



Forest guardian: Protecting indigenous populations of the Amazon also helps protect the entire ecosystem. (Photo: JialiangGao, www.peace-on-earth.org (CC BY-SA 4.0).)

Piperno and colleagues conclude that ancient residents did not impact the inter-riverine areas of the Amazon basin, making up 95% of the total surface, as much as they did many riverside locations studied by archaeologists. They conclude that “our vegetational and fire history from this previously unstudied, remote region joins the increasing body of evidence that deforestation and fires during the prehistoric period and subsequent vegetation recovery upon European Contact were not so widespread and intense as to have contributed significantly to decreasing atmospheric CO₂ levels and the onset of the Little Ice Age.”

Moreover, they suggest that the current composition of these remote forests is not mainly the result of human influences. Although they acknowledge the limitation that more subtle manipulations or planting of certain species of fruit and nut trees may go unnoticed in the phytolith record, the authors come to the overall conclusion that “the activities of present and past societies in the MP-A [study area] have not strongly altered the community composition and structure of the species-diverse forests over perhaps thousands of years of utilization.” They refer to these societies, who used the resources of the forest sustainably over many centuries, as “a positive force in maintaining forest integrity and biodiversity.”

Stewards of the forest

The finding that a sustainable life in and with the Amazonian rainforest is possible chimes with the idea promoted by non-government organisations working to protect the Amazon that indigenous groups maintaining traditional lifestyles, including more than 100 uncontacted tribes (*Curr. Biol.* (2015) 25, R635–R638), are the best stewards of the Amazonian rainforest, preserving it both as a functioning ecosystem and as their own home.

As organisations like Survival International have highlighted on the occasion of the recent ‘Uncontacted Tribes Week’ (June 19–25), the forests and their people face the same threats, and efficient measures that protect one will also help the other.

Many know the endangered paradise of Amazonia from the work of Brazilian photographer Sebastião Salgado, who has just published a new volume of pictures and opened an exhibition at the Philharmonie de Paris, France, and who runs a family reforestation project at his family farm in Aimorés. In a recent interview with *The Guardian*, Salgado expressed optimism that quintessential wilderness can survive, noting that we have only destroyed “a little bit of the periphery. The heart is there yet. To show this pristine place, I photograph Amazônia alive, not the dead Amazônia.”

Michael Gross is a science writer based at Oxford. He can be contacted via his web page at www.michaelgross.co.uk

My word

What emotions might be like in other animals

Joseph E. LeDoux^{1,2}

Fresh off the success of *On the Origin of the Species* in 1859 and *The Descent of Man* in 1870, Darwin published *The Expression of the Emotions in Man and Animals* in 1872. In the latter, he extended his theory of evolution by natural selection to mind and behavior, and especially to emotions, arguing that we humans inherited our emotions from our mammalian ancestors. Though little was known about the nervous system at the time, Darwin proposed that emotional inheritance occurred by way of conservation of elements of the nervous system in the mammalian lineage.

Darwin’s ideas about emotions were based on his observations of similar behavioral (especially facial) expressions in emotional situations in people around the world. In accounting for this, he adopted the commonsense assumption that most people then (and now) have about emotions — that they are states of mind that cause behavioral expressions. Why else would we flee from danger if not because we feel afraid?

Darwin also noted some similarities in behavioral expressions between humans and other mammals, leading him to conclude that our emotions are states of mind inherited from them. But he often described animal behavior in human emotional terms: cheerful, proud, scornful, content, jealous, contemptuous. A reporter once asked him why he talked this way: in response, he said it was kinder, and that the public was more likely to accept animals being like humans, than humans being like animals.

Darwin’s romantic approach to animal behavior was quite anthropomorphic, and had a profound impact on the course of the new field of animal psychology that was emerging in the late 19th century. His acolyte, George Romanes, referred to behavior as the ambassador of the animal mind. The continuing influence of Darwin’s views on emotion research is one of the

reasons why the nature of emotions is one of the most contentious topics in the study of mind and behavior today, especially in relation to the question of animal emotions. In this My word, I explore key issues in the current debate, and suggest how current understanding of human emotions, and their underpinnings in the brain, might provide a novel approach for illuminating what emotions in other animals *might* be like.

