness, a mysterious extra ingredient that animals don't have. This would be an avenue towards dualism or panpsychism. You choose.

Is the issue then solved by showing similar behaviour based on similar neural processes between man and animal? No. Critical to understanding consciousness is that it is a contrast. A contrast with the unconscious (Lamme, 2020). Without it, when we would always see everything that hits our eyes, when we would never lose consciousness eight hours per day, we would probably have never noticed it exists. This contrast is its defining characteristic, so it's the presence

or absence of such contrasts we should study in animals, chart whether they are similar in terms of behaviour and neural mechanisms. In the accompanying article, I do that for sleep, anaesthesia, blindsight, masking, and rivalry, which are all prominent paradigms to study the contrast in humans. And if that contrast is present, we should conclude that also in these animals there are then two 'what it is likes', two types of states, two types of experience: conscious versus unconscious, seeing versus not seeing (Lamme, 2018).

Will their 'seeing' be similar to ours? Of course not, as conscious experience is naturally determined and constrained by the make-up of sensory equipment, its neural processing, and the neural architecture underlying it. But that some of their life goes on 'in the dark', while other parts are 'in the light', is the inescapable conclusion we should then draw.

8. Andrew V. Lee

Here's a philosophical puzzle about investigating animal consciousness. The conscious experiences of animals are sometimes radically different from the conscious experiences of humans. Take, as examples, the proprioceptive experiences of octopuses or the echolocation experiences of bats. Now, according to conventional wisdom, in order to think about what it's like to have an experience, one must have had that experience (or a sufficiently similar one). But if we humans cannot even think about what it's like to be an octopus or a bat, how could we ever hope to study their conscious experiences?

Well, consider an analogous case. Someone who was born blind is unable to grasp what it's like to see red. But they can still acquire some knowledge of visual phenomenology: in particular, they can still grasp how visual experiences are structured. Suppose, for example, that the blind person were told that visual experiences are perspectival representations of regions of three-dimensional space, that different visual features may be bound to a single visual object, that colours are experienced as spatially extended over the surfaces of objects, or that colour experiences vary along three dimensions of similarity. These are claims about the phenomenal character of visual experiences. Yet these claims — at least, their structural components — are accessible to the blind person, in the same way that structural facts from other scientific domains are accessible to them.

I think we stand to the exotic experiences of bats and octopuses in roughly the same way that the blind person stands to the visual experiences of the sighted. There may be some aspects of the target experiences that are inaccessible to individuals who cannot themselves undergo those experiences. But there are other aspects — namely, the way that those experiences are structured — that remain within reach. If we were to discover that the echolocation experiences of bats have four dimensions of variation, or that their similarity relations can be captured by a specific kind of metric space, or that the temporal character of those experiences is discrete rather than continuous, then we would acquire some interesting and substantive knowledge about what it's like to be a bat.

A natural reaction is to point out that conscious experiences involve more than merely structure: the structural knowledge described above still leaves us in the dark about the intrinsic qualities of the target experiences. I believe this reaction points towards an important truth. Perhaps there are aspects of octopus and bat experiences that we will never understand, unless we ourselves were to grow tentacles or develop sonar abilities. But that doesn't make the study of animal experiences hopeless. Conscious experiences are more than mere collections of qualities; those qualities are organized into rich structures. That structure is tractable, even when the qualities themselves are not. And that gives us plenty to discover in the study of animal consciousness.

9. Matthias Michel

Spinoza once wrote:

no one has hitherto determined what the body is capable of; *i.e.* experience has hitherto taught no one what the body can do solely by the laws of nature considered as corporeal only, and what it cannot do unless it be determined by the mind... Hence when people say this or that motion of the body arises from the mind, which has an empire over the body, they do not know what they are saying, and merely confess in specious words that they are ignorant of the true cause of that action. (Spinoza, 1677/2020, Part III, p. 166)

No one has hitherto determined what the unconscious mind is capable of. This makes non-human animal consciousness difficult to assess in cases in which we cannot induce consciousness from the presence of brain structures analogous to those supporting consciousness in humans — as in fish, insects, or decapod crustaceans, for instance. In those cases, behavioural indicators are all we have. And we don't know which behaviours should be interpreted as indicating conscious-

ness, and which should not, as long as we don't know what unconscious minds can do.

