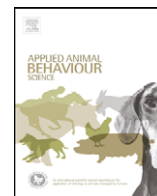




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Cognitive bias as an indicator of animal emotion and welfare: Emerging evidence and underlying mechanisms[☆]

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ABSTRACT

Accurate assessment of animal emotion (affect) is an important goal in animal welfare science, and in areas such as neuroscience and psychopharmacology. Direct measures of conscious emotion are not available, so assessment of animal affect has relied on measures of the behavioural and physiological components of affective states. These are important indicators but have some limitations (e.g. measuring emotional arousal rather than valence (positivity vs negativity)). Human psychology research suggests that changes in cognitive function (information processing) can also be reliable indicators of emotional state (especially valence). For example, people in negative states attend to threats, retrieve negative memories, and make negative judgements about ambiguous stimuli more than happier people. Here we review a new research area investigating the possibility that such affect-induced 'cognitive biases' also occur in animals. We focus on a novel 'judgement bias' paradigm in which animals are trained that one cue predicts a positive event and another cue predicts a less positive/negative event, and are then presented with ambiguous (intermediate) cues. The hypothesis is that animals in a negative affective state will be more likely to respond to ('judge') these ambiguous cues as if they predict the negative event (a 'pessimistic' response), than animals in a more positive state. Recent studies of rats, dogs, rhesus monkeys, starlings and humans provide face-value support for this hypothesis. We discuss the strengths and weaknesses of the affect manipulation treatments used in these studies, and the possibility that treatment-induced changes in feeding motivation, general activity and learning are responsible for the effects observed, and we consider whether the type of bias observed and the precise design of the judgement bias task can provide information about different types of affective state. Judgement biases may result from the influence of affect on decision-making processes including attention to and perception of the ambiguous cue, evaluation of the value and probability (expected utility) of the outcomes of different responses, and action selection. Affect might also modulate general tendencies of loss, risk and ambiguity aversion, hence biasing decisions. We discuss these possibilities in relation to theory and findings from neurobiological and psychological studies of decision-making, in order to better understand the potential mechanisms underlying judgement biases. We conclude with some specific recommendations for study design and interpretation, and suggestions for future research in this area.

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1. Introduction

Concerns for animal welfare are generally based on the assumption that non-human animals can subjectively experience emotional (affective) states and hence can

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suffer or experience pleasure (Dawkins, 1990; Mendl, 2001; Mendl and Paul, 2004; Boissy et al., 2007). Recent political and legal statements echo the basis of these concerns. For example, European legislation aims 'to ensure improved protection and respect for the welfare of animals as *sentient beings*' (italics added; European Union, 1997. Treaty of Amsterdam, Protocol on Protection and Welfare of Animals (p. 110)), and the Australian government's strategy for animal welfare covers the care and use of 'all sentient species in Australia', where a sentient animal is defined as 'one that has the capacity to have feelings and to experience suffering and pleasure' (Australian Government, 2008. Australian Animal Welfare Strategy (p. 7)). Although direct measurement of subjective emotional experiences is not currently possible (for a different view, see Wemelsfelder, 1997), the development of accurate proxy measures is therefore an important goal in animal welfare science, as well as in other disciplines such as neuroscience and psychopharmacology (Panksepp, 1998; Mendl and Paul, 2004; Rolls, 2005; Lawrence, 2008).

Most emotion researchers consider that emotions arise in situations that are 'important' to the organism, in the sense that they may influence its survival and reproductive success. The primary function of emotions in these contexts is widely hypothesised to be to guide the animal's behavioural decisions in order to achieve survival goals – the attainment of valuable resources/rewards, and the avoidance of harm/punishment – perhaps by providing a 'common currency' that the animal uses to determine which behaviour or sequence of behaviours is most likely to enhance survival (e.g. Ortony et al., 1988; Cabanac, 1992; Oatley and Jenkins, 1996; Cardinal et al., 2002; Rolls, 2005).

