

## A framework for the study and assessment of animal emotions

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A recent review of animal emotion suggests that, as in humans, emotions may tell animals about how dangerous or opportunity-laden their world is, and guide the choices that they make [14]. This has implications for the conceptualisation, study and measurement of animal emotion. In many scientific disciplines, ranging from neuroscience to psychopharmacology to animal welfare science, a better understanding of the emotional states of non-human animals is an important goal. For example, from an animal welfare perspective, if we understand how housing and management impact on the emotional states of animals, we can design or recommend new procedures that help to enhance well-being. Understanding and assessing the emotional states of other species is a challenging task. The conscious experience of emotion is essentially private, and currently we are not able to measure it directly, not even in other people. However, in addition to the conscious feeling of emotion, emotional responses have other components including changes in behaviour, physiology and neural function, and these can be measured. It is of course possible that other species may show these measurable aspects of emotional responses without experiencing conscious emotions at all. Unfortunately, we cannot know for sure whether and which other species have conscious experiences, and this question is a separate one that is beyond the scope of this article. However, if they do, then measurable behavioural, physiological and neural responses might be useful proxy indicators of these emotional experiences. Traditionally, much research on animal emotion has measured these responses to assess how animals react to situations designed to induce specific emotional states. This approach has viewed emotions as discrete entities (e.g. 'fear') that arise in response to specific stimuli, and reflect the coordinated activity of 'emotional systems' (e.g. the 'fear system') rooted in the circuitry of particular brain areas, and serving specific adaptive functions. The control, and behavioural and physiological expression, of certain discrete emotions, notably 'fear' and 'anxiety', has been comprehensively studied in animals by neuroscientists such as Panksepp [16] and LeDoux [10].

While this *discrete emotions* approach has greatly advanced our understanding of specific emotional states, it has inevitably been piecemeal. Positive emotions in particular have been less well studied. Furthermore, the study of discrete emotions does not provide an over-arching framework, or 'structure' of emotion, that allows the relationships between different affective states to be conceptualised, and that can provide *a priori* predictions, with cross-species applicability, for how these states are manifested and hence how they can be measured. *Dimensional theories of emotion*, which have become prominent in the field of human psychology, offer a potential framework that can address some of these issues, and we believe that they can complement the discrete emotions approach and further our understanding of animal emotions. Dimensional approaches, based on analysis of reports of subjective emotional experiences in people, conceptualise emotional states as lying in two or three-dimensional space. All such models suggest that a critical, and defining, dimension of emotion is 'valence' (whether the emotion is positive or negative). The influential 'core affect' model of Russell [18] and colleagues suggests that the other major dimension is 'arousal' (how activated the individual is). Discrete emotions can thus be represented in this two dimensional model according to their arousal and valence, as shown in figure 1. For example, 'excitement' or 'happiness' are positive states of high arousal, while 'relaxed' is a low arousal positive state.