Contemporary emotion theory

The flagrant calling upon of conscious explanations of behavior was a major factor that led to the behaviorist revolution in psychology, which resulted in a strict ban of all talk of mental states during much of the first half of the 20th century. Emotion research did not cease in psychology, but it took a different form. Rather than being about the subjective conscious feelings that people experience, emotions were redefined as behavioral responses to stimuli. By the early 1960s, though, behaviorism was on the wane, and the topic of emotion was returning in earnest to psychology in two forms. One was so-called basic emotions theory, and the other, cognitive theory.

In the tradition of Darwin, basic emotions theory proposed that a small number of primary emotions are common to all humans by virtue of our species having inherited the same ‘affect programs’ (*hypothetical* innate neural structures) that underlie these emotions from our mammalian ancestors^{1,2}. Affect programs were said to be involved in both controlling behavioral (especially facial) and physiological body responses and the conscious experience of the emotions. Like Darwin, many said that the emotional stimulus activates the affect program and elicits the mental state of emotion, which causes behavior. But others adopted William James’ notion that the emotional stimulus, *via* the affect program, elicits body responses, and feedback signals from these responses define the emotional experience³. A common list of basic emotions includes fear, happiness, anger, sadness, surprise, and disgust, but the list varies some between theorists. In addition to primary emotions, basic emotions theories also typically postulate secondary emotions — envy, jealousy, pride, contentment, and so on — that are said

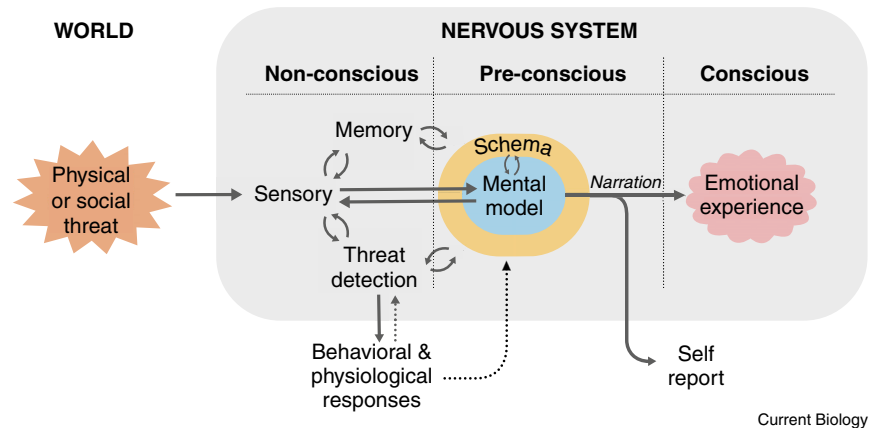


Figure 1. My cognitive view of emotion.
See the text for details.

to be learned individually and influenced by one’s culture.

The other approach to emotion reflected the new cognitive movement in psychology, which had supplanted behaviorism. Stanley Schachter and Jerome Singer proposed that emotions result from the cognitive interpretation of situational factors which, for them, included the external physical and social context, and physiological responses in the brain and body⁴. For example, if one notices their heart is beating fast in the context of the rapid approach of an angry aggressive person, fear results. But if one’s heart is beating similarly fast after exercise, no emotion needs to be attributed.

Contemporary representatives of the cognitive approach fall into two categories. Appraisal theories assume that the emotion one experiences is a function of cognitive appraisals. While innate affect programs perform a primitive, non-cognitive kind of appraisal, cognitive appraisals are learned and culturally influenced, and depend on attention, memory, concepts, predictions and decision-making^{5,6}. These define one’s momentary experience in terms of specific categories similar to those of basic emotions theories, but the experience arises from individual cognition rather than innate programs inherited from animals.

Constructionist theories draw upon similar cognitive processes, but are less wed to specific emotion categories. These, instead, emphasize how signals resulting from interactions between arousal (high to low) and valence (positive to negative) allow us to

conceptualize emotional experiences by assigning everyday emotion words to our experiences⁷.

