



Review

Measuring emotional processes in animals: the utility of a cognitive approach

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Abstract

Contemporary researchers regard emotional states as multifaceted, comprising physiological, behavioural, cognitive and subjective components. Subjective, conscious experience of emotion can be inferred from linguistic report in humans, but is inaccessible to direct measurement in non-human animals. However, measurement of other components of emotion is possible, and a variety of methods exist for monitoring emotional processes in animals by measuring behavioural and physiological changes. These are important tools, but they have limitations including difficulties of interpretation and the likelihood that many may be sensitive indicators of emotional arousal but not valence—pleasantness/unpleasantness. Cognitive components of emotion are a largely unexplored source of information about animal emotions, despite the fact that cognition–emotion links have been extensively researched in human cognitive science indicating that cognitive processes—appraisals of stimuli, events and situations—play an important role in the generation of emotional states, and that emotional states influence cognitive functioning by inducing attentional, memory and judgement biases. Building on this research, it is possible to design non-linguistic cognitive measures of animal emotion that may be especially informative in offering new methods for assessing emotional valence (positive as well as negative), discriminating same-valenced emotion of different types, identifying phenotypes with a cognitive predisposition to develop affective disorders, and perhaps shedding light on the issue of conscious emotional experiences in animals.

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1. Introduction

When people experience a change in their emotional state or mood, there are concomitant changes in the way they think about the world (Bower, 1981; Mathews and MacLeod, 1985; Mellers et al., 1999). These cognitive changes occur in relation to emotions triggered briefly and discretely by known objects, and in relation to ongoing moods and longer-term emotional states associated with clinical affective disorders (Nygren et al., 1996; Mathews et al., 1996). They have been demonstrated in numerous tasks involving attention, perception, memory, expectations and risk assessment (Mathews and MacLeod, 1994; Mineka et al., 1998; Schwarz, 2000; Lerner and Keltner, 2000). Such tasks have been proposed as tools for assessing emotions and emotional reactions, particularly for people who might be unwilling or unable to give accurate self-report of the way they feel (Mayer and Bremer, 1985; Kuykendall et al., 1988; Parrott and Hertel, 1999). The purpose of this paper is to go one step further than this, and to review the potential value of using cognitive changes to assess emotion and mood states in non-human animals (hereafter, animals). We argue that theory and findings from this area of human psychology and cognitive science will help progress research on animal emotion, and that investigation of the role played by cognition in the generation and expression of emotional states in animals is critical to further development of our understanding of the processes and functions of affective systems in animals.

First, we consider definitions of the terms ‘emotion’ and ‘cognition’. We then briefly summarise methods by which animals’ affective states are currently measured, and their limitations. We then present an overview of the cognition–emotion associations that occur in humans, and discuss theoretical accounts of these associations. Following this, we describe studies that have investigated cognition–emotion associations in animals, and show how theory and data from

human research can provide a framework for generating novel non-linguistic techniques for measuring animal emotion. In concluding, we consider what cognitive methods for assessing animal affect might tell us about conscious emotion in animals.

1.1. Definitions

In this paper, we use broad definitions of both emotion and cognition, while acknowledging that some of the researchers whose work we discuss may use these terms in more specific ways. We follow Shettleworth’s (1998) comprehensive definition of cognition as referring to ‘the mechanisms by which animals acquire, process, store and act on information from the environment’. This definition can incorporate many different types of information processing, ranging from sensory perception and mechanisms of associative learning through to conscious, rational, linguistically based thought processes.

Emotions refer to processes which are likely to have evolved from basic mechanisms that gave animals the ability to avoid harm/punishment and seek valuable resources/reward (Panksepp, 1994; Rolls, 1999; Cardinal et al., 2002). For example, Rolls (1999) proposes that emotions are ‘states elicited by rewards and punishers, including changes in rewards and punishments’. Emotions include adaptive behavioural, physiological and neural processes and, in humans at least, they include a conscious subjective component—the *feeling* of the emotion (but see Zajonc (1994) and Winkelman and Berridge (2004)). Many scientists appear to be uncomfortable about using the term emotion when referring to animals, for fear that they automatically imply anthropomorphic assumptions of human-like subjective experience. Indeed, some psychologists maintain that the word emotion is best restricted to those states that clearly *do* include subjective feelings (Clore et al., 1994). To sidestep this issue, expressions like

‘emotional processes’ are used as code for the ‘not necessarily conscious emotion’ that occurs in animals (LeDoux, 1996). We too use this expression, but we also use the term emotion with the proviso that its use does not necessarily imply accompanying conscious, subjective states (Hinde, 1985; Berridge, 2003). Whenever we consider the conscious experience of emotion, we mention this explicitly.

‘Affect’ is another term commonly used by emotion researchers. Some (Clore et al., 1994; Berridge, 2003) regard affect as essentially involving the psychological qualities of pleasantness or unpleasantness (i.e. valence). However, we use the term here to refer to behavioural and physiological responses (and in conscious beings, feelings) that can vary both in terms of valence (pleasantness/unpleasantness) and also intensity (arousing or activating qualities). Indeed, valence and intensity/arousal can be considered to be the core features of affective and emotional processes.

The terms affect and emotion are often used interchangeably, and we will use them in this way. However, they are sometimes given specific and distinct meanings. In human research, affective states in their pure form can be viewed as largely equivalent to ‘free-floating’ mood states (Watson et al., 1988; Russell, 2003). On the other hand, emotion in its strictest sense refers to affective states that are *attached in some way* to an object. Thus, emotions are likely to involve a greater degree of information processing (e.g. appraisal of the object) than pure affective or mood states, and may also incorporate actions or ‘action tendencies’ (Frijda, 1986; Öhman et al., 2000) towards the object concerned (e.g. in anger, the tendency to hit). When we want to make a distinction between free-floating affect or mood, and object-focused emotions, we will make this clear in the text.

1.2. A componential view of emotion

As should be clear from the above, human emotional processes and their outcomes are now generally regarded as multifaceted, comprising physiological, behavioural and subjective components (Lerner and Keltner, 2000; Frijda, 1986, 1988; Izard, 1977; Plutchik, 1980; Tomkins, 1980; Ekman, 1984; Scherer, 1984; McNaughton, 1989; Smith and Lazarus, 1993; Lang, 1993; Bradley and Lang, 2000; Clore and Ortony, 2000). For example, fear may involve not only a subjective feeling of dread or terror, but also increased heart rate, sweaty palms, a facial grimace and an increased tendency to run away. Although these different components usually act in concert, they are potentially dissociable, not always operating as a functional whole (Meadows and Kaplan, 1994; Reisenzein, 2000). Emotional processes can thus be viewed as adaptive events or states that are likely to occur across the animal kingdom, but that may or may not have subjective components, depending on the species and circumstances involved (LeDoux, 1994, 1996).

Such an outlook renders the non-conscious processes involved in emotional functioning open to empirical investigation, even in animals for whom conscious emotional experiences cannot be proven to occur (LeDoux, 1996), and allows independent investigation of the different facets of an emotional event (LeDoux, 1996; Tooby and Cosmides, 1990; Levenson, 1994; Öhman, 1999).

This componential view of emotion also identifies a cognitive component—changes in *information processing* that occur in conjunction with changes in affect—to be an integral part of the emotional process (Clore and Ortony, 2000). This is in line with predominantly human-based cognitive theories of emotion, and with the ever increasing body of evidence linking biases in cognitive processing with affective state (Mathews and MacLeod, 1994; Mineka et al., 1998; Schwarz, 2000). But the blurring of boundaries between cognitive and affective processes remains controversial. Some take the view that emotional processes cannot occur independently of cognitive processes arguing that, for example, the mere act of identifying a stimulus is a cognitive process which must occur before an emotional response can be made (Forgas, 2000), or that cognitive evaluations of stimuli are always involved in emotions (Lazarus, 1999). Others argue that cognitive and emotional processes are essentially distinct, both conceptually and neurobiologically. Panksepp (2003), for example, strongly supports the traditional delineation of cognitive and affective processes in humans and animals alike. Although conceding that cognition and affect are often inextricably linked in normal humans, he regards the two systems as ultimately independent: functionally, anatomically, pharmacologically and phylogenetically. In particular, he regards the affect system as essentially subcortical, visceral and embodied. The cognitive system, although often working in concert with affect, he views as essentially cortical, evolutionarily more recent, and likely to show more variation across (e.g. mammalian) species. Zajonc (1980, 2000) asserts a similar position with respect to humans, arguing that affective states can be induced with no cognitive involvement whatsoever (‘preferences without inferences’; see also Russell (2003)).

We agree that subcortical systems are central to the generation and expression of emotion and affect, but we also agree that in humans at least, cortical, cognitive processes are often intimately involved in the production and output of affective and emotional states. It is therefore of interest and importance to investigate whether and to what degree such processes are also involved in the affective states of animals. The extent to which our advocacy of research into cognition–emotion links in animals may be taken to support one or other position is unintentional. We merely propose that such links are of both practical and theoretical interest, and may in due course offer emotion researchers an extra dimension to the cognition–affect debate.

