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Constructing nonhuman animal emotion

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Scientists and lay-people alike have long been fascinated with the emotional lives of nonhuman animals. To date, scientific approaches to the study of ‘animal’ emotion have assumed that emotions are biologically evolutionarily conserved, hardwired and have discrete behavioral and physiological outputs. According to this view, emotions and their outputs are homologous across species, allowing humans to accurately perceive (or ‘read’) animal emotion using our own concepts of what emotions are. In this paper, I discuss the challenges to that perspective and propose using an alternative theoretical approach to understand animal emotion. Adopting this alternative approach, which represents a collection of similar theories (referred to as ‘Theories of Constructed Emotion’), changes the questions that we ask about animal emotion, how we study emotion across phylogeny and advance translational science, and how we understand the evolution of emotion.

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The idea that a small set of emotions is biologically hardwired, evolutionarily conserved, and has discrete and specific behavioral and biological outputs has dominated the study of affect in human and nonhuman animals (herein, ‘animals’) [1[•],2–7]. This ‘Classic View of Emotion’ (CVE) is intrinsically appealing, most notably because it stipulates that it is possible to understand animals’ emotions by measuring behavioral and biological outputs and categorizing them into human emotion categories (e.g. freezing equals fear). This approach, however, is problematic for several reasons. In the present paper, I review the problems inherent with the CVE for studying animal emotion and introduce a set of emotion theories collectively known as Theories of Constructed Emotion (TCE; for reviews: [8,9^{••}]) as an alternative framework for understanding the affective lives of nonhuman animals and the evolution of emotion.

Challenges to the Classic View of Emotion as a model for animal emotion

The primary problem associated with applying CVE to animals is that it assumes that there must be consistent, discrete, and specific markers of emotions — each emotion must have a distinct and reproducible signature of behavior, physiology, or both. However, such signatures do not exist in humans. While some individual studies have found evidence of mappings between emotions and outputs, meta-analyses, which provide a comprehensive gestalt view of the entire literature do not. The correspondence between outputs and emotions does not exist in humans in the autonomic nervous system [10–13], the central nervous system [14[•],15–18], or facial behavior [10,19]. Variation in human emotion outputs is the norm and not the exception. The only way to know with confidence what emotion a human is experiencing is to ask him to report on his state using symbols (words). Such reports are impossible for most, if not all, animals.

Potent human beliefs about the realness of our emotional experience and perception of emotions in others reflect the remarkable capacity of humans to use conceptual knowledge and to infer mental states ([20] for a recent review on mental inference). Inferring emotion in animals based on our perception does not ensure that animals have those emotions (for a similar argument [21^{••},22^{••}]). Our human perceptions are real. But, the realness of our perceptions does not confer realness of the animals’ experience. Thousands of years of human history demonstrate that how humans perceive the world does not necessarily reveal the reality of the world — for example, the earth is not flat and the sun does not orbit around the earth. It may be argued that the case of emotions is no different. When human emotion concepts are applied to animals we are engaging in human perception and mental inference — not data collection. Perception of emotion in animals is the act of ‘seeing human’ where it may or may not be.

Theories of Constructed Emotion as a model for animal emotion

Given the variation in the manifestation of emotions in humans (i.e. there are not consistent mappings^a between outputs and emotions) and that seeing emotion in animals reflects the human capacity for mental inference and not (necessarily) animals’ capacity for emotion, an alternative approach to the study of animal emotion is clearly warranted. TCE provide a promising alternative. While

^a Even if one argues that the evidence for mappings requires more data or better methods, the logical choice is to not assume that emotions exist in other animals, but to adopt an approach that does not require such assumptions until evidence is found.

specifics differ across theories, one general premise is consistent: emotions are not modules or hardwired circuits, but rather emerge from a combination of ingredients [23–29] (for reviews: [8,9^{**},30]). Those ingredients are supported by neural circuits which are not necessarily modular and can be indexed via biological and behavior measurements.