My approach to emotion

I have long been in the cognitive camp when it comes to emotional experience^{8,9}. My approach incorporates aspects of appraisal and constructionist theories, and starts with the assumption that emotions are conscious experiences that emerge in biologically or psychologically significant situations. Key to the experience is the integration of perceptual and memory signals with signals related to brain and body states to form situational, self, and emotion schema. The latter coalesce into a non-conscious, or more precisely, pre-conscious, mental model of the emotional situation. The output of the model is a narrative that constitutes the penultimate pre-conscious antecedent of the conscious emotional experience, and that is also antecedent to verbal self-report (Figure 1).

The narration can be about immediate experience or about memories. The conscious emotional experience resulting from the narration is either of a particular categorical type of emotion — fear, joy, anger, jealousy, envy, pride — or a less well-defined state of distress or well-being. Because emotional situations can change moment-to-moment, the schemata, mental model, and narration can also change. As a result, the conscious experience can vacillate in real-time as well — distress may become fear or anger, or fear may suddenly become anger, jealousy or embarrassment.

The view that narration and self-report are both pre-conscious is contrary to conventional wisdom, which typically has narrations and reports as post-conscious. One consequence of my view is that the experience and report may diverge to some extent as a result of differences in the post-narrative processing that is required to generate conscious awareness and speech. Despite the fact that reports are not perfect mirrors of experience, they are very useful and are considered the gold standard for scientifically assessing conscious experiences¹⁰, a fact of scientific life that poses challenges for research seeking to study emotional experiences in non-human animals.

Emotions in the brain

The emotion that has been studied most extensively in terms of neural circuitry is fear. Decades of animal research has implicated the brain area called the amygdala, and interconnected downstream areas, such as the hypothalamus and periaqueductal gray region, in the expression of behavioral and physiological body responses elicited by threatening stimuli^{8,11}. Importantly, imaging studies of amygdala neural activity, and studies of patients with amygdala damage, confirm that core findings from the animal research apply to humans¹².

Neuroscientists have generally been more interested in the brain circuits controlling behavioral and physiological responses than in conscious feelings. But some have, in the spirit of Darwin, argued that the brain mechanisms that control the responses are also responsible for the conscious experience of emotions. Indeed, the amygdala and connected downstream targets, like the periaqueductal gray area, have come to be synonymous with the fear affect program, and are often also assumed to be involved in the conscious experience of fear. The late neuroscientist Jaak Panksepp¹³, for example, wrote that “the mechanisms of affective experience and emotional behavior are intimately intertwined in comparatively ancient areas of the mammalian brain”, proposing specific subcortical circuits for each of several basic emotions in animals and humans.

Nico Tinbergen, the pioneering ethologist, once pointed out that proposals about conscious feelings

in animals are “merely a guess about the possible nature of the animal’s subjective state”¹⁴. Indeed, many in the consciousness field believe that conscious experiences can only be studied with scientific rigor in humans, because findings from animal studies really only reveal how brain circuits control behavioral physiological responses. And in humans, the evidence for subcortical programs being responsible for conscious feelings is weaker than is sometimes claimed^{8,15–17}.

Some neuroscientists, me included, place greater emphasis on cortical circuits, especially circuits involving prefrontal cortex (PFC) that contribute to cognitive processes such as working memory, in understanding conscious emotional experiences^{8,9,15–17}. Positive correlations between the experience of fear and neural activity have been found in both PFC and in the amygdala¹⁸. However, studies directly comparing cortical and amygdala involvement using neural decoding have shown that PFC activity is more explicitly associated with consciously experienced fear than is amygdala activity, while the latter is more related to physiological responses¹⁹.

Nevertheless, such correlations do not prove that PFC activity plays a causal role in the experience. More compelling is evidence from direct electrical stimulation of brain areas in humans. Studies in the 1960s found that stimulation of the amygdala elicited fearful experiences, but the techniques used were primitive by today’s standards, and there were other methodological and interpretative problems (for discussion, see¹⁶). Recent studies using more sophisticated methodology found that electrical stimulation of the amygdala elicited body responses, but only infrequently resulted in self-reports of fear²⁰, while stimulation of several areas of PFC elicited reports of fear and other emotional experiences²¹. Although I emphasize prefrontal areas, temporal and parietal lobe representations are also involved, and may, when PFC is damaged, compensate to some extent.

Kinds of consciousness

So far, I have treated emotional consciousness as a single kind of experience. But different kinds of experience can, and often do, occur simultaneously. In evaluating the role of

cortical versus subcortical brain areas in emotional consciousness, distinctions between kinds of consciousness may offer a more subtle understanding.