2. The measurement of emotional processes in animals

Measurement of the emotional or affective state of an animal is of interest to researchers in a number of fields, including affective neuroscience, psychopharmacology, evolutionary zoology, comparative psychology and animal welfare science. Although the ultimate goals of these disciplines are different, the challenge of reliably establishing the on-going affective state or emotional reaction of an animal to a stimulus or situation, is essentially the same. The problem is simple. Humans, on the whole, can verbally report how they feel, and this is generally accepted as the ‘gold standard’ indicator of their current subjective emotional state. Animals, however, are unable to provide this information. Indeed, we cannot be sure whether non-human animals actually *feel* anything at all (Dawkins, 1993; Macphail, 1998). Nevertheless, functional, behavioural, anatomical and physiological continuities between humans and many non-human animals are considerable, allowing exploration of affective states in animals regardless of whether or not, and in what way, they may be consciously experienced.

A wide variety of methods have been employed in attempts to measure the affective states of animals. Although affective research of one kind or another has been conducted on a number of different species, work in this area has focused predominantly on the measurement of mammalian affect (Haug and Whalen, 1999). For the purposes of this review, therefore, we will restrict our consideration to the measurement of emotional or affective states in mammals. It is also worth pointing out that, apart from some notable exceptions (Carter, 2001; Knutson et al., 2002), the majority of research into emotion measurement in animals has focused on negative states, particularly fear, anxiety, and ‘stress’. As a result, our review will also predominantly consider the assessment of these negative processes.

LeDoux (1996) suggests that, ultimately, the best objective way to reliably and accurately measure someone’s current emotional state will be to look directly at the processes going on in the brain. The study of the neurobiological substrates of animal affect is a burgeoning area (Rolls, 1999; LeDoux, 1996; Panksepp, 1998; Gray and McNaughton, 2003; Berridge, 1996; Bechara et al., 2000). There is a wealth of knowledge about the actions of certain parts of the brain such as the amygdala, thalamus, ventral tegmental area, ventral pallidum, nucleus accumbens, anterior cingulate cortex, peri-aqueductal grey, hippocampus, and pre-frontal cortex in affective processing (Rolls, 1999; Cardinal et al., 2002; LeDoux, 1996; Berridge, 1996, 2003; Panksepp, 1998; Gray and McNaughton, 2003; Bechara et al., 2000; Phillips et al., 2003; Davis and Whalen, 2001). Techniques such as lesioning, electrical stimulation, single cell recording and microdialysis are helping to establish the neurobiological mechanisms and systems that underlie emotional processes. It is quite possible that LeDoux’s

vision of looking directly at brain processes to assess emotion will become a reality in the future, and PET and fMRI scanning procedures are beginning to make it possible now, particularly in studies of humans but also in studies of non-human primates (Andersen et al., 2002; Takamatsu et al., 2003). Furthermore, indirect measures of asymmetries in brain activity during emotional processing, partially supporting the theory that the right hemisphere is dominant in this activity, are also being used in animals (e.g. visual field bias (Casperd and Dunbar, 1996); asymmetries in tympanic membrane temperature (Parr and Hopkins, 2000)). However, the practical assessment of ongoing emotion or mood states in animals, whether in the laboratory or in more naturalistic conditions, continues to rely on a catalogue of more ‘remote’ measures, often used in concert with one another. These measures are primarily of the behavioural and physiological components of emotion.

2.1. Physiological measures of affective state

Physiological measures of emotion often correspond to those commonly used in the study of stress. The term stress is used in different ways by different researchers, and there is no widely accepted definition (for detailed discussion see Kopin (1995), Toates (1995), McEwen (2001) and Moberg (2000)). Broadly speaking, it refers to a state that is induced by a challenge to homeostasis and the organism’s ability to survive and reproduce, the challenge coming from a ‘stressor’ (Moberg, 2000; Ramos and Mormède, 1998). However, this is too inclusive for some, and definitions incorporate stipulations about the duration of homeostatic perturbation, the physiological systems involved in the response to the stressor, whether the state is necessarily aversive or can actually be pleasant, and so on (Toates, 1995).

Although the focus and interests of stress researchers have tended to be somewhat different from those of emotion researchers, there is clearly considerable overlap between the two topics, primarily because the study of stress is generally viewed as the study of responses to situations that are likely to be aversive in some way and hence to evoke negative affective states. Stressful situations or protocols are used as models for affective disorders such as depression (Koolhaas et al., 1997; Willner, 1997a; Irwin, 2001), and researchers often use affective terms such as ‘anxiety’ or ‘frustration’ to label the emotional states that might be associated with measured behavioural or physiological stress responses (Ramos and Mormède, 1998; Elder and Menzel, 2001). Conversely, researchers who are primarily interested in emotional processes often use changes in stress physiology as indicators of emotional states. This overlap is most evident in the study of fear and anxiety where the neurophysiological substrates of these emotional states—the amygdala and associated systems—have clear effects on the classical stress neuroendocrine systems; the hypothalamic-pituitary-adrenal (HPA) and sympathetic-adrenal-medullary (SAM) systems

(LeDoux, 1996; Bradley and Lang, 2000; Gray and McNaughton, 2003; Davis and Whalen, 2001; Boissy, 1995). Because much animal emotion research has focused on these types of affective state, it follows that the physiological indicators used to measure animal emotion will usually include those employed by stress researchers.

These physiological measures include measures of HPA function (e.g. levels of ACTH, glucocorticoids, response to dexamethasone, ACTH, and CRH challenge tests), changes in sympathetic and autonomic function such as alterations in heart rate, blood pressure, catecholamine levels, skin conductance and skin temperature, and other measures of neuroendocrine activity, including levels of circulating oxytocin, vasopressin, prolactin, and opioid peptides (Bradley and Lang, 2000; Carter, 2001; Davis and Whalen, 2001; Boissy, 1995; Süer et al., 1998; Aureli et al., 1999; Parr, 2001; Blanchard et al., 1998; Landgraf and Wigger, 2002; Bradshaw et al., 1996). Other physiological correlates of reported affect in humans such as activity of facial muscles (e.g. corrugator and zygomatic (Bradley and Lang, 2000)) could also be of use in animals if related facial expressions can be identified (Berridge and Robinson, 2003).

The use of physiological measurements as indicators of affect in animals requires that certain methodological issues are adequately addressed. For example, the time course of physiological responses in relation to a trigger event, and the effects of individual and diurnal variations in baseline levels must be accounted for (Schrader and Ladewig, 1999; von Borell and Ladewig, 1992; Ruis et al., 1997). Likewise, the possibility that sampling methods themselves (e.g. blood collection) may provoke confounding emotional reactions also has to be guarded against (Broom and Johnson, 1993). More importantly, interpretation of physiological measures in terms of emotional state is not always straightforward. Situations likely to induce *different* affective states may give rise to the *same* physiological responses. For example, cortisol levels may rise in both fear inducing situations and in response to sexual activity, and also in apparently affectively neutral situations such as during elevated activity (Toates, 1995; Broom and Johnson, 1993; Rushen, 1986, 1991; Dawkins, 2001). Similarly, increases in heart rate may reflect activity, as well as anticipation of both punishing and rewarding stimuli (Marchant et al., 1995; Baldock and Sibly, 1990; Baldock et al., 1988), and physiological changes may correlate poorly with how strongly an animal avoids an aversive stimulus (Dawkins, 2001; Rushen, 1996). It is likely that at least some and perhaps many physiological indicators primarily reflect arousal (or intensity of affective stimulation) and so, on their own, offer limited precision in differentiating between highly arousing but differently valenced states such as fear and sexual attraction. Measures of multiple physiological indicators coupled with observations of behaviour may help aid interpretation of the animal's affective state (Broom and Johnson, 1993).

Most physiological measures tend to be interpreted as measuring negative rather than positive affect, although there are some exceptions (e.g. changes in oxytocin levels and their relationship to positive social experiences and decreased reactivity to stressful situations (Carter, 2001)). Thus, current physiological indicators offer limited opportunities for the assessment of positive affect. Furthermore, in humans, some individuals showing physiological emotional responses are apparently unaware of (fail to report) any accompanying change in subjective emotional state (Lane et al., 1997; Stone and Nielson, 2001), indicating dissociations between the gold standard of verbal report and established measures of physiology.

2.2. Behavioural measures of affective state

Measurements of spontaneously occurring behaviour can be used to assess the functionally relevant action tendencies (Frijda, 1986) that accompany particular emotional states. Thus, at the simplest level, approach and avoidance behaviour may be used to gauge the general valence (pleasantness/unpleasantness) of a stimulus to an animal, while freezing, attacking, exploratory and consumptive behaviours may indicate the presence of more specific, object-directed emotions. Other relevant forms of spontaneous behaviour include vocal or facial expressions. Facial expressions, particularly in response to pleasant and unpleasant taste stimuli, have been shown to be homologous in a variety of mammalian species, including humans, chimpanzees, and even mice and rats (Berridge, 1996; Berridge and Robinson, 2003). In cattle, eye white exposure may act as an indicator of frustration mediated via sympathetic control of eyelid opening (Sandem et al., 2002). Vocal expression of apparently valenced affective states has also been identified in species such as rats, pigs and cattle (Knutson et al., 2002; Weary and Fraser, 1997; Watts and Stookey, 2000; Blumberg and Sokoloff, 2001; Panksepp and Burgdorf, 2003; Manteuffel et al., 2004; Zimmerman and Koene, 1998; Zimmerman et al., 2000), and it has been suggested that affect intensity is reflected in the calls of some primates (Rendall, 2003).