I have a good idea of what conscious minds can do since conscious mental states accompany my daily perceptual and cognitive activities. In the absence of consciousness, however — for instance, during dreamless sleep or general anaesthesia — my mind can't seem to do much. I have yet to catch it in the midst of some complex perceptual or cognitive activities in those instances.

From there, it's only a small step to the conclusion that my mind couldn't perform all these activities without being a conscious mind. And from there, it's another small step to the conclusion that non-human animal minds have to be conscious to engage in similar activities.

But a correlation between a given conscious state and a given behaviour doesn't imply that this conscious state drives that behaviour. When you see your cup of coffee and reach to grasp it, it might seem to you that your conscious percept guides your motor action. Yet, research on the two visual streams indicates that motorguidance is mediated by an unconscious visual state (Goodale and Milner, 2005). When you experience fear and suddenly freeze, it might seem to you that your conscious fear causes you to freeze. Yet, the two systems model of fear suggests that this behaviour is triggered by an unconscious defensive survival circuit (LeDoux and Pine, 2016).

Nor is it necessarily the case, if a conscious state does cause a behaviour, that it causes it in virtue of being a *conscious* state. Perhaps the same behaviour could have been caused by an unconscious analogue. The phenomenon of blindsight, for instance, has revealed that several visual functions can be performed both consciously and unconsciously (Weiskrantz, 2009).

To have valid indicators of consciousness, we should strive to discover what unconscious minds can do. The study of non-human animal consciousness should start at home — in humans, by identifying those capacities for which conscious mental states make a difference in virtue of being *conscious* mental states.

10. Françoise Wemelsfelder

A defining feature of the notion of consciousness is that it evokes a subjectivity/objectivity differentiation which makes it difficult to find suitably 'neutral' ground for its study. Animal scientists of course

place great emphasis on 'objectivity', and, assuming that animals cannot verbally report their subjective experience, use mechanistic criteria and methods to assess their brain, behaviour, and intelligence (Daston and Galison, 2007).

However, the problem here is that the development of mechanistic thought in early twentieth-century animal science was driven specifically by the motivation to oust consciousness as an explanatory factor from scientific analysis (Crist, 1999). This foundation, still at work in modern science, implies that however we end up defining consciousness, it is most likely to be understood as basically another functional element, another cog, in the complex machinery of life. But this, it seems to me, threatens conceptual implosion. To search for that elusive extra 'consciousness factor' ('qualia', 'intention', 'mind', 'feeling') that presumably qualifies a system as 'more-than-mechanical' seems self-defeating: can a particular functional property of a machine lift that machine out of its machine-like existence? This seems incoherent. Like studying ice in an oven — the question melts the answer.

Of course elucidating mechanisms of consciousness is meaningful and has led to impressive progress in uncovering cognitive and emotional capacities in a wide range of animal species, including invertebrates such as octopuses and bees (Barron and Klein, 2016; Birch, Schnell and Clayton, 2020). The point, however, is that to find consciousness-in-action in the first place, so we can address and engage with animals' subjective lives, what we need is a consciousness-facilitating, not -resisting, language, to be accommodated by scientists in their work.

What could anchor such a language? Assuming there is indeed 'something it is like for a bat to be a bat' (Nagel, 1974), animals qualify not merely as objects, but, moreover, as subjects-of-a-life (Regan, 1983). That is, to themselves, each other, and humans, they first and foremost manifest as *someone*, an 'I/you' rather than an 'it' — fellow sentient beings with whom communication and meaningful encounter is, with concerted effort, possible (Buber, 1937). To enter this conceptual arena is thus to ask, not 'what is consciousness', but 'who are you'? A question requiring not rigorous experimental control, but the opposite: giving animals opportunities to freely express themselves, let them be agents of their own experience, and establish grounds for communication.

This is how pioneering primatologists such as Jane Goodall (1990) and Barbara Smuts (2001) engaged with the wild chimpanzees and

baboons they studied, but as a generic principle it should hold across the animal kingdom — there will be something it is like to be a butterfly too. Humanities scholars (e.g. anthropologists, philosophers) have begun to ask how animals can 'flourish' alongside humans in 'morethan-human communities', using a language envisioning a sharing of sentient worlds, for example through 'convivial conservation' (Acampora, 2006; Bastian *et al.*, 2016; Büsher and Fletcher, 2019).