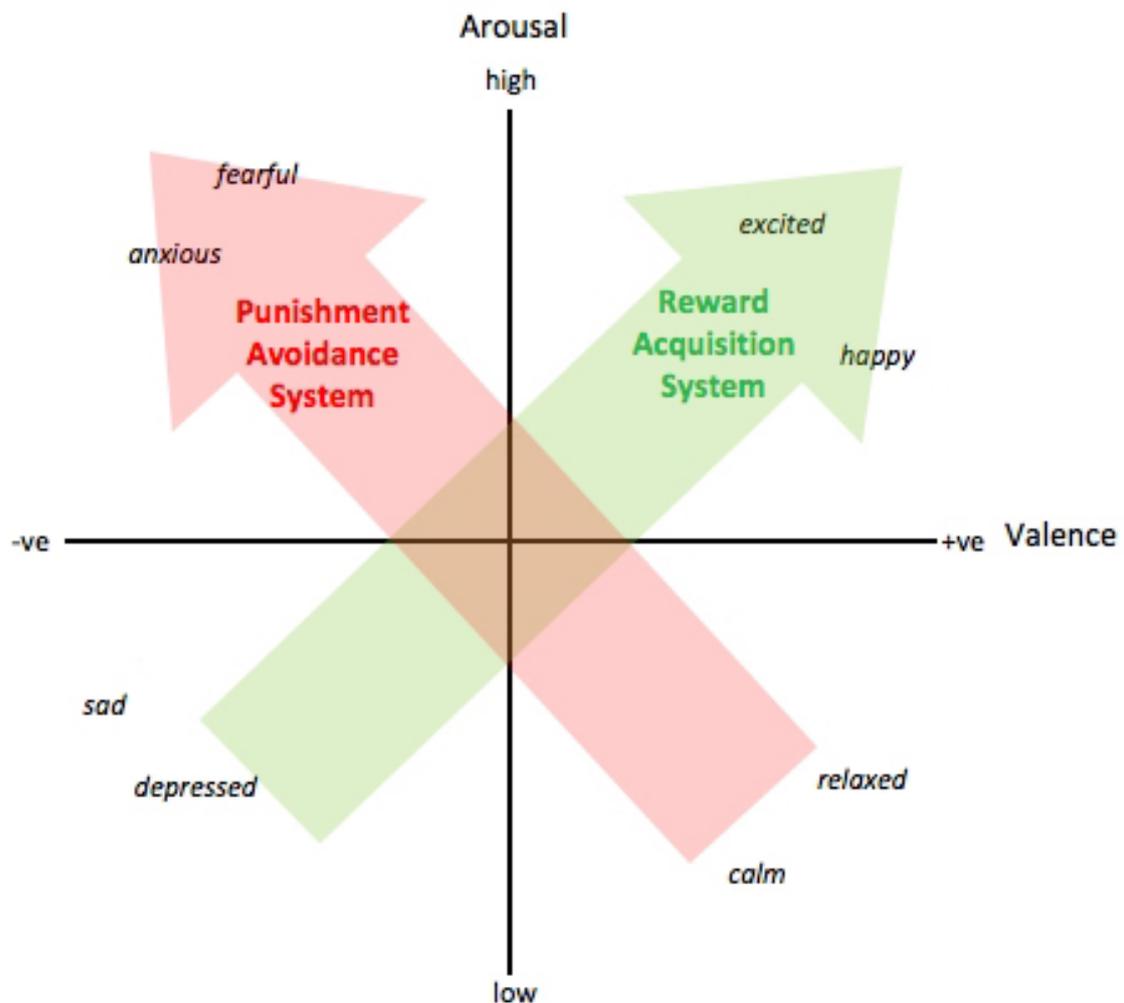


Figure 1. Core affect dimensional model of emotional states. Words in italics indicate the possible locations in core affect space of discrete emotions. Arrows indicate how the activation of putative fundamental neurobiological systems controlling reward acquisition and punishment avoidance may map on to emotional states. Adapted from reference [14].

Research by psychologists and neuroscientists suggest that the activity of two types of core neurobiological systems may map on to this two-dimensional space as shown in figure 1. These systems are concerned with two fundamentally and evolutionary ancient survival functions – the acquisition of fitness-enhancing ‘rewards’ (i.e. resources important for survival such as food, mates etc.) and the avoidance or minimisation of fitness-threatening ‘punishers’ (i.e. predators, competitors). Activation or deactivation of the reward acquisition system may correspond with high arousal positive states (e.g. in the presence of reward) and low arousal negative states (e.g. in the absence of reward) respectively. The mesolimbic dopaminergic system may be an important component of such a system. Activation and deactivation of the punishment avoidance system may correspond with high arousal negative states (e.g. in the presence of a predator) and low arousal positive states (e.g. in the absence of threats), respectively. Circuits in the peri-aqueductal gray, amygdala, anterior cingulate and other brain regions may be important components of this system.

This core affect dimensional model of emotion allows us to integrate discrete emotions into a ‘higher order’ overall emotional structure. Following appraisal theorists such as Scherer [19], we suggest that anticipation of rewarding and punishing events, occurring through appraisal of events, generates short-term discrete emotions that likely function as rapid behavioural and physiological responses designed to maximise survival chances. Each discrete emotion is located in core affect space according to its arousal and valence properties. As argued by Cabanac [5] and others, we suggest that location in core affect space may act as a common currency allowing comparisons between different discrete emotions when behavioural decisions need to be made. We further propose that, over time, an organism’s location in core affect space will change according to its motivations and emotions which, in turn, are determined largely by its environmental circumstances, and also by any predisposition to respond to these circumstances in a particular way. Thus, an animal in an environment full of threatening events will tend to inhabit the top left corner of core affect space (i.e. high arousal negative states such as ‘fear’ and ‘anxiety’). A stress-susceptible individual may inhabit a more extreme top-left hand location than one that has a more relaxed personality.