In order to study emotional states scientifically, the development of accurate measures is an essential first step. The measurement of subjective experience in non-human species is fraught with difficulty, and debates continue as to whether and which non-human animals (hereafter 'animals') have the capacity for such experience (e.g. Carruthers, 1989; Kennedy, 1992; Griffin, 1992, 1998; Macphail, 1998; Baars, 2001; Bermond, 2001; Panksepp, 2005). However, emotional states are recognised by human psychologists as being multifaceted and comprising other 'components' in addition to subjective experience, namely behavioural and physiological changes (e.g. Plutchik, 1980; Ekman, 1984; Scherer, 1984; Frijda, 1988; Smith and Lazarus, 1993; Clore and Ortony, 2000; Lerner and Keltner, 2000). For example, the emotion of fear includes the subjective experience of fear, but also the expression of freezing or fleeing behaviour, and alterations in physiology such as changes in heart rate, blood pressure, and circulating glucocorticoids. In humans, linguistic report can be used as a measure of a person's subjective emotional experience that is likely to be as reliable an indicator as any (though not infallible), but this is clearly not possible in animals. Instead, behavioural and physiological indicators form the basis for nearly all current indicators of animal emotional states (e.g. approach/avoidance behaviour; vocalizations; play behaviour; behavioural tests such as open field, elevated plus maze

(EPM), light–dark box test, sucrose consumption, forced swim; indicators of hypothalamic–pituitary adrenal (HPA) and sympathetic–adrenomedullary (SAM) activity; other endocrine indicators such as oxytocin; see Paul et al., 2005).

These indicators offer a great deal of information. However, they are not free from problems of interpretation (Paul et al., 2005). Some may be good measures of emotional arousal (intensity, or how 'activated' the animal is), but less good measures of emotional valence (whether the emotional state is positive or negative; see Watson et al., 1988; Russell, 2003). For example, HPA and SAM activity may increase in a range of situations including those that are likely to have quite different emotional valence (e.g. meeting a predator vs meeting a sexual partner) or which may be affectively neutral (e.g. increased locomotor activity) (Rushen, 1986, 1991; Baldock et al., 1988; Marchant et al., 1995). From an animal welfare perspective these are significant problems because, although the arousal and intensity of emotional states are important to know about, whether these states are positive or negative for the animal (valence) is the critical measure.

A related issue is that many measures lack *a priori* hypotheses for how they should change according to the animal's emotional state (specifically, its valence). This can make interpretation of tests, and translating them from one species to another, difficult. For example, does a decreased latency to stop swimming in the forced swim test reflect a state of depression or despair, or does it represent an adaptive coping response (Cryan and Mombereau, 2004)? What are the predictions for tests designed to measure anxiety-related 'wall-hugging' thigmotaxis (e.g. open field test, EPM) or preference for dark areas (e.g. EPM, light–dark box test) when adapted for use in a diurnal species with low fear of light or open spaces (cf. Janczak et al., 2002)?

Other limitations include few measures of *positive* affective states, despite these being of increasing interest in animal welfare research (Boissy et al., 2007; Yeates and Main, 2008), and the finding that, in humans, linguistic report of subjective emotion may dissociate from other indicators of emotional state. For example, some people report no change in subjective emotional experience while exhibiting clear physiological indicators of an emotional response, while others report emotional experiences in the absence of the expected physiological changes (e.g. Patrick et al., 1993; Stone and Nielson, 2001). While such dissociations provide valuable information about the relationships between components of emotion, they also raise uncertainty as to the extent to which existing behavioural and physiological indicators map on to the subjective emotional states which lie at the heart of animal welfare concerns.

Given the above issues (described in more detail by Paul et al., 2005), there is clearly room for the development of new methods for assessing animal emotion. One major growth area is the study of neural correlates of emotional responses both in humans (primarily using functional magnetic resonance imaging) and animals (using a range of techniques including single-cell recording, lesioning

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