A particularly useful way of characterizing the different kinds of conscious states is Endel Tulving’s²² three-way partition between auto-noetic, noetic, and anoetic states. Each is said to depend on a different form of memory: auto-noetic consciousness depends on episodic memory; noetic consciousness on semantic memory; and anoetic consciousness on procedural memory.

For illustrative purposes, consider the three kinds of states in relation to what you might experience in the presence of a dangerous stimulus, such as a snake at your feet^{9,15–17}. Using semantic memory, you would recognize the stimulus as the kind of animal you know of as a snake, and you would likely conceptualize the stimulus and situation as potentially dangerous. The result would be an instance of *noetic* consciousness about danger, including awareness of the relation of danger to the experience of fear. With the addition of episodic memory, that is, memories about your ‘self’, ‘you’ become part of the experience —you conceptualize that you may be harmed by the snake. The experience, at this point has become an *auto-noetic* state of reflective self-consciousness in which you feel afraid of what may happen to you.

While noetic states can occur without becoming auto-noetic states, auto-noetic states typically depend on the kind of semantic conceptual knowledge that comes with noetic states, including semantic autobiographical memory. Not all auto-noetic states are emotional states, but all full-fledged emotional states are auto-noetic states.

Auto-noetic emotional states are the kinds of emotional state we encounter in our minds when we think of ourselves as having emotional experiences, and that we talk about when we share our emotions with others. And they are the kinds of emotional feelings we read about in novels or poetry, as when Jane Austin, in *Persuasion*, wrote, “you pierce my soul. I am half agony, half hope...I have loved none but you”.

Anoetic states are quite distinct from both auto-noetic and noetic ones. Tulving characterized the difference in terms of three ways of ‘knowing’: ‘self-knowing’

comes with auto-noesis; ‘fact-knowing’ with noesis; and ‘non-knowing’ with anoesis. In other words, auto-noetic and noetic states have explicit conscious content, but anoetic states do not.

I was, for some time, puzzled about why Tulving referred to anoetic states as conscious states, given that he called them states of ‘non-knowing’, and connected them to procedural memories, which are generally considered to be non-conscious states. In an email to me, he explained that he used ‘consciousness’ to mean the condition of being alive and responsive to stimuli (this is typically referred to as creature consciousness in the literature), as opposed the condition of having a conscious experience with explicit content (this is called mental state consciousness in the literature). So, for Tulving, anoetic states are indeed implicit, procedural states of creature consciousness that control behavior unconsciously.

This clarification provides an interesting perspective on the controversy about the brain basis of emotions between basic emotions and cognitive theorists. For example, Panksepp and Marie Vandekerckhove specifically called upon Tulving’s anoetic states to account for primal emotional conscious feelings that emerge from subcortical circuits²³. Given the exchange I had with Tulving, one could say that Vandekerckhove and Panksepp simply misunderstood Tulving’s opaque concept. But they had a different agenda.

Vandekerckhove and Panksepp viewed anoesis as a fluid boundary between the conscious and unconscious mind. Specifically, they treated subcortical neural states as being responsible for a form of emotional consciousness that is so primitive that it is typically overshadowed by cognitive states of emotional consciousness and hence not noticed in humans. But in lower mammals, they said, these primal states are what conscious emotions are. While I think Vandekerckhove and Panksepp were indeed on to something important functionally, I think they got the anatomy wrong.

Higher-order emotional experiences

For several years I have been attempting to integrate Tulving’s model into the higher-order theory of consciousness.