TCE vary in their emphasis on which ingredients are required for emotions to emerge. For example, some theories focus on the importance of emotion concepts (what we know about emotions), which the brain constructs on an ongoing manner based on past experiences to serve as predictive signals for incoming sensory information [22^{**},29]. Other theories highlight the importance of the language (symbolic representations) that is used to represent emotion concepts [26,31]. Yet, other theories focus on the importance of social relationships for the emergence of emotion [32,33] or the cognitive representation of situations in which emotions occur [25]. At the core of TCE is ‘affect’ — a global state characterized by valence and arousal that forms the basis of emotions [34,35]. Stimuli are said to have ‘affective value’ when they can perturb an individual’s allostasis, creating an ‘affective state’. The perturbation of allostasis is therefore the mechanism that produces affect. Thus, affective value is a barometer indexing an organism’s idiographic relationship to the environment. Critically, affect allows for efficient navigation of the environment in order to meet survival needs by signaling which stimuli and conspecifics may be harmful or beneficial. This occurs via the generation of probabilistic inferences about which stimuli are relevant for allostasis [36]. The mechanism by which emotions emerge is therefore the application of conceptual information to the representation of one’s affective state [37]. For humans, symbolic representations (words) increase the accessibility of, and shape the content of, concepts; they also allow for concepts, and the experiences that they represent, to be socially shared [38–41]. See Table 1.

The promise of using TCE to understand animal emotion is that assumptions about what counts as evidence for specific emotions in animals are no longer necessary. Instead of trying to measure emotions in animals, we investigate emotion’s ingredients using behavioral and physiological responses (see below), and map their presence and emergence across phylogeny. Affect is likely present in most non-plant organisms, although in those lacking nervous systems or with simple nervous systems (e.g. ganglion only) it may appear in rudimentary form. For example, bacteria move toward positive things (e.g. food) and away from negative ones (e.g. acid), indicating that they can use signals about affective value to guide behavior (see [42] for a discussion). In humans and other primates, encoding of physiological information is integrated into affect via an anatomical network that includes insula, orbital frontal cortex and anterior cingulate cortex [36,43–46,47^{*},48]. A detailed discussion of the networks that support affect is beyond the scope of this paper, but see [48]. Anatomical regions that integrate peripheral physiological information exist in non-primate mammals (e.g. [49]) and may exist in non-mammals from less studied lineages (e.g. corvids, see [50]). Increased complex anatomical connectivity that develops over phylogeny likely leads to increasingly complex representations of bodily or arousal information that are available to be integrated into affective states [51].

While affect is omnipresent in the animal kingdom, less is known about the other ingredients that are hypothesized to be critical for the emergence of emotion according to TCE. Animals have concepts that allow them to navigate their environments, including understanding the behaviors of conspecifics. For example, macaque monkeys have conceptual information that allows them to differentiate between kinds (see [52]) and are capable of modifying their understanding in contextually flexible ways, much like humans (e.g. understanding that the meaning of a specific facial behavior differs by context [53]). Corvids can solve multi-step problems that require

Table 1

Proposed psychological ingredients of emotion and their presence in animals

| Ingredient | Definition | Present in? |
|----------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------|
| Affect | The state that results from perturbations of allostasis; it is characterized by valence and arousal. | All animals. May exist in rudimentary forms in animals with simple nervous systems (e.g. mosquitoes) or no nervous systems (e.g. bacteria). |
| Conceptual knowledge | Probabilistic organization of what we know about emotions based on our past experiences that serve as prediction signals in the construction of emotion. Emotion concepts are abstract and socially shared. | While all animals have concepts, the extent to which abstract, socially shared concepts exist in species other than humans is not known. |
| Language | Socially agreed upon symbols used to represent concepts. | Humans. Learning studies suggest that other animals (e.g. great apes, parrots, and dolphins) have the capacity to acquire human-like language. |
| Social context | Relationships between both in-group and out-group conspecifics. | Any animal whose home range overlaps with other conspecifics. |

creating tools and performing actions outside their typical behavioral repertoire [50], suggesting that they are able to abstractly represent the use of novel objects and actions. Many similar examples in the animal kingdom exist (for a discussion, see Chapter 12 [22**]). But, the question is whether animals (generally), or which animals (specifically), have abstract concepts that represent physical sensations which are also socially shared [22**] — in other words, emotion concepts. It is also unknown whether species that may have the capacity for emotion concepts have the capacity to symbolically represent them such that they can be shared socially. Some animals have demonstrated the capacity to use human-like symbols for objects and actions after significant training (great apes, e.g. [54]; e.g. parrots [55]; e.g. dolphins [56,57]) — indicating that, at the very least, the neural resources for symbolic representation are present. Only a small number of species have the documented capacity to make mental inferences (for a review: [58**]) — a feature required for the social sharing of conceptual information. Further research is clearly warranted.