Often, the affective significance of a behaviour is determined by the observer's evaluation of the context in which it occurs. Thus, behaviour occurring in response to thwarting of motivation to feed or drink may be interpreted as indicating frustration (Sandem et al., 2002; Zimmerman and Koene, 1998; Zimmerman et al., 2000; Bokkers et al., 2004; Haskell et al., 2001). Play behaviour tends to occur in situations where the animal's other requirements are satisfied (Martin and Caro, 1985; Fraser and Duncan, 1998; Spinka et al., 2001), and appears ebullient and energetic hence prompting suggestions that it is an indicator of positive affect (Fraser and Duncan, 1998; Spinka et al., 2001). Behaviours which occur consistently in a variety of contexts that appear to have the same affective valence, and which do not appear in oppositely valenced situations are

likely to be more reliable indicators. Nevertheless, interpretation of spontaneous behaviour in affective terms is not straightforward. Approach behaviour may be directed towards threatening and dangerous things such as competing conspecifics and predators (Humphrey and Kemble, 1974; Humphrey, 1972; Krams and Krama, 2002; Fitzgibbon, 1994; Walling et al., 2004) as well as valued and positively reinforcing stimuli (Tanimoto et al., 2004). Vocal and facial expressions have probably evolved to have communicative functions, and may be strongly influenced by the presence of an ‘audience’ and hence not necessarily bear a direct, one-to-one correspondence with an actual affective state, but rather with the need to communicate an affective state (Kraut and Johnson, 1979; Marler and Evans, 1996; Zimmerman et al., 2003).

Alongside measures of spontaneous behaviour, behavioural tests are commonly used in the study of animal emotion, especially in the fields of psychopharmacology and neuroscience. These serve to standardise observational and stimulus techniques, and enable a degree of test validation (e.g. testing effects of well-established anxiolytics and anxiogenics on behaviour in novel anxiety tests) and comparison across different test populations. They include tests of unconditioned responses such as the open field, elevated plus maze, hole board, black and white box, and social interaction test (Ramos and Mormède, 1998; Landgraf and Wigger, 2002; File, 1996; Rodgers, 1997; Hendrie et al., 1996), the vast majority of which are designed to measure negatively valenced states, particularly anxiety and fear. While the reliability and validity of these tests is strengthened by pharmacological and cross-test ‘validation’, there are still problems of interpretation that have been discussed at length by many others (Ramos and Mormède, 1998; File, 1996; Rodgers, 1997; Hendrie et al., 1996; Archer, 1973; Walsh and Cummins, 1976). For example, does activity in the open field reflect escape or exploratory motivation and hence different associated affective states (Archer, 1973)? Is behaviour following a test or a particular treatment more informative than that occurring during it? Hendrie et al. (1996) suggest that behaviour following encounters with predator stimuli may be a better indicator of anxiety states than behaviour occurring during encounters which may more accurately reflect a state of ‘panic’. Species and strain differences also influence interpretation. For example, avoidance of open arms in the elevated plus maze may more closely reflect anxiety in some species than others (Janczak et al., 2002). Strain, conditions at the time of testing, and the laboratory environment may also have a strong influence on the behaviour shown in the test (Crabbe et al., 1999; Hogg, 1996).

A number of tasks have been developed that allow animals to indicate their affective or emotional state in the form of an unconditioned or learnt response to a specific stimulus. For example, affective startle potentiation represents a dramatic, automatic modulation of a defensive

reflex, in which an animal’s normal tendency to interrupt behaviour with a jump or jolt in response to a sudden stimulation (e.g. burst of loud noise), is enhanced in the context of an already negative affective state (Lang et al., 2000). The particular usefulness of this lies in the fact that in humans it is closely associated with subjective reports of both the valence of an ongoing affective state, and its arousing qualities (Cook et al., 1992; Cuthbert et al., 1996). In addition, startle responses may also be attenuated in individuals experiencing positive affect (Koch, 1999). It therefore has the potential to be a valuable indicator of individual variation in affective responsiveness and affective state. However, it is not yet used for the practical measurement of animals’ affective states as frequently as the more traditional behavioural tests outlined above.

Learnt responses can indicate animals’ affective reactions by demonstrating whether a particular stimulus acts as a positive or negative reinforcer (e.g. conditioned place preference, conditioned suppression (Rolls, 1999; Cardinal et al., 2002; Dantzer and Baldwin, 1974)). These tests primarily indicate the affective value of the stimulus to the animal. In experimental psychology and animal welfare research, related tests of preference for, or avoidance of, stimuli have been used to investigate how highly animals value resources (e.g. flooring, nesting substrates (Blom et al., 1996; Sherwin and Glen, 2003; Phillips et al., 2000)). These have been further developed to incorporate measures of how hard animals will work to get at or avoid resources, borrowing theory from the microeconomics of human consumer demand (Lea, 1978; Dawkins, 1990; Sherwin and Nicol, 1997; Mason et al., 1998; Houston, 1997; Kirkden et al., 2003). Their use has been particularly influential in animal welfare research, in which establishing the affective value of behavioural and resource requirements of animals is paramount (Dawkins, 1990). However, even here, interpretations are not always straightforward. For example, behavioural expressions of ‘wanting’ and ‘liking’ may well be controlled by separate neural systems (Berridge, 1996; Berridge and Robinson, 2003). Therefore, how hard an animal works to access a resource (wanting) need not reflect the core positive affect (liking) it experiences when accessing the resource. Similarly, as mentioned earlier, animals may be motivated to gain access to potentially dangerous, as well as rewarding, stimuli.

Finally, a number of animal models of affect and affective disorder have been developed in which exposure to environmental conditions is designed to induce a certain state. These are often concerned with depression-like states and include exposure to chronic mild stress, social defeat, forced swim, conflict situations, and inescapable aversive stimuli (Koolhaas et al., 1997; Willner, 1997a; Maier and Seligman, 1976; Millan and Brocco, 2003; Cryan and Mombereau, 2004). In some of these paradigms, specific behavioural tests are used to assess the state induced. For example, sucrose consumption is used as a measure of anhedonia—a common correlate of human depression.

The persistence or disappearance of conditioned place preferences is also studied in this context (Willner, 1997a; Papp et al., 1991). Again, problems with validity, reliability, and interpretation exist and have been discussed at length by others. These include the extent to which the techniques really do induce the putative affective state (Deakin, 1997), and how to interpret behaviour observed in associated tests. For example, cessation of swimming behaviour in the forced swim test has been interpreted as indicating a state of depression or despair, and also an adaptive change in the animal's behaviour that helps it to cope successfully with the situation (see Cryan and Mombereau (2004)). The usefulness of consumption of sucrose as an indicator of an anhedonic depressed state in the chronic mild stress paradigm has been hotly debated (Willner, 1997a,b; Reid et al., 1997; Moreau, 1997; Hagan and Hatcher, 1997).

In conclusion, the many and varied methods available to researchers wishing to assess animals' affective or emotional states and reactions to stimuli can, when taken together, offer a great deal of information. Nevertheless, there are often limitations to the interpretations that can be made on the basis of any one measure. As a result, judgements concerning possible affective states are greatly strengthened if based on more than one measurement technique. Any inconsistencies that occur between data obtained by different methods, or when using the same methods with different species or individual animals, may also offer important information concerning the variety of potentially dissociable systems that contribute to affective reactions.

Overall, the measurement of affective state in animals is a large and expanding part of modern biological and biomedical science, and of importance in fields as diverse as the development of new psychoactive drugs, the characterisation of novel genetic strains of mice, and the assessment of animal welfare. Many techniques are available, primarily based on measurement of behavioural and physiological components of affect, but all have limitations. Our purpose in the rest of this paper is to highlight the additional role that can be played by information gleaned from human studies of the interactions between affective and cognitive processes. Based on these studies, new methods for measuring affective states in animals, which directly consider the cognitive component of emotional processes, can be developed. Such methods, we propose, will offer practical new means for assessing animal emotion, and also contribute significantly to our understanding of the functionally interlocking processes of affect and information processing that have emerged in the course of evolution.

3. Cognitive components of emotional processing in humans

Cognitive processes can be regarded as 'components' of human emotion states or events, both in the form of

appraisals which can trigger the occurrence of particular emotions, and cognitive *outputs* which can result from emotional states. To effectively interpret findings regarding emotion–cognition links in animals, and to drive further research in this area, attention must be paid to the processes by which affective states and cognitive processes interact. Human-based research in this area offers a starting point from which to undertake such investigations.

There is ample evidence to show that links between emotion and cognition, in humans at least, occur in both causal directions, with cognitive manipulations influencing felt affect (Mathews and MacLeod, 2002) and affective manipulations influencing cognitive processing (Hinde, 1985; Forgas, 2000). In fact, psychological theorists in this field have followed largely independent courses, depending on the particular body of data they are seeking to explain. Those studying cognitive biases in the context of experimentally induced emotion have developed theories to account for the ways in which an emotion can give rise to particular cognitions and processing styles (Bower, 1981; Schwarz and Clore, 1983). Those studying clinically or temperamentally anxious or depressed populations have concentrated on the processes by which cognitions and cognitive biases (e.g. appraisal tendencies) influence the occurrence and perpetuation of pathological emotions (Mathews and MacLeod, 2002; Beck et al., 1979).