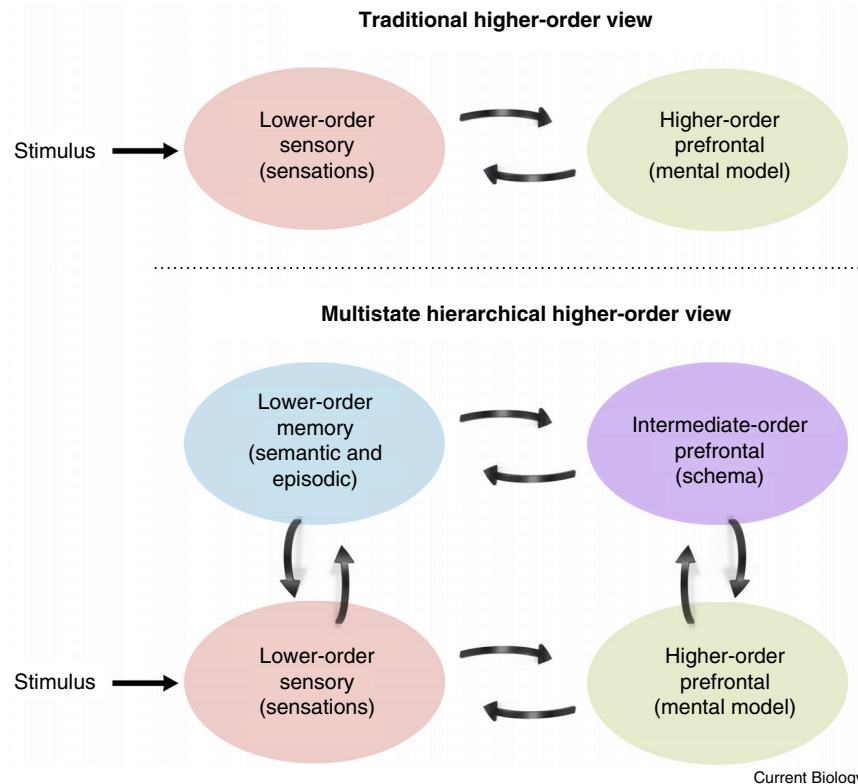


Figure 2. Traditional and multistate hierarchical higher-order theories of consciousness.

The traditional theory postulates that consciousness arises from a higher-order representation of a single kind of lower-order state. My multistate hierarchical hypothesis proposes several layers of re-representation especially involving memory. For further discussion see^{17,25–27}.

According to higher-order theory, lower-order information becomes conscious when it is cognitively re-represented, especially by PFC circuits^{15,17,24–26}. A key feature of higher-order theory is that the re-representation is not itself the conscious experience. It is instead a pre-conscious antecedent of consciousness. For example, a higher-order account of visual perception assumes that a non-conscious state of secondary visual cortex becomes conscious when cognitively re-represented by PFC, and, in particular, by lateral PFC areas, especially the dorsal and ventral lateral areas and the lateral frontal pole (Figure 2, top). The higher-order state is, in effect, what I referred to above as the pre-conscious mental model that is antecedent to a conscious experience (Figure 1).

I recently proposed that this traditional higher-order view, which posits a single lower-order state, is too simple — that multiple levels of re-representation, especially involving memory and related conceptual processes, may

be required between a conventional lower-order state and the higher-order re-representation^{9,25–27}. I refer to this as a *multistate hierarchical higher-order view* (Figure 2, bottom).

In the case of visual perception, for example, the modified view proposes that sensory information alone is insufficient to noetically know what an object is — that semantic memory must be integrated with sensory information to conceptualize and categorize what is being sensed. And to have an auto-noetic experience of what the object means to you, episodic self-memory has to be integrated with the sensory/semantic representation. These integrations, I suggest, occur by way of transmission of signals from visual cortex to memory processing areas in the temporal and parietal lobes that, in turn, connect with what can be thought of as intermediate PFC areas. Included are insula, orbital and medial (i.e. anterior cingulate and ventromedial) PFC. These then connect with lateral PFC higher-order circuits^{9,25–27} (Figures 2 and 3).