We hypothesise that longer-term ‘mood’ – affective states that, unlike short-term emotions, are not tied to a specific event but are ‘free-floating’ – result from cumulative experience of an animal’s location in core affect space. We can liken them to a ‘running’ mean of positions occupied in core affect space. For example, an individual in a plentiful environment with few predators will tend to have a mood state whose valence and arousal properties are located in the right half of core affect space. We suggest that an important function of these mood states is to provide information about the type of environment that the organism is living in – the probability of threats and opportunities – and how well it is coping, and that this information is used to inform appropriate decisions in novel and ambiguous situations. For example, an individual in an environment where it has experienced high levels of threat will have a mood state in the top left corner of core affect space (e.g. an anxious mood) and is likely to benefit from avoiding an ambiguous stimulus such as a rustle in the grass which could well indicate a predator, in comparison to an individual in a safe environment with a mood state in the bottom right hand corner for whom a negative judgement of the stimulus is likely to result in wasted time and energy. Similarly, individuals in plentiful environments with mood states in the top right hand corner will benefit from a more ‘optimistic’ response, exploring the source of the rustle for potential prey, relative to individuals with mood states in the bottom left corner (e.g. a depressed mood) who may benefit more from conserving energy until circumstances change, as suggested by Nesse [15]. In a sense, therefore, mood state can thus be conceptualised as reflecting past experiences and, thereby, the possible future probabilities of outcomes of decisions in particular situations. Bayesian decision-making theory suggests that optimal decisions result if animals take this distribution of probabilities into account when making decisions and update it according to the new information acquired. If so, mood state may act as a proxy ‘Bayesian prior’ that summarises past experience and likely future probability of outcomes and thus guides decisions. By influencing appraisals of events, mood states also influence the resulting emotional responses, emphasising the bi-directional relationship between short-term discrete emotions and longer-term moods.

By bringing discrete and dimensional approaches to the study of animal emotion together, we believe that the framework allows us to see how discrete emotions are structured relative to each other, and how short-term emotions and long-term moods are related. The framework also recognises the role of positive emotions, which have previously received limited attention in animal studies, and emphasises that affective states are strongly influenced by the organism’s environment and its experiences. Finally, and importantly, we believe that the framework suggests new ways of assessing animal emotion and mood. Based on our hypothesis that mood states can guide decision-making in ambiguous circumstances, we suggest that animals in a positively valenced mood are likely to interpret ambiguous stimuli positively (make ‘optimistic’ judgements), while those in a negatively valenced mood will show more ‘pessimistic’ judgements. Furthermore, those whose mood is, for example, in the top-left hand corner of core affect space will be particularly likely to show increased expectation of punishing events, while those in the bottom-left corner will specifically show decreased anticipation of rewarding events. Both are forms of ‘pessimism’, but subtly different.

Studies of humans are in line with these predictions. Many studies show that people in depressed or anxious moods have more negative expectations about the future and are more likely to make negative judgements about ambiguous stimuli [17]. There are even data to suggest that subtly different forms of pessimism occur as our model predicts; anxious people (equivalent to a top-left corner mood state) are indeed more likely to expect negative events while depressed people (bottom left corner mood state) are less likely to expect positive events. Recently, we have developed a way of assessing ‘optimistic’ and ‘pessimistic’ decision-making in animals. Our ‘judgement bias’ task, developed initially in studies of rats [9], involves training animals to perform a particular response (e.g. press left lever) when presented with a particular stimulus (e.g. tone A) to obtain a positive outcome (e.g. food), and to perform a different response (e.g. press right lever) when presented with a different stimulus (e.g. tone C) to avoid a relatively negative outcome (e.g. no food). Once trained, we then present the animal with ambiguous intermediate stimuli (e.g. tone B) and hypothesise that, for example, animals in a more positive state will tend to judge these stimuli positively, or ‘optimistically’, in this case by pressing the left lever to indicate they are anticipating a good outcome.

Results from a variety of species, including rats [3] [4] [8] [9], dogs [12], sheep [6] [7], starlings [1] [2] [11], and others [see 13] appear to support our hypothesis, suggesting that ‘optimistic’ and ‘pessimistic’ decision making may be useful new indicators of animal emotion and welfare. Because decision-making of this sort can be measured objectively, this allows us to use decision-making in response to ambiguity as an indirect, but objectively measurable, indicator of the more elusive emotional states that influence it. An important point here is to clarify what is meant by ‘optimistic’ or ‘pessimistic’ decision-making. In our studies animals show ‘optimistic’ decisions in the sense that they make choices which indicate that they are expecting the better of two outcomes in an ambiguous situation. However, this is not to imply that they have conscious optimistic thoughts like humans. As mentioned earlier, we cannot know for sure what they are thinking. In humans at least, research shows that optimistic or pessimistic decisions are useful indicators of an individual’s emotional state and, if the species we are studying is capable of conscious emotional experience, our conclusion would be that an ‘optimistic’ animal is likely to be in a more positive mood than a ‘pessimistic’

one.