But accommodating such relational language in animal science will not be easy. Fundamentally, as a starting point, it will require acknowledgment of the dynamic whole animal, the animal-as-agent, as a legitimate unit for observation and assessment. It is the animal having the experience, not the ears, tail, or even the brain; whatever goes on physically, only the whole living being reflects the 'you' to whom we relate and whose expressivity we wish to understand (Hacker, 1993). Through the centuries there have been scientists arguing that qualitative characterizations of how animals express wanting, feeling, and thinking should be accommodated in research, alongside mechanistic language. However, given the near-absolute primacy of mechanistic thought, scientists remain wary of anthropomorphic projection, and mostly prefer to mechanize descriptions of sentient expressivity: animals' experiences become 'affective states', feeling good or bad translates as emotional 'valence', thought as 'cognition', meaningful action as 'behaviour'... with ultimately 'the brain' absorbing the animal's agency and sentience as the presumed generator of 'consciousness' (Crist, 1999).

But whose consciousness? Why write animals out of their sentience this way — why not invite them to express it, guided by what has been described by philosophers as a moral practice of attentive 'interspecies etiquette' (Cheney and Weston, 1999; Warkentin, 2010)? Creating conditions and languages that give voice to, or in anthropological terms 'foreground', other sentient perspectives strikes me as the opposite ofanthropomorphic projection (Midgley, Wemelsfelder, 2012). If animal scientists could imbue their deep knowledge of animal lives with the greater conceptual freedom and creativity exercised by humanities scholars, there is huge potential for finding fertile epistemic grounds for discerning and honouring what life is like for non-human animals.

Efforts to develop Qualitative Behaviour Assessment (QBA), a science-based 'whole-animal' method for assessing non-verbal emotional expressivity (e.g. as relaxed, anxious, content, etc.), is but one way of exploring this potential (Wemelsfelder, 2007; Fleming *et*

al., 2016). Accommodating animal sentience will inevitably propel scientists into wider moral and epistemic domains of engagement, and there is no reason why this could not still involve the intellectual rigour and evidence-based analysis scientists are accustomed to.

11. Oryan Zacks, Simona Ginsburg, and Eva Jablonka

Two major ways of studying consciousness are (i) investigations of the global state of consciousness (such as the state of being asleep, under aneasthesia, or being awake), by following the behavioural, cognitive, and neural correlates of this state, and (ii) investigations of the contents of consciousness — which include awareness of specific sensory perceptions, affects, and the sense of self. Like global consciousness modes, the contents of consciousness too can be studied at the behavioural/learning, cognitive, and neural levels in conditions that distinguish between conscious and non-conscious contents.

According to the theory of consciousness one endorses, evolutionary comparative studies of consciousness can shed light both on the origin of consciousness and on the attributes of different types and levels of consciousness (minimal, imaginative, and symbolic, with all their many variations). These methodologies can also be used to track consciousness during individual development, as the level and sometimes also the specific contents of consciousness are transformed.

In our paper we focus on imaginative consciousness, using an evolutionary and comparative approach. A survey of the literature uncovered the scarcity of studies of imaginative cognition: the range of species investigated is very small, experimental designs are sometimes not comparable, and sample sizes are small, so it is difficult to consider intraspecific variations. Extending the range and scope of studies of imaginative cognition is needed, and it is important to go beyond the vertebrate phylum and study imaginative consciousness in other taxa (e.g. cephalopods, maybe some arthropods).

Our survey also showed that the 'when' aspect of episodic-like memory (ELM) has not been sufficiently studied, and it is not clear how integration over time is represented in the brain. Are there temporal maps that are distinct from spatial maps, or is the representation of time an extension of the representation of space?

The relation between the existence and activity of a default mode network (DMN) and ELM may be of relevance to the study of prospection, since DMN activity has been correlated with planning. Analogues of DMN are therefore expected to be found in non-mammalian imaginative species.

Another promising way to investigate imaginative consciousness is to study the cognitive capacities that partially overlap with it or enable it, such as causal learning. We expect that animals with imaginative consciousness, in whatever taxon, will exhibit goal-directed behaviour. We also expect that causal learning, dreaming, and control of emotions will cluster with ELM (these capacities either imply or enable imaginative consciousness), while theory of mind, prospection, and pretend play will depend on it, and will be present only in some imaginatively enriched taxa.

These predictions can be tested and will help us to understand the cognitive architecture of imaginative consciousness, as well as define the dimensions of imaginative consciousness in different taxa.

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