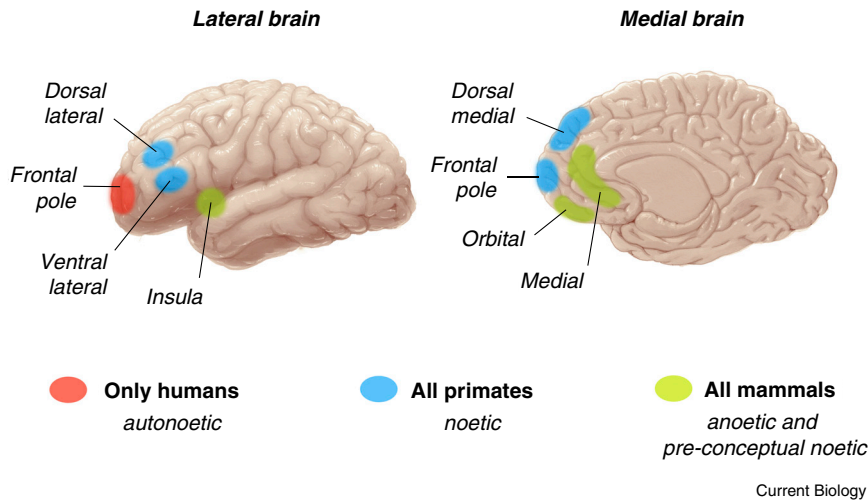


Figure 3. How human brains can help us think about what animal consciousness might be like.

All mammals possess insula, orbital, and medial areas of PFC (medial PFC includes the anterior cingulate and ventromedial areas) (green). Primates alone have medial frontal pole, dorsal and ventral lateral, and dorsal medial areas of PFC (blue). Only humans possess the lateral frontal pole area (red). Better understanding of the neural underpinnings of different kinds of consciousness (anoetic, noetic, autonoetic) in humans might shed light on the kinds of conscious capacities that might be possible in other mammals, given the kinds of brains they possess. All anatomical depictions are approximate. For further discussion see text and references^{17,25,26}.

The intermediate PFC areas have been implicated in a variety of functions, including the encoding of body states, stimulus and response values, and the self, and also in the capacity to mentalize and to gate conscious access to lower-order information^{28,29}. A concept that subsumes all of these is their role in the formation of schema, complex collections of memories about specific things, such as external situations, one's emotions, and one's self, including one's body.

For example, stimuli signifying danger activate semantic and episodic memories in the temporal and parietal lobes, as well as the amygdala threat-processing circuitry. Via connections to the intermediate PFC areas, situational, self and fear schema are formed and help shape a conception of what the situation is about in relation to you and how you might feel and act in such a situation. Individual schema are integrated into a pre-conscious emotional (fear in this case) mental model that narrates the content of the autonoetic fearful conscious experience.

The main difference between an emotional and a non-emotional mental model is the presence of an emotion schema that adds emotion content to the mental model. This is what makes

the mental model an emotional mental model, and the experience an emotional autonoetic emotional experience²⁶.

What about anoetic consciousness? In a recent *My word*²⁶, Hakwan Lau and I proposed that, like any other experience, anoetic conscious experiences result from re-representation of lower-order events. But unlike noetic and autonoetic conscious states, which are based on lower-order explicit memories with content, the lower-order events involved in anoetic consciousness are procedural states that have resulted from innate wiring, accumulation of statistical regularities through deep learning, or simple associative learning, and lack explicit content. These states accompany all explicit conscious experiences, from the simplest noetic perception of what a sensory stimulus is to the most complex autonoetic emotional experiences.

When these first-order events are re-represented in intermediate PFC areas, the result is, I propose, an anoetic conscious experience that exists as a mental shadow on the border between consciousness and unconsciousness. As others have said, they reside in the background of explicit consciousness, giving noetic and autonoetic states a feel of 'warmth and intimacy', to use an

expression by James. While these states are not about anything in particular, they exude familiarity, and make it possible for one to know their explicit (noetic and autonoetic) mental states are theirs²⁶.

Diving deeper into anoesis

Contrary to what has been said about my views, I do not claim that non-human animals are mindless robots that lack conscious experiences. My point, instead, is that while it is likely the case that non-human animals have some form of consciousness, it is difficult, maybe impossible, to scientifically study animal consciousness^{10,15-17}.

Just as I am often misunderstood as someone who denies animal consciousness, I think Panksepp's views about animal emotions have also been misunderstood. Because he was so adamant about animal emotion, it was assumed he meant that emotional experiences in animals are similar to the kinds of emotional experiences that humans refer to with everyday vernacular words, such as fear or sadness. But, in fact, he maintained that emotions in animals are qualitatively different from canonical human emotional experiences. For example, he and Vandekerckhove²³, using Tulving's language, referred to emotions in animals as rudimentary anoetic states of "unknowing consciousness".