In summary, we believe the framework proposed in our paper [14] provides a useful way of conceptualising animal emotion that also has implications for the measurement of this elusive but very important aspect of the life of other animals.

## References

1. Bateson, M., Matheson, S.M. 2007. Performance on a categorisation task suggests that removal of environmental enrichment induces 'pessimism' in captive European starlings (*Sturnus vulgaris*). *Anim. Welfare* 16, 33-36.
2. Brilot, B.O., Asher, L., Bateson, M. 2010. Stereotyping starlings are more 'pessimistic'. *Anim. Cogn.* 13, 721-731.
3. Burman, O.H.P., Parker, R., Paul, E.S., Mendl, M. 2008. A spatial judgment task to determine background emotional state in laboratory rats, *Rattus norvegicus*. *Anim. Behav.* 76, 801-809.
4. Burman, O.H.P., Parker, R.M.A., Paul, E.S., Mendl, M. 2009. [Anxiety induced cognitive bias in non-human animals](#). *Physiol. Behav.* 98, 345-350.
5. Cabanac, M. 1992. [Pleasure – the common currency](#). *J. Theoret. Biol.* 155, 173-200.
6. Doyle, R.E., Fisher, A.D., Hinch, G.N., Boissy, A., Lee, C. 2010. Release from restraint generates a positive judgement bias in sheep. *Appl. Anim. Behav. Sci.* 122, 28-34.
7. Doyle, R.E., Hinch, G.N., Fisher, A.D., Boissy, A., Henshall, J.M., Lee, C. 2010, in press. Administration of serotonin inhibitor p-Chlorophenylalanine induces pessimistic-like judgement bias in sheep. *Psychoneuroendocrinology*.
8. Enkel, T., Gholizadeh, D., von Bohlen und Halbach, O., Sanchis-Segura, C., Hurlemann, R., Spanagel, R., Gass, P., Vollmayr, B. 2010. [Ambiguous-cue interpretation is biased under stress and depression-like states in rats](#). *Neuropsychopharmacology* 35, 1008-1015
9. Harding, E. J., Paul, E. S., Mendl, M. 2004. [Animal behavior - Cognitive bias and affective state](#). *Nature* 427, 312-312.
10. LeDoux, J. 1996. *The Emotional Brain*. New York, NY: Simon and Schuster.
11. Matheson, S. M., Asher, L., Bateson, M. 2008. Larger, enriched cages are associated with 'optimistic' response biases in captive European starlings (*Sturnus vulgaris*). *Appl. Anim. Behav. Sci.* 109, 374-383.
12. Mendl, M, Brooks, J, Basse, C, Burman, O, Paul, E, Blackwell, E., Casey, R. 2010. [Dogs showing separation-related behaviour exhibit a 'pessimistic' cognitive bias](#). *Curr. Biol.* 20, R839-R840.
13. Mendl, M., Burman, O. H. P., Parker, R. M. A., Paul, E. S. 2009. Cognitive bias as an indicator of animal emotion and welfare: Emerging evidence and underlying mechanisms. *Appl. Anim. Behav. Sci.* 118, 161-181.
14. Mendl, M., Burman, O.H.P., Paul, E.S. 2010. [An integrative and functional framework for the study of animal emotion and mood](#). *Proc. Roy. Soc. B.* 277, 2895-2904.
15. Nesse, R.M. 2000. Is depression an adaptation? *Arch. Gen. Psychiat.* 57, 14-20.
16. Panksepp, J. 1998. *Affective Neuroscience. The Foundations of Human and Animal Emotion*. New York: Oxford University Press.
17. Paul, E. S., Harding, E. J., Mendl, M. 2005. [Measuring emotional processes in animals: the utility of a cognitive approach](#). *Neurosci. Biobehav. Rev.* 29, 469-491.
18. Russell, J. A. 2003. [Core affect and the psychological construction of emotion](#). *Psychol. Rev.* 110, 145-172.
19. Scherer, K.R. 2001. Appraisal considered as a process of multi-level sequential checking. In: K.R. Scherer, A. Schorr, T. Johnstone, (Eds), *Appraisal Process in Emotion: Theory, Methods, Research*, pp.92-120. Oxford: Oxford University Press.