3.1. Cognitive appraisals and emotion

Researchers interested in the processes by which emotions arise from cognitions have tended to focus on the role of appraisals (Frijda, 1986; Scherer, 1984; Oatley and Johnson-Laird, 1987; Ortony et al., 1988; Lazarus, 1991). Appraisals are essentially the assessments that an individual makes about the relevance of a stimulus (object, event, situation, etc.) to him or herself at a particular point in time (Scherer, 1984; Oatley and Johnson-Laird, 1987; Lazarus, 1966, 1991; Arnold, 1960; Roseman, 1984; Smith and Ellsworth, 1985). Unlike sensory experiences, emotional experiences do not represent physical features of the world, and there are no sensory receptors for emotional value (Clore and Ortony, 2000). So 'appraisals' of some kind need to be made in order to assign emotional meaning or value to stimuli, making use of relevant and available information to determine the appropriate response: for example, to approach or to flee, to feel pleasure or fear.

The issue of whether or not all appraisal processes can be regarded as strictly 'cognitive' is a controversial one (Forgas, 2000; Lazarus, 1999; Panksepp, 2003; Zajonc, 1980, 2000; Lane et al., 2000), although this depends in large part on the definition employed for the term cognition. The origins of some 'complex' emotions, such as regret or guilt, clearly appear to depend on high-level cognitive (probably conscious) reflections regarding, for example, explicit memories and self-concepts (Johnson-Laird and Oatley, 1989; Smith and Kirby, 2000). Such emotions are

not only determined by appraisal cognitions, they are defined by them and, presumably, would not exist (in that form) without them. Evidently, these complex cognition–emotion interactions which rely on high level conceptual and linguistic processing are of limited relevance to animal emotion research. But this does not mean that some kind of appraisal process does not play a critical role in the generation of emotional responses in many non-human species. In humans, some stimuli appear to elicit affective responses almost automatically, and others require only minimal exposure to elicit a response (e.g. a subliminally presented photograph of a snake or spider will elicit a fear response in phobic individuals—(Öhman and Soares, 1993)). Thus, simple basic emotions, such as fear, can be triggered extremely rapidly, on the basis of limited perceptual information, prior to, and even without, any conscious recognition of the emotion-provoking stimulus taking place (LeDoux, 1996; Öhman and Soares, 1993; Gray, 1999). Such processes are still regarded by many as a form of cognitive appraisal (but see Zajonc (1980, 2000) who disagrees), but are nevertheless very different from the conscious thought processes that are by necessity concerned with more complex emotions. The generation of basic emotions such as fear in animals might rely on similar non-conscious appraisal processes.

However, appraisal theorists propose that emotions usually arise, not just as a result of direct effects of perceptual information (e.g. see snake—feel fear), but also according to an evaluation of what a piece of perceptual information means to that organism at that moment in time. Thus, a range of cognitive dimensions, determined during the appraisal process, differentiates emotional experiences beyond mere valence (positivity vs. negativity) (Lerner and Keltner, 2000). For example, Scherer (1984) postulates that human emotions are determined on the basis of a series of five stimulus evaluation checks for: novelty, intrinsic pleasantness, goal need/significance, coping potential, and norm/self-compatibility. Smith and Ellsworth (1985) propose certainty, pleasantness, attentional activity, control, anticipated effort and responsibility. Rolls (1999) puts forward a similar classification scheme based on reward and punishment contingencies, which applies to both human and non-human animals. Within this, different emotions arise depending on the reinforcement contingency, and whether the reinforcer is positive or negative. Thus, emotions associated with the presentation of a negative reinforcer include apprehension, fear and terror; those associated with the omission or termination of a positive reinforcer include frustration, anger and rage (Millenson, 1967; Gray, 1975).

Other appraisal theorists propose much more complex lists of stimulus checks occurring in the appraisal process. In fact, it is likely that there are multiple levels of appraisal processing, ranging from rapid evaluations (e.g. of angry faces or dangerous animals), which are immediately relevant to approach or avoidance and take place even prior to conscious perception, to subtle and complex

evaluations (e.g. of interpersonal communications) which are slower and probably take place with conscious involvement (Öhman and Soares, 1993; Leventhal and Scherer, 1987; Morris et al., 1999). At whatever level, however, there exists the possibility for existing cognitive biases to influence these appraisal processes and thus influence the type and strength of emotion that occurs.

Beck's Schema Theory proposes that affective disorders such as depression can be initiated and perpetuated by the inappropriate processing of incoming, affectively relevant information (Beck et al., 1961, 1979; Beck, 1967). According to this view, vulnerability to emotional disorders is characterised by pathological 'schemata', cognitive structures not dissimilar to appraisal tendencies, which influence a person's perceptions, interpretations and memories (Kovacs and Beck, 1978). For depression the predominant schemata are thought to involve negative views of the self, the world and the future. For anxiety disorders, the principle schemata are proposed to be to do with vulnerability and danger. Williams et al. (1997) have suggested that, in such vulnerable individuals, stressful life events are more likely to trigger a 'vigilant' processing mode, in which attention is captured (and held more tenaciously) by relatively mild threatening cues. Consequently, these individuals will be exposed to a stream of information about possible dangers, leading to increased anxiety. In less vulnerable people, the same event may be insufficient to trigger a shift from the default 'avoidant' mode, in which threatening information is largely ignored. Mathews and McLeod (2002) tested this hypothesis by inducing attentional and interpretative biases experimentally, without directly affecting anxiety levels. These biases did not induce mood changes by themselves, but did cause changes in reported anxiety state by influencing how novel, emotionally significant information was encoded. These findings are concordant with the notion that cognitive biases influence or change emotional responses, by altering the processing (appraisal) of affective information.

Clearly, the ways in which animals appraise, evaluate and weight the significance of incoming information are likely to affect their emotional responses. Furthermore, any bias in these cognitive evaluative processes will affect how strongly and in what direction such effects occur. Appraisal theory frameworks could be used as a starting point for developing methods to differentiate emotional states in animals according to the profile of stimulus checks that they carry out (Dantzer, 2002; Desiré et al., 2002a; see below). Research into appraisal mechanisms may therefore further enhance our understanding of animal emotions, and our ability to measure them.

3.2. Cognitive outputs and emotion: cognitive bias

Cognitive outputs of emotion are the numerous information processing changes or biases that are observed amongst humans in whom particular emotions or moods

have been induced or reported (Mathews and MacLeod, 1994; Mineka et al., 1998). People in such studies are either clinically diagnosed with an affective disorder (e.g. depression), known to score high or low on a particular affective trait (e.g. trait anxiety), or have an emotion induced experimentally for the purposes of the experiment (e.g. fear, happiness, sadness). The former, clinical group is particularly interesting because their subjective emotions are likely to be powerful and thus to be most strongly associated with measurable cognitive biases or variations. However, one complication is that such biases may result directly from the personalities of the individuals concerned (e.g. depression-prone cognitive style (Beck, 1967; Gotlib and Krasnoperova, 1998)), rather than being associated directly and causally with the predominant emotions themselves. Studies that experimentally manipulate mood are the most amenable to control and therefore offer the best chance of identifying mechanisms involved in emotion-induced cognitive biases. But they too have their problems in that the emotions or moods induced are sometimes weak and short lived and so any measured effects can be subtle and mild. Notwithstanding these problems, a wide variety of cognitive biases associated with emotion have been found using each of these different subject groups. These can be grouped roughly into three main categories: attention biases, memory biases and judgement biases.

3.2.1. Attention biases

The primary functions of fear and anxiety are to avoid danger and protect the body from harm (Lang et al., 2000), so we would expect anxious or fearful cognitive biases to relate particularly to perceptual vigilance. Numerous experimental studies have shown that this is indeed the case: anxious people are particularly prone to bias their attention towards threatening information (for reviews, see Mathews and MacLeod (1994), Mogg and Bradley (1998) and Kindt and van den Hout (2001)). A variety of cognitive tasks have been employed to detect these emotion-related attention biases in humans. The two most widely used are visual dot probe tasks (MacLeod et al., 1986) and modified Stroop colour naming tasks (Mathews and MacLeod, 1985). In the former, participants are briefly presented with two words on a screen, followed by a dot probe appearing in the location of one of the preceding words. Anxious participants are usually faster than non-anxious subjects at detecting dot probes which replace threat words rather than neutral words, consistent with an attentional bias occurring towards threatening information (MacLeod et al., 1986; Mogg et al., 1992; Keogh et al., 2001).

In the modified Stroop colour naming task, words are presented in different colours, and participants are required to name the colour but ignore the meaning of the word. Patients with generalized anxiety disorder (GAD) have been found to be slower at naming the colour of threatening words compared to neutral words, suggesting that a greater degree of processing is being applied to these words, thus

interfering with the colour naming task (Mathews and MacLeod, 1985; Mogg et al., 1989). Further research using the Stroop and dot probe tasks has shown that anxious individuals show a processing bias for threat stimuli even when their awareness of these stimuli is restricted by the use of brief (e.g. 14 ms) masked visual displays (Mathews et al., 1996; Mogg et al., 1993, 1994, 1995; Bradley et al., 1995; MacLeod and Rutherford, 1992; MacLeod and Hagan, 1992). On the basis of such findings, it has been concluded that anxiety is particularly associated with shifts in attention towards threat, and that this shift often occurs as a result of automatic attentional capture arising from pre-conscious processing (Williams et al., 1997; Bradley et al., 1997).