If other animals have conscious emotions, I believe the essence of what these would be is very similar to what Vandekerckhove and Panksepp propose — primitive states of unknowing (content-lacking) consciousness. But perhaps William James' term, 'fringe of consciousness', which Vandekerckhove and Panksepp also used at times, is more fitting, since it suggests that anoetic emotional states, being on the border between consciousness and unconsciousness, are different from explicit, content-laden, autonoetic emotional states about one's self that fill the mind.

What human brains suggest about what animal emotions might be like

Although we cannot know what other animals experience, if the above framework is roughly correct, it would provide a foundation for speculating about what an animal *might* experience, given the kind of brain it has. A way to proceed in this vein would be to

mount a concerted effort to better understand the processes that underlie autozoetic, noetic, and anoetic states in relation to human emotions, and then to characterize the circuits responsible in our brains. This knowledge about human emotions, when compared with known anatomical similarities and differences between the brains of humans and other mammals, would provide an empirically based approach for speculating about emotions across species (Figure 3).

One prediction from such an approach is that, in the human brain, procedural processes associated with anoetic consciousness involve anatomical regions common to all mammals, including subcortical brain circuits involving areas such as the amygdala, hypothalamus, periaqueductal gray, and their connections with the intermediate PFC areas. A second prediction is that a simple form of non-verbal, pre-conceptual noetic awareness about stimulus and response values acquired through reinforcement learning may involve connections between what is called the extended amygdala and the intermediate prefrontal areas. Third, non-verbal noetic awareness of objects and events based on cognitively acquired conceptual knowledge may involve known interactions between temporal lobe memory systems and the intermediate PFC areas. This capacity and circuitry is well developed in primates, but could exist, to some extent, in some other mammals. Fourth, it is known that primates possess PFC circuits that differ significantly from those present in non-primate mammals, but that are similar in human and non-human primates. Included are dorsal and ventral lateral PFC, and dorsal medial PFC, and the medial frontal pole. These differences may underlie the ability of primates, compared to other mammals, to flexibly use conceptual knowledge to form content-rich noetic states of consciousness. Finally, circuits that differ most between humans and non-human primates (the lateral frontal pole) have been implicated in abstract mentalization and subjective self-awareness, and may contribute to autozoetic self-consciousness, which many believe is a unique, or at least an especially well-developed, human capacity.

Too often, the existence and nature of animal emotions has been assumed from intuitions about what animals must experience, given similarity of the way we and they respond behaviorally to certain classes of stimuli. But as Tinbergen said, such conclusions are mere guesses about the possible nature of the animal's subjective state. Romanes' idea that behavior is an ambassador of the mind is not wrong; it is just too broad since we know that, in humans, some behaviors, such as those that are often associated with emotions, are not caused by conscious feelings^{9,17}. If we cannot rely on overt behavior alone to tell us what a human is feeling, why do we think behavioral responses in animals reveal their inner experiences?

Judging what an animal is feeling on the basis of what we might feel in a comparable situation is fine as a way of interacting with our pets, but it is not the way to do science. Just as physicists do not rely on intuition alone to understand the universe, or biologists, life, we should not rely solely on intuition when it comes to the science of mind. While we can turn to verbal reports to back our intuitions in humans, we don't have this luxury in animal research.

The approach proposed here would still only result in speculations about the emotional experiences of animals. But the speculations would be constrained by empirical facts about the relation of mind to brain, rather than simply being the result of romantic presuppositions about what we think the relation of behavior to mind should be.