Ideally, the search for the ingredients of emotion across phylogeny would be conducted using ‘translational tools’ — indices that can be deployed across species and within species across context (e.g. wild versus captive) without having to modify operationalized definitions of emotions, emotion-related processes, or affect for each species or having to anthropomorphize. For example, we can measure the timing or the magnitude of behavioral responses (i.e. ‘affective reactivity’ as in [59]) simply by counting the number of unique behaviors that occur in response to stimuli thought to have affective value. Physiological responses also give evidence about the encoding of affective value [60–62]. Starting with human data about the intrinsic brain networks that are related to self-reported affective experience [48], we can investigate whether those networks are present in other species (e.g. as has been done for the ventral salience network in humans [63] and macaques [46]). Eye tracking can also be deployed in a wide variety of species to index visual attention to stimuli with affective value (e.g. [64,65,66*]).

Theories of Constructed Emotion and the evolution of emotion

Adopting TCE radically shifts how we understand the evolution of emotion (EvoEmo). Based largely on human data or theory alone (rather than comparative data), the predominant EvoEmo argument claims that emotions emerged to meet specific evolutionary challenges resulting in modular programs that have discrete predictable causes and outputs and are consistent across species (e.g. [6,67]). For example, fear is thought to occur when freezing or fleeing is the best response. Most EvoEmo theories posit that the modules were hardwired during the Pleistocene era which began ~1.8 million and ended ~11 700 years ago [6,67]. This confers homology in emotions across species

that existed *in the evolutionary past*. What this also means is that emotions could have first evolved in a very different natural and social world — conferring adaptability for a very different ecological niche.

Ultimately, existing EvoEmo hypotheses conflict with what we know about how evolution functions. Evolution acts on variability [68]; hardwired emotion programs would not allow for variability in responding. Thus, as new evolutionary challenges manifested, species that did not have an emotion program to meet that specific challenge would fare poorly. According to TCE, however, because emotions are not hardwired modules, evolution could not have acted on them directly [23]. Instead, evolution selected for the ingredients of emotion, and in some species, further for a flexible conceptual system that itself is adaptable to any ecological niche. This allows emotions to emerge in a contextually dependent way that reflects the evolutionary and adaptive challenges faced by a particular organism at a particular point in time and space. Species that only required affect to survive, only developed affect (e.g. fruit flies on one extreme). Species that benefited from the social sharing of experience developed emotions that were linked to symbolic representations (e.g. humans on the other extreme). Concepts for specific emotions developed as a result of experiences in particular environments and particular evolutionary challenges.

When shared socially, emotions would allow groups to understand evolutionary challenges without having to experience them directly, potentially subserving the development of the large groups that are characteristic of human societies. Living in groups affords both advantages (e.g. reduced predation risk, cooperation) and disadvantages (e.g. disease transmission, competition); optimal group size is predicted by a balance of these competing factors (for a review and discussion [69]; for a recent empirical example [70]). Human groups exceed optimal size [69]. Language has been proposed to be an important feature in the development of large groups because it allows for social bonding with less effort and time than non-linguistic forms of social bonding (e.g. grooming) [71]. While language, generally, may serve a social bonding function, being able to communicate about allostasis-relevant stimuli and experiences would confer a significant adaptive advantage. Emotions may therefore have evolved in part to support this capacity, and in turn, support living in such large groups. This idea can be empirically tested in the future using phylogenetic comparative approaches that are aimed at ancestral state reconstruction [72].

Conclusion

Perhaps most critically, TCE do not restrict the nature of animal emotion to human emotion. Anthropomorphic perspectives have traditionally been levied on the basis that *not*

applying human concepts to animals denies animals' true capacities, which is morally questionable (e.g. [73,74]). This perspective sets humans as the standard, eliminating the possibility that animals may have unique capacities that far surpass our own or concepts that arise from completely experiences which in turn support the emergence of unique emotions that humans do not have. This idea is supported by the fact that many animals inhabit niches unlike those of humans, and thus face evolutionary challenges that humans will never experience. Constructing animal emotion leaves open the possibility that there is a discrete emotion associated with say, sensing the vibrations a dying family member's voice hundreds of miles away (as might be the case for cetaceans and elephants), or an emotion that results from the physiological consequences of a 250 m deep dive that has turned up a favorite food (as may be the case for California sea lions). Constructing emotion recognizes that the human capacity for emotion does not carve nature at its joints, but rather that humans exist as part of a dynamic animal kingdom shaped by changing environments, experience, and evolution's ability to act on variation over time.

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Conflict of interest statement

Nothing declared.

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