3.2.2. Memory biases

The literature concerning associations between emotions and memory spans a wide range of methodological approaches and topics of interest (e.g. autobiographical memories, 'flashbulb' memories, implicit and explicit memories), and demonstrates strong links between a variety of emotions and the storage, consolidation and retrieval of memories (Christianson, 1992; Cahill and McGaugh, 1996, 1998; Reisberg and Heuer, 1995; Hamann et al., 1999; Uccros, 1989). There is considerable evidence that events which induce positive or negative emotions are more readily remembered than those which are emotionally neutral. Variation in the amount of attention paid to the original event, and in consolidation of the event memory, are probably the prime sources of this bias (Cahill and McGaugh, 1996, 1998; Reisberg and Heuer, 1995; Christianson et al., 1991; Cahill et al., 1994). Extreme examples of this are 'flashbulb' memories, which are particularly vivid recollections of the circumstances in which participants were first informed of traumatic events (e.g. the assassination of President Kennedy (Brown and Kuluk, 1977)), and whose formation appears to be facilitated by the intensity of participants' personal affective responses (Conway et al., 1994). Although it was originally thought this flashbulb effect enhanced memory for many unrelated details surrounding the emotion-inducing news, it now seems that only memory of centrally important details are in fact improved (Reisberg and Heuer, 1995). This is consistent with the finding that, compared with memories for emotionally neutral stimuli, the central features of traumatic stimuli are more accurately recalled, whereas peripheral details are more poorly recalled (Clifford and Hollin, 1981; Christianson and Loftus, 1990).

Although the majority of this type of research concerns emotional *material* giving rise to processing biases, it may also have relevance to processing biases caused by emotionally aroused *individuals* dealing with emotion-neutral material. Such individuals are likely to be experiencing elevated activation of the HPA and SAM systems, and it is known that these systems play an important role in memory modulation, both in humans and other animals. For example, moderate elevations in the activity of HPA

and SAM systems enhance consolidation and storage of information in long-term memory, while very high or low levels of HPA or SAM activity have detrimental effects on memory formation (Davis and Whalen, 2001; Cahill and McGaugh, 1996, 1998; Hamann et al., 1999; Cahill et al., 1994; McEwen and Sapolsky, 1995; Erickson et al., 2003; Gold, 1992, 1995; Lupien and McEwan, 1997; de Kloet et al., 1999; Nielson et al., 1996; van Stegeren et al., 1998; de Quervain et al., 2000; Mendl, 1999; Mendl et al., 2001). The role of the amygdala in facilitating storage of emotional memories has also been established in humans and animals (Hamann et al., 1999, 2002; Gallagher and Chiba, 1996; Adolphs, 1999; Ferry et al., 1999; Roozendaal et al., 1999). These findings indicate that individuals in different states of emotional and associated physiological arousal are likely to encode information in memory in different ways.

Of special relevance to this paper is the finding that negative affective states are associated with a heightened ability to retrieve information about negative events—a form of *mood congruent* memory (Bower, 1981; Beck, 1967; Gotlib and Krasnoperova, 1998). From a functional perspective, sadness and depression can be thought of as states that involve the need to revise an expectation or plan that has failed (Williams et al., 1997). So we would expect sadness or depression-related cognitions to be particularly concerned with the processing of memories, especially those related to events of failure or loss. This is borne out by findings that, in contrast to the pattern seen in emotion-related attention, there is more evidence demonstrating an association between depression and memory than between anxiety and memory (Mathews and MacLeod, 1994; Mineka et al., 1998). For example, both depressed and anxious individuals have been shown to have an elevated tendency to report negative autobiographical memories (Clark and Teasdale, 1982; Burke and Mathews, 1992). But depressed participants have also been shown to be better at recalling emotionally negative stimuli within word lists (Denny and Hunt, 1992; Watkins et al., 1992), while anxious patients do not seem to show this tendency (Mathews and MacLeod, 1994).

3.2.3. Judgement biases

Research into the effects of emotions on judgement making in humans has focused on a number of areas, including interpretations of ambiguous stimuli, expectations about the future, and risk-taking (Nygren et al., 1996; Mathews et al., 1989; Loewenstein et al., 2001). As complex, multi-layered processes, judgements may be affected by emotions in a number of ways. For example, emotion effects may act directly on the judgement or risk assessment process itself, or indirectly, through biases in the attention and memory processes that pertain to it (Segerstrom, 2001).

Anxious individuals tend to bias their interpretations of ambiguous stimuli. A sentence such as ‘The doctor examined little Emma’s growth’ is more likely to be

interpreted positively by individuals with low trait anxiety, and negatively by high trait-anxious individuals (Eysenck et al., 1991). Similarly, clinically anxious patients are more likely to offer threatening spellings of homophones (e.g. die/dye, guilt/gilt, pain/pane) than non-anxious individuals (Mathews et al., 1989). Subjective probability assessments also appear to be affected by current emotional state. That is, people in happy moods tend to overestimate the likelihood of positive outcomes and events, and underestimate the likelihood of negative ones (Nygren et al., 1996; Wright and Bower, 1992). Individuals in sad moods show the reverse pattern (Wright and Bower, 1992; Johnson and Tversky, 1983).

MacLeod and Byrne (1996) investigated the positive and negative expectations of anxious, mixed anxious-depressed and control individuals. Participants were given one minute to think of as many future positive experiences as possible, and another minute to think of as many future negative experiences as possible. Anxious and anxious/depressed participants generated more negative future experiences than controls. In a similar study, a non-clinical sample of undergraduates, varying in levels of self-reported depression (measured by the Beck Depression Inventory (Beck et al., 1961)), were presented with a target individual on a computer screen and required to give yes/no responses to the possibility of good or bad future events occurring to them (Andersen et al., 1992). Compared to their non-depressed peers, depressed students demonstrated significantly more predictions of negative events occurring. Using a more abstract test of subjective probabilities, Nygren et al. (1996) asked participants to guess their chances of winning a betting game. Those who had had their mood elevated by receiving a bag of sweets at the outset of the experiment were more optimistic about their chances of winning.

3.2.4. Theoretical perspectives on the effect of emotions on cognitions

The possible mechanisms by which cognitive outputs of emotion arise have been addressed by a number of theorists. We consider them here because they provide frameworks for interpreting emotion–cognition links in animals. The affect priming theories of Bower (Bower, 1981, 1991; Forgas and Bower, 1988; Bower and Forgas, 2000) and Isen (Isen, 1984, 1987; Clark and Isen, 1982) consider memory and judgement biases in particular, proposing that they result from emotions directly facilitating attentional access to appropriate, mood-related cognitions. Essentially, this approach hails from semantic network theory, in which associated memories are thought to be made preferentially available through a process of ‘spreading activation’ (Anderson and Bower, 1973). Each distinct emotion is proposed to have a specific ‘node’ or unit in memory that collects together the numerous memories (semantic and episodic) that are connected to it by associative pathways (Bower, 1981). Thus, when feeling sad, one is more likely to remember sad events and to think about issues that have

unhappy implications. Distributed network theory is an alternative to semantic network theory that could also be applied to cognition–emotion links (Plaut and Booth, 2000). This proposes that each item in memory is represented by a diffuse network of activation unique to itself. Different items have different networks of activation, but those that are more closely associated have more overlapping networks. Therefore, activation of one item will increase the likelihood of other items also becoming activated if they share a high percentage of network.

Despite being highly influential within clinical psychology research, associative network theories of emotion–cognition links are essentially descriptive rather than explanatory (Williams et al., 1997), and do not demonstrate *how* the cognitive, subjective, behavioural and physiological components of emotion relate to one another, beyond the proposition that many of these associations are likely to occur at automatic, non-conscious levels of processing.

An alternative view is taken by the ‘affect-as-information’ hypothesis (Schwarz and Clore, 1983, 1988, 1996; Wyer and Srull, 1989; Clore and Parrott, 1991; Clore, 1992). This regards the subjective component of emotion as being directly involved in the production of cognitive outputs of emotion (see also the ‘affect infusion model’ (Bower and Forgas, 2000; Forgas, 1992, 1995; Forgas and Bower, 1987), ‘risk as feelings’ (Loewenstein et al., 2001), and the ‘somatic marker hypothesis’ (Damasio, 1994) for similar views). The particular empirical focus of these models has been the role of emotion in the making of judgements, such as preference assessments or decisions regarding risk. Rather than making a judgement simply on the basis of recalled features of a target, it is proposed that individuals effectively ask themselves ‘how do I feel about it?’ The subjective experience of felt emotion is thereby the intermediary through which emotional states are thought to influence judgements or decisions. Evidence in support of this comes from findings that people in a variety of experimental settings mistake covertly induced or unattributed emotional feelings as direct reactions to target stimuli, and make inappropriate judgements or decisions accordingly. For example, Schwarz and Clore (1983) found that, when interviewed over the telephone on a pleasant, sunny day, subjects made more positive evaluations of their happiness and life satisfaction than did subjects who were interviewed on a rainy, overcast day. However, when their attention was directed to the probable source of their mood (the weather) by a prior question about it, weather/mood effects on life satisfaction evaluations disappeared. If it *is* the subjective component of emotion that mediates this sort of effect, the exact process by which this is done remains unclear. Subjective emotions and cognitions would need to be brought together in attention (presumably with working memory involvement) in order to do this, and such a view implies that subjective emotions would have to occur, even in animals, in order for cognitive biases to take place.