REFERENCES

- Tomkins, S.S. (1962). *Affect, Imagery, Consciousness, Volume 1: The Positive Affects* (New York: Springer).
- Ekman, P. (1980). Biological and cultural contributions to body and facial movement in the expression of emotions. In *Explaining Emotions*, A.O. Rorty, ed. (Berkeley: University of California Press), pp. 73–102.
- Carvalho, G.B., and Damasio, A. (2021). Interoception and the origin of feelings: A new synthesis. *BioEssays* 43, 2000261.
- Schachter, S., and Singer, J.E. (1962). Cognitive, social, and physiological determinants of emotional state. *Psychol. Rev.* 69, 379–399.
- Scherer, K.R. (1984). Emotion as a multicomponent process: A model and some cross-cultural data. *Rev. Personal. Social Psychol.* 5, 37–63.
- Ortony, A., Clore, G.L., and Collins, A. (1988). *The Cognitive Structure of Emotions* (Cambridge University Press: Cambridge).
- Barrett, L.F., and Russell, J.A., eds. (2015). *The Psychological Construction of Emotion* (New York: Guilford Press).
- LeDoux, J.E. (1996). *The Emotional Brain* (New York: Simon and Schuster).
- LeDoux, J.E. (2020). Thoughtful feelings. *Curr. Biol.* 30, R619–R623.
- Dehaene, S., Lau, H., and Kouider, S. (2017). What is consciousness, and could machines have it? *Science* 358, 486–492.
- LeDoux, J. (2007). The amygdala. *Curr. Biol.* 17, R868–R874.
- Phelps, E.A. (2006). Emotion and cognition: Insights from studies of the human amygdala. *Annu. Rev. Psychol.* 57, 27–53.
- Panksepp, J. (1998). *Affective Neuroscience* (New York: Oxford University Press).
- Tinbergen, N. (1951). *The Study of Instinct* (New York: Oxford University Press).
- LeDoux, J.E., and Brown, R. (2017). A higher-order theory of emotional consciousness. *Proc. Natl. Acad. Sci. USA* 114, E2016–E2025.
- LeDoux, J.E. (2015). *Anxious: Using the Brain to Understand and Treat Fear and Anxiety* (New York: Viking).
- LeDoux, J. (2019). *The Deep History of Ourselves: The Four-Billion-Year Story of How We Got Conscious Brains* (New York: Viking).
- Zhou, F., Zhao, W., Qi, Z., Geng, Y., Yao, S., Kendrick, K.M., Wager, T.D., and Becker, B. (2020). Beyond fear centers — a distributed fMRI-based neuromarker for the subjective experience of fear. *bioRxiv*, <https://doi.org/10.1101/2020.11.23.394973>.
- Taschereau-Dumouchel, V., Kawato, M., and Lau, H. (2020). Multivoxel pattern analysis reveals dissociations between subjective fear and its physiological correlates. *Mol. Psych.* 25, 2342–2354.
- Inman, C.S., Bijanki, K.R., Bass, D.J., Gross, R.E., Hamann, S., and Willie, J.T. (2018). Human amygdala stimulation effects on emotion physiology and emotional experience. *Neuropsychologia* 145, 106722.
- Raccah, O., Block, N., and Fox, K.C.R. (2021). Does the prefrontal cortex play an essential role in consciousness? Insights from intracranial electrical stimulation of the human brain. *J. Neurosci.* 41, 2076–2087.
- Tulving, E. (2005). Episodic memory and autonoesis: Uniquely human? In *The Missing Link in Cognition*, H.S. Terrace and J. Metcalfe, eds. (New York: Oxford University Press), pp. 4–56.
- Vandekerckhove, M., and Panksepp, J. (2011). A neurocognitive theory of higher mental emergence: From anoetic affective experiences to noetic knowledge and autozoetic awareness. *Neurosci. Biobehav. Rev.* 35, 2017–2025.
- Lau, H., and Rosenthal, D. (2011). Empirical support for higher-order theories of conscious awareness. *Trends Cogn. Sci.* 15, 365–373.
- Brown, R., Lau, H., and LeDoux, J.E. (2019). Understanding the higher-order approach to consciousness. *Trends Cogn. Sci.* 23, 754–768.
- LeDoux, J.E., and Lau, H. (2020). Seeing consciousness through the lens of memory. *Curr. Biol.* 30, R1018–R1022.
- LeDoux, J.E. (2020). How does the non-conscious become conscious? *Curr. Biol.* 30, R196–R199.
- Koban, L., Gianaros, P.J., Kober, H., and Wager, T.D. (2021). The self in context: Brain systems linking mental and physical health. *Nat. Rev. Neurosci.* 22, 309–322.
- Huang, Z., Tarnal, V., Vlissides, P.E., Janke, E.L., McKinney, A.M., Picton, P., Mashour, G.A., and Hudetz, A.G. (2021). Anterior insula regulates brain network transitions that gate conscious access. *Cell Rep.* 35, 109081.

¹Center for Neural Science and Department of Psychology, New York University, New York, NY 10003, USA. ²Departments of Psychiatry and Child & Adolescent Psychiatry, NYU Langone, New York, NY 10016, USA.
E-mail: jel1@nyu.edu