A challenge to the affect infusion model comes from the ‘affective primacy hypothesis’ of Zajonc (1980, 1984, 1994) and Winkielman et al. (1997). This proposes that, when eliciting stimuli are presented at the pre-conscious level (i.e. masked, subliminal presentations of affective words or pictures), affective biases and preferences can be induced, even when there has not been enough processing time to elicit identifiable, subjective feelings. Winkielman et al. (1997) showed that, after viewing 10 ms presentations of smiling faces, participants rated neutral Chinese ideographs more positively than they did after viewing frowning faces, neutral polygons or blank slides. But self-reports revealed that these participants were not consciously aware of any feeling reactions to the primes or the targets. This experiment appears to demonstrate that subliminal priming can produce affective reactions that are not represented as subjective feeling states, a direct contradiction of the affect infusion model. This does not exclude the affect infusion model’s prediction that many judgements are still made on the basis of subjective emotional assessments (how do I feel about it?) when target stimuli are presented supraliminally, but Winkielman et al.’s findings (1997) suggest that it may also be possible for emotional biases in judgements to be made without reference to subjective emotion (see also Berridge and Winkielman (2003)).

In conclusion, emotional modulation of cognitive processes appears to have adaptive value by helping, for example, a fearful or anxious individual to attend to, memorise and make judgements about threatening circumstances or stimuli. There is no reason to suppose that such effects are restricted to humans. On the contrary, it is easy to envisage the value that such processes could have for most animal species, and the selective pressures favouring their evolution. Indeed, emotional arousal effects on memory acquisition and consolidation appear to be similar in both humans and other animals, and to have the same underlying neural and neuroendocrine mechanisms, indicating a degree of phylogenetic continuity in these processes at least. Data from human studies indicate that some emotional modulation of judgements may rely on conscious experience of affect, though other studies indicate that at least some effects can occur without conscious involvement. If conscious involvement is necessary in humans, as some theorists argue, this raises the intriguing possibility that any similar processes in animals may also rely on some form of conscious experience of affect. Further research into cognition–emotion links thus represents an avenue for increasing our understanding of affective processes in animals, and for developing new indicators of affective state such as cognitive bias in attention, memory or judgement. A major challenge in following this route will be to develop relevant non-linguistic tasks, as the majority of methods used to study these issues in humans depend on the use of language. In the following section, we consider how the findings and theory discussed here can be applied to

the study of animal emotion, and how non-linguistic tasks can be designed to ask relevant questions.

4. Measuring the cognitive component of emotion in animals

As we outlined earlier, a wide variety of physiological and behavioural measures are currently used to indicate the emotional or affective states experienced by animals, though all have their limitations. Cognitive components of emotion are a relatively unexplored potential additional source of information about animal emotions (Toates, 1995; Mendl and Paul, 2004). Most of the cognitive outputs of emotion that have been studied experimentally in humans involve language-based tasks. However, many are not necessarily dependent on language, and could, with appropriate modifications, be studied in animals. Investigating the types of appraisal processes that animals go through in generating emotions may also offer important insights into the nature of animal affect (Dantzer, 2002; Desiré et al., 2002a). Below, we detail a number of ways in which measurement and manipulation of cognitive processes in animals may provide new information about animal emotion.

4.1. Appraisal processes in animals

Appraisal theories of emotion generation have been developed almost exclusively within the human context, with most research being conducted using linguistic reports of people's experiences of emotions and their antecedents (Scherer, 1999). But this does not mean that the stimulus checks thought to give rise to particular, discrete emotions in humans do not also occur in animals (see Rolls (1999)). Leventhal and Scherer (1987) proposed that appraisal processing takes place at three different levels—the sensorimotor (automatic triggering of reactions to adaptively significant stimuli), the schematic (automatic triggering of learned reactions to previously encountered stimuli) and the conceptual (non-automatic, consciously processed reactions). Dantzer (2002) and Desiré et al. (2002a) suggest that at least the first two of these, the sensorimotor and the schematic levels of appraisal processing, are also likely to occur in non-human animals. They also suggest that a significant number of the stimulus checks or criteria proposed by appraisal theorists such as Scherer (2001) are likely to be utilized by animals in the generation of emotions. Examples of these include suddenness, familiarity, predictability, intrinsic pleasantness, discrepancy from expectation and capacity for control. By investigating how far animals can distinguish between and respond to these different factors, the range of emotions that such species are likely to 'undergo' may be estimated (Dantzer, 2002; Veissier et al., 2002). Moreover, by presenting animals with situations for which the likely appraisal

checks have been experimentally manipulated, and at the same time monitoring their physiology and behaviour, direct relationships between presumed appraisals and measurable emotional outcomes can be established. Using such an approach, Desiré et al. (2002b) have recently demonstrated that lambs produce differential emotional responses to suddenness and novelty.

This approach has clear advantages over interpretations of physiological and behavioural measures based simply on how a person might feel in a similar situation. It also offers a framework for assessing subtle emotional differences that may occur between animals in objectively similar situations. For example, as noted by Dantzer (2002), a sow should not feel 'frustrated' at the absence of nesting material if she has never had the opportunity to experience relevant substrates. She may experience agitation and negative affect, because of an unfulfilled motivation to nest build, but without the stimulus check for 'discrepancy from expectation', an actual emotion akin to what people call frustration should not arise. Such a hypothesis could be tested experimentally by comparing animals that have and have not had the opportunity to develop an 'expectation' about appropriate nesting substrates. Of interest would be whether 'frustrated' and 'agitated' sows actually show different physiological and behavioural expressions of their state.

Studies such as these, in which objectively determined or experimentally manipulated appraisal criteria are matched with resultant physiological and behavioural responses, should offer insights into the emotions that particular animals undergo in particular situations, the profile of behavioural and physiological changes that can be used to identify them, and the range of emotions that different species are capable of overall. They will also offer the opportunity to investigate whether individual variation in appraisal tendencies ('Schema' (Beck et al., 1979; Beck, 1967)), and hence predispositions to particular interpretive biases that may render animals more or less vulnerable to affective disorders similar to depression, exist in animals as well as humans.

4.2. Attention biases in animals

Increased tendencies to respond defensively to sudden novel stimulation can, in general terms, be interpreted as emotional modulation of attention. Affective potentiation of the startle response is an example of this. Humans and many other species demonstrate a rapid, protective, interruption response when exposed to a sudden stimulus such as a loud noise. This response, often measured as an eye blink in humans, and whole body 'jumps' in rodents, tends to occur faster, and has greater magnitude, during negative affective states (Lang et al., 1998). The emotional potentiation of the startle response has been investigated extensively in recent years and is of particular interest to animal emotion measurement given its ubiquity across

humans and non-human species. However, it is arguable whether the relatively primitive startle reflex (Bradley and Lang, 2000; Lang et al., 1998) should be classified as a *cognitive* process and hence an indicator of cognitive bias. More relevant may be changes in active searching for threats as occurs during directed attention/orienting and vigilance behaviours.

In animal research, vigilance has usually been measured in terms of general alertness and scanning behaviour. In field studies, levels of vigilance behaviour—visual scanning—appear to increase in threatening circumstances (e.g. as distance to safe cover increases, or when near to a feature that obstructs the view of potential threats (Lazarus and Symonds, 1992)), and decrease in situations where threat is lower (e.g. in large groups where predation danger may be diluted or detected early (Elgar, 1989; Quenette, 1990) but see Treves (2000)). Consequently, vigilance may be a useful indicator of anxiety or fear states. For example, elevated ‘head-up’ time and pronounced opening of the eyes—presumably to enable better vision—have been observed in domestic cattle exposed to threatening or frustrating situations, and may be a useful measure of negative affective states (Sandem et al., 2002; Welp et al., 2004).

Neural processes underlying enhanced vigilance and attention during fear inducing situations may involve the amygdala and associated structures. There is growing evidence that the amygdala plays an important role in attentional processes, perhaps by lowering neuronal thresholds in sensory systems, and by influencing orienting behaviour, particularly to stimuli which have acquired affective value (Davis and Whalen, 2001; Holland and Gallagher, 1999). However, it is becoming clear that these effects are not just restricted to negative affective states, but also include situations in which the stimuli to be attended to are positively valenced (Hamann et al., 1999, 2002; Holland and Gallagher, 1999), and may even occur in ‘emotionally neutral’ contexts or when stimuli are emotionally ambiguous (Davis and Whalen, 2001; Hamann et al., 2002). At a behavioural level, it is also evident that enhanced vigilance behaviour can occur outside fear-inducing predator detection situations, and may conceivably include vigilance for positive stimuli such as potential mates or food sources. In primate species in particular, the targets of vigilance may be especially diverse (Treves, 2000). Therefore, an increase in vigilance per se may be of limited value in indicating the valence of the subject’s affective state, but rather reflect general levels of arousal.

In human research on cognitive bias, vigilance is usually studied in terms of directed attention towards specific threat stimuli (e.g. valenced words), rather than general levels of undirected alertness and scanning behaviour. For example, subjects experiencing negative affect are more likely to attend to negative or threatening stimuli. These findings can be used as a basis for developing new methods to probe the valence of emotional states in animals. The majority of experimental research in humans has used linguistic stimuli

such as neutral and threat related words and is therefore not directly applicable to animal research. However, modified, non-linguistic methods could be designed and, in some human studies, pictorial stimuli have been used (Yiend and Mathews, 2001; Mogg et al., 2000; Ioannou et al., 2004). For visually oriented species, picture stimuli, representing appetitive resources or threatening objects (e.g. predators), could be presented to animals pre-trained to respond rapidly to dots (or other shapes) occurring on a display screen. It would then be possible to observe whether animals in (environmentally or pharmacologically) induced negative affective states are, like anxious humans, more likely to detect the dot when it is presented in the same location as a threatening stimulus. The same procedure could be carried out for animals in positive affective states. It might even be possible to develop similar methods that utilize auditory or olfactory stimuli.

Alternatively, tests could be developed to assess how ongoing attention-demanding tasks (e.g. signal detection tasks for food reward) are interrupted by threatening or neutral stimuli. The hypothesis would be that threatening stimuli would be more demanding of attentional resources in animals in a negative affective state and hence lead to poorer performance in the task in comparison to animals in a relatively positive affective state. Stimuli with similar psychophysical properties could be given affective value by previous contingent or non-contingent presentation with negative or positive events, hence allowing control for any intrinsic effects of stimulus characteristics per se (Stormark and Hugdahl, 1996; Fulcher et al., 2001). If developed, such studies could offer additional, experimentally controllable means by which to assess cognitive components of emotions in captive animals. Moreover, they could also determine the similarities or dissimilarities that exist between people and animals in attention and emotion associations.

4.3. Memory biases in animals

Studies of the emotional modulation of memory in animals form an extensive literature. The main purpose of this work has been to investigate the neuroendocrinological processes by which emotions might influence memory storage, consolidation and retrieval (Cahill and McGaugh, 1996, 1998; McEwen and Sapolsky, 1995; Mendl, 1999; Mendl et al., 2001; Kim and Diamond, 2002; Sandi et al., 1997). A major finding of these studies is that administration of the classic stress hormones, the catecholamines (e.g. adrenaline) and glucocorticoids (e.g. cortisol), around the time of a to-be-learned event can enhance memory for that event (Cahill and McGaugh, 1996, 1998; Gold, 1992; Sandi and Rose, 1994). These hormonally mediated effects appear to influence both memory acquisition, partly by increasing attention towards emotional stimuli (Lupien and McEwan, 1997; Mendl, 1999), and memory consolidation into long-term memory stores (Sandi et al., 1997), and likely interact with amygdala and hippocampal processes in achieving

their effects (Ferry et al., 1999; Roozendaal et al., 1999; Quirarte et al., 1997).

The implication of these findings is that an animal experiencing moderate natural elevations of catecholamines and/or glucocorticoids will show enhanced memory for negative, and also positive (Packard and White, 1990) and neutral, events. However, as was emphasised earlier, elevations in levels of these hormones may occur in both positive and negatively valenced situations, and indeed it is clear from human studies that enhancement of emotional memory storage occurs for both good and bad stimuli or events (Hamann et al., 1999). This is not surprising if it is considered that this memory modulating effect has adaptive value (Cahill and McGaugh, 1998), and that memories for emotionally arousing stimuli, irrespective of whether they are positive (e.g. sexual, food related) or negative (e.g. predation threat), are more likely to contribute to survival and reproduction than memories of neutral stimuli. Therefore, enhanced memory performance may be a more reliable indicator of an individual's level of emotional arousal rather than the valence of its emotional state. Moreover, very low, very high, or chronically elevated levels of catecholamines and glucocorticoids appear to have disruptive effects on memory processes (Cahill and McGaugh, 1996; McEwen and Sapolsky, 1995; Gold, 1995; de Kloet et al., 1999; Kim and Diamond, 2002; Bodnoff et al., 1995; Woodson et al., 2003) and this adds complexity to the interpretation of affective influences on memory.

This work has not, however, focused explicitly on the possibility that an animal's emotional state might be assessed or characterised by the type of memory it preferentially retrieves. The finding in human clinical research, that sad or depressed individuals show enhanced retrieval of *mood congruent* (i.e. sad, upsetting) memories, has received little attention in animal studies. Again, the linguistic nature of such research presents a significant challenge to anyone attempting to design parallel experimental paradigms for use with animals. But if this (and additional problems arising from the confounding effects that manipulating emotional states akin to depression may have on the behavioural expression of memories) can be overcome, such research will be important for determining the full nature of emotion and memory links in animals, and for providing measures that more accurately reflect affective valence as well as arousal. Given that there are clearly many similarities between humans and non-humans in the emotional modulation of memory, it would be surprising if, for example, enhanced retrieval of negative memories was not also a facet of depressed states in animals.

An example of a method for investigating this possibility would be to expose animals to positive and negative events (on separate occasions, balanced for order, and ensuring all animals were in a similar motivational and affective state (Dickinson and Balleine, 1995)) in the same context, and then, at a later time, re-expose them to this context. The prediction would be that animals in a negative/depressed

state during re-exposure would be more likely to behave as if they retrieved information about the negative event, than animals in a neutral state, with animals in a positive affective state being most likely to behave as if remembering the positive event. In other words, like depressed humans, they would show a bias in retrieval from memory of information that was congruent with their current mood. Event-specific responses (e.g. move to shelter/back of pen in response to negative event; move to front of pen in response to positive event) could be trained during initial exposures to aid interpretation of responses made during re-exposure. Although this approach is unlikely to be without problems (e.g. effects of affective state on memory would need to be separated from any general effects on motivation), we believe that further comparative research needs to be conducted in this area in order to inform our understanding of the phylogenetic origins of memory-emotion links, and to develop novel cognitive measures of emotional state in animals.

4.4. Judgement biases in animals

Judgements or decisions on how to respond to a particular stimulus or situation are complex processes, often involving attention, memory and other aspects of cognition and perception. Therefore, the task of seeking emotion biases in the judgements of animals is likely to be a particularly complex one, further complicated by the reliance in much human research on linguistic measures of judgement (Wright and Bower, 1992). For our purposes, the key findings from the human studies are that people reporting negative emotions appear to make negative judgements about ambiguous (usually linguistic) stimuli or anticipated events, while happy people show the opposite bias.

Broadly speaking, some of the behavioural tests of anxiety, such as the open field and elevated plus maze, could be thought of as measuring responses to ambiguous situations in animals. However, many factors potentially contribute to the ambiguous nature of these situations including, for example, whether there is a predator waiting to strike in the exposed areas, whether there is an escape route, whether there is a familiar or unfamiliar conspecific nearby, and so on. Furthermore, the responses shown—for example, emergence into an open field, ambulation in the field—may reflect calm exploration or attempts to escape. Interpretation in the terms that we are interested in here—whether the animal made a negative or positive judgement about the likely outcome of the situation or encounter—is thus not easy to make.

Measures of 'risk taking' in animals may be of more use in this respect. Various anxiety tests include measurements of 'risk-taking behaviour' such as stretching out of a protected area to monitor a more open area (Blanchard et al., 1998; Quartermain et al., 1996), and these can provide an indication of how tentative the animal is about its decisions,

although again the precise motivations underlying the decisions may not be clear. A different approach to the study of risk taking has been followed by behavioural ecologists interested in whether animals opt to select a 'variable resource' where, for example, either a small or a large amount of food may be present, vs. a 'constant resource' where an intermediate amount (the mean of the small and large amount) is guaranteed (Kacelnik and Bateson, 1996). Studies have examined how the animal's motivational state (often its hunger state) influences its decisions, initially following predictions that, under conditions where the animal's bodily resources are so low that it requires the large amount of food to survive, it should be risk prone (opt for the variable resource), whereas under other circumstances it should be risk averse (Barnard and Brown, 1985; Caraco et al., 1980). Support for this hypothesis has been equivocal, and there have been interesting differences in the responses to variability in reward size as compared to variability in delay to reward, which some researchers have explained in terms of the mechanisms of psychological measurement of time and quantity, rather than adaptive choice making behaviour (Kacelnik and Bateson, 1996). Overall, this approach, while being directly interested in the influence of an animal's current state on its choices, uses a very specific scenario of risk (variability vs. constant/guaranteed reward), and the choices made are difficult to interpret in the terms we are interested in (i.e. as predicting that a positive or negative thing will happen).

In the absence of obviously suitable existing techniques, we have recently developed a novel method to investigate the possibility that animals may show emotional biases in judgements similar to those found in humans. The method is based on a discrimination task. The animals are first trained to make an operant discrimination between a tone of one frequency (2 or 4 kHz) that signals the arrival of a 'good event' (e.g. food), and a tone of another frequency (4 or 2 kHz) that signals a 'bad event' (e.g. no food and a brief burst of white noise). To get the food, the animal must perform a particular operant response (e.g. lever press) and to stop the noise from sounding, it must perform a different response (e.g. nose poke, or no response). This training thus sets up a specific association between one cue, a positively valenced event and a specific operant response, and another cue, a negatively valenced event, and a different response (e.g. 2 kHz/food/lever press vs. 4 kHz/noise and no food/nose poke). Once the animal has reached a criterion performance on the discrimination task, it can then be exposed to ambiguous, non-rewarded, probe tones of intermediate frequency to the training tones (e.g. 2.5, 3 and 3.5 kHz), to see how it responds to these. The hypothesis under test is that those animals experiencing a negative affective state will be more likely to interpret the ambiguous probe tones as predicting the arrival of a bad event—just as depressed people tend to make negative 'pessimistic' judgements about ambiguous and future events—while those in a positive affective state will show

the opposite response. This task thus provides a start point for animal studies of affective biases in judgements.

In Harding et al.'s study of rats (Harding et al., 2004), the responses trained were lever pressing to access food, and a null response to stop the white noise being played. Once they had reached criterion performance on the discrimination task, half of the trained rats were exposed to unpredictable housing conditions designed to induce a mild negative affective state (Willner, 1997a). The aim was to investigate whether these animals differed from controls in their responses to the intermediate probe tones. Compared with controls, the rats experiencing unpredictable conditions were slower to show the lever press response to intermediate (ambiguous) tones that were close to the food tone, and to the food tone itself, and tended to show fewer responses to these tones (Harding et al., 2004). Other tests indicated that these differences were unlikely to be due to differences in feeding motivation (a possible explanation for reduced responding to the food tone itself), general activity, body weight, and response accuracy to the training tones (Harding et al., 2004). Overall, these findings indicated that rats in conditions likely to induce negative affect were less ready to respond to the ambiguous stimuli as signalling the arrival of the good event. This compares with the findings that depressed or anxious people interpret ambiguous stimuli negatively and have reduced expectations of positive events. The precise mechanisms underlying these findings remain to be explored. For example, it is not yet clear whether the observed effect concerns reduced positive affect or increased negative affect, or whether memory processes, or 'risk assessment' processes underlie it. Furthermore, there is a need to repeat the procedure using, for example, different combinations of operant responses (e.g. lever press vs. nose poke), different discriminative stimuli, and different good and bad events to confirm the robustness of the findings. But the principle is illustrated: affective judgement biases can be sought in animals. The technique can be developed and adapted for other species, and unlike many indicators of animal emotion, it may be able to detect correlates of positive, as well as negative, moods such as an enhanced expectation of positive events.

Another technique that can be loosely described as assessing judgements about stimuli by measuring anticipatory behaviour towards them, has recently been developed by Spruijt et al. (2001). They hypothesise that a common currency system for measuring pleasure exists to evaluate and control the relative importance of different motivational priorities at any one time. This system may have its neural basis in interacting opioid and mesolimbic dopamine systems involved in the control of liking (assessing affective value of a stimulus) and wanting (initiating and integrating appropriate appetitive behavioural response) respectively (Berridge, 1996). When animals are experiencing short-term stress due to rewarding stimuli being in short supply, they hypothesise that the system becomes sensitised and that

this can be measured as enhanced anticipatory behaviour to a cued reward. In long-term absence of reward (chronic stress), they hypothesise that the system shuts down and reduced anticipatory behaviour to cued reward is observed (anhedonic-like response). Studies have shown that rats exposed to social stress and/or isolation exhibit a reduced frequency of behavioural transitions between the presentation of a conditioned stimulus predicting a sucrose reward and the arrival of that reward, indicating reduced anticipatory behaviour (van den Berg et al., 2000; von Frijtag et al., 2000). The rationale behind this approach is quite different to that developed by Harding et al. (2004), but both suggest that changes in ‘judgements’ about stimuli or their predictive cues can be used as indicators of affective or stress states.

5. Conclusions

In humans, appraisals or cognitive processing of some kind appear to be involved in determining the occurrence of emotional events. Cognition is also a critical part of the expression or output of emotional processing. Biases in judgement, memory and attention have been repeatedly shown to vary according to emotional state. Indeed, even basic sensations such as pain appear to include cognitive components or correlates (Rainville, 2002).

Within clinical psychology, considerable interest has been paid to exploration of the cognitive components of emotional and affective states. The possibility that such cognitive biases generate or perpetuate pathological, negative emotional experiences through biased appraisal and elaboration has received particular attention (Beck et al., 1979; Beck, 1967). In experimental psychology, on the other hand, most emphasis has been placed on developing models for explaining the processes by which emotions may affect cognitions. Here, the relative roles of subjective emotions and automatic, non-conscious emotional processes in determining cognitive outputs have been a point of particular focus. Finally, neuropsychological and neuropharmacological researchers have considered the mechanics of cognition–emotion links, investigating the roles played by certain brain regions and stress hormones in determining the modulating effects of emotion (especially ‘stress’ or anxiety) on cognitive functions, such as the acquisition and consolidation of memories.

We believe that emotion–cognition links also have a significant role to play in all areas of animal-focused emotion research. Dantzer (2002) and Desiré et al. (2002a) have already proposed the investigation of appraisal processes in animals. In particular, they suggest that, by inducing certain emotions by the controlled use of stimuli with a known and limited set of appraisal criteria, it should be possible to broadly identify which types of emotions different species are capable of undergoing. In this way, the behavioural and physiological outputs that uniquely

characterise particular emotions can be investigated (Dantzer, 2002).

Information regarding animals’ emotional and affective states can also be explored in the future by tapping the cognitive *outputs* of emotions. Several lines of evidence indicate that affective state modulates attention in animals, but new methods are required to identify attentional changes that reflect valence as well as arousal. Likewise, affective state appears to influence memory encoding and consolidation in animals, and tests of memory retrieval bias may provide novel measures of the valence of ongoing mood states. Harding et al. (2004) have started to investigate judgement biases by using an ambiguity task to discriminate between rats whose emotional or mood states are temporarily manipulated. Similar tasks have also been developed by Spruijt et al. (2001). Further cognitive tasks still need to be designed, and their efficacy at detecting differences in attention, memory or judgement processes will have to be reviewed. But the potential is clearly present for the development of new, non-linguistic, experimental paradigms that can be used with animals (and also with humans, including those who are non-literate and non-linguistic) to investigate emotionally induced cognitive biases.

These cognitive approaches will offer novel paradigms for assessing affective or emotional states of animals for whom behavioural and physiological measures may be inconclusive or imprecise (e.g. many current measures may be better indicators of emotional arousal than valence). Because cognitive biases occur in humans experiencing generalised affective states as well as specific, object-oriented emotions, they may be particularly useful for detecting subtle, on-going mood states in animals, which are currently more difficult to assess than object-focused emotional responses. Moreover, they have the potential to discriminate between similarly valenced but different types of emotion or mood state which have different cognitive appraisal profiles or induce different types of cognitive bias (e.g. depression and anxiety).

Another area where assessment of cognitive outputs of emotion may prove particularly valuable is in the assessment of positive emotion or affective states in animals. These are rarely discussed in animal emotion research, both because biomedical and animal welfare concerns have led researchers to focus on studies of negative affective states, and because positive emotions generally appear to be difficult to assess behaviourally and physiologically. Although the human cognition–emotion literature has also focused predominantly on negative emotions, there are now enough studies showing positively valenced biases, particularly in judgement and decision-making (Nygren et al., 1996; Anderson and Bower, 1973), to expect that similar findings could be achieved with animals. Finally, knowledge of cognitive bias may also identify individuals with a predisposition to interpret events in ways that are more or less likely to induce negative affect, thus allowing

identification of phenotypes that are vulnerable to affective disorders such as depression (Beck, 1967).

In addition to the flow of information from human to animal research, it may also turn out that findings and techniques from animal studies can inform human theory and experiment. For example, non-linguistic techniques developed to assess cognitive bias could have applications in the study and treatment of non-verbal or linguistically impaired children and adults. We hope that the ideas and approaches outlined in this paper will encourage a fruitful two-way exchange between those working in the animal and human fields of emotion research.

5.1. Cognition, consciousness and subjective emotion

We have so far avoided any detailed discussion of the implications that investigation of cognition emotion-links might have for our understanding of the possible subjective emotional experiences of animals. But ultimately this will be a key issue. We can certainly study emotional processes in animals without concerning ourselves directly with whether or not any of those processes result in conscious experiences for the animal concerned. LeDoux (1994, 1996) takes this view, further proposing that emotions become subjective, or conscious, only in animals which possess the capacities for both emotion and consciousness. This may or may not include the majority of mammals and other non-human animals—LeDoux refuses to be drawn into such speculations. Others take an opposing view, suggesting that the subjective component is likely to be a fundamental part of the emotional process, with ‘felt’ emotion of some kind occurring in all species who ‘do’ (behaviourally, physiologically) emotion (Panksepp, 1994). Whichever approach is correct, however, the issue of whether and in which species subjective emotional experiences occur is vitally important, both for our ethical treatment of animals, and for our understanding of the phylogenetic origins of felt emotional experience.

If research in animal emotion is to progress significantly, difficult empirical and philosophical issues concerning the occurrence of subjective emotion need to be addressed. Investigating every facet of emotional events in animals, including cognitive components, will provide a more complete picture than is currently available of the similarities and differences that exist between human and non-human emotional processes as a whole. As a result, we might come closer to understanding the role of subjective experience in the emotions of all species. Of particular relevance here is the possible applicability of the affect-as-information hypothesis (Schwarz and Clore, 1983, 1988), the affect infusion model (Forgas, 1992, 1995) and the somatic marker hypothesis (Damasio, 1994) to the understanding of emotion–cognition links in animals. While other theories propose fairly simple, ‘mechanistic’ causal routes by which emotions influence cognitions (Bower, 1981; Isen, 1984), these models suggest that it is felt, *conscious* emotion

itself which is necessary for (certain) affective biases in cognitive processing to occur. If they are correct, studying the cognitive processes and outcomes associated with emotional states may be particularly illuminating with regard to the subjective experience of emotion in animals. These models propose a functional relationship between conscious affect and cognitive biases. So, animals showing such biases either challenge the validity of these models, or question the arguments of those who believe that animals do not consciously experience their emotions. Either way, research in this area is likely to be important for a complete understanding of both human and animal emotion.

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