# Animal Welfare and Affective States

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## Introduction: the central role of positive and negative feelings in animal welfare

"*Let us not mince words: animal welfare involves the subjective feelings of animals.*"
(Dawkins 1990)

In this book, we follow the view that Marian Dawkins so succinctly summarised over 30 years ago; we are concerned about animal welfare because we are concerned that animals have *subjective experiences* akin to suffering. Take a look at the cheeseburger shown in Figure 1.1. If animal welfare troubles you, you'll probably be worried about the welfare of the organisms that provided the patty and cheese but not about those that made up the bread and garnish. Why is this? All the organisms were likely reared under unnatural conditions, their growth and physiology were adjusted through the use of chemicals (and by genetic selection and modification), and their lives were cut short when 'harvested'. Yet although they all had a challenging time, this matters to us when the organisms were animals but not when they were plants, because most of us believe that plants, lacking a nervous system, cannot consciously experience suffering[1]. The capacity to suffer is therefore core to our concept of animal welfare. More broadly it is the capacity for *sentience*, the ability to subjectively experience *feelings*, both positive and negative.

[1] Some researchers argue, controversially, that plants may have a form of conscious experience (Segundo-Ortin and Calvo 2023 and commentaries therein), or that nervous systems are not required for an organism to be sentient (Reber and Baluska 2021). This is a live debate, and the consensus may change with time but a telling conclusion from Segundo-Ortin and Calvo (2023) is that if plant sentience were to be established, the ethical treatment of plants would then need to be considered; sentience is thus key to welfare concerns.

**Figure 1.1** The cheeseburger of welfare concerns. Source: Created using Canva.

Identifying which species are sentient is a challenging enterprise, and one we return to at the end of the chapter. However, there is a broad consensus that, assuming that a species is sentient, it is the stuff of sentience – *affective states* – that is the determinant of animal welfare. Affective states are *valenced* mental experiences – ones that are positive, pleasant and rewarding, or negative, unpleasant and punishing. They include *emotions* and *moods* such as fear, happiness, sadness and anger. They also include the affective components of sensations such as pain, thirst, hunger and sickness, which are sometimes referred to as *homeostatic emotions* (Craig 2003), *homeostatic feelings* (Damasio and Damasio 2022) or *primordial emotions* (Denton et al. 2009), and which reflect interoceptive evaluation of the state of the body. To assess animal welfare, we must therefore be able to assess these states. And to assess affective states, we must further clarify what they are. This is the focus of the current chapter.

But first, why are affective states so central to animal welfare? It has been said of such experiences, at least for humans, "*No aspect of our mental life is more important … . They are what make life worth living, or sometimes ending*" (Scarantino and De Sousa 2021). The idea that these subjective states also play a pivotal role in other species' well-being has a long history, that includes Jeremy Bentham's (1789) famous quotation "*The question is not, Can they reason? nor, Can they talk? but, Can they suffer?*"; Russell and Burch's (1959, p. 23) aspiration to "*aim at well-being rather than the mere absence of distress*"; UFAW's original mission "*to promote humane behavior towards wild and domestic animals … so as to reduce the sum total pain and fear inflicted on animals by man*", the 1965 Brambell Committee's concerns for "*the physical and mental well-being of the animal*"; and today's Five Domains' framework, with its goal of "*an ultimate assessment of the overall welfare state of the animals, understood in terms of what they (are) likely to experience subjectively*" (Mellor et al. 2020). Minimising negative subjective states such as fear or pain, and promoting positive subjective states such as contentment, is thus seen as synonymous with improving the quality of animals' lives (see also Duncan 1993; Mason and Mendl 1993; Dawkins 1998;

Rushen 2003; Mendl and Paul 2004; Broom 2007; Kirkwood 2007; Mason and Veasey 2010; Browning 2020, for similar views of animal welfare).

This is also evident in real-world guidelines and legislation. Estimating the severity of laboratory animals' negative states and suffering is a crucial part of the ethical review process for much animal-based research, and ensuring good well-being is core to many farm assurance and food labelling schemes. Furthermore, the capacity for *sentience* is now enshrined in legislation in several countries as the key factor underpinning our animal welfare obligations (e.g. EU Treaty of Amsterdam (EU 1997); New Zealand Animal Welfare Act (New Zealand Government 1999) and UK Animal Welfare (Sentience) Act (UK Government 2022)). It is also implicit in the way that many animal species receive levels of protection that plants do not (e.g. Canada has two federally-influential animal care councils, the Canadian Council on Animal Care and National Farm Animal Care Council, but no equivalents for plants). This feelings-centred view of animal welfare is thus widespread and conventional. It relies on two assumptions, additional to the animals in question being sentient: first, that positive and negative feelings matter to animals, and therefore have ethical weight (see Wittgenstein 1953; Singer 1976; Midgley 1984); and second, that we can detect or measure them in some way, so that welfare can be assessed. The latter, the process of objective assessment, is the focus of this book.

To begin, this opening chapter will delve into what affective states actually are. First, we consider two main ways in which they have been conceptualised: (i) as a collection of discrete, modular states such as 'fear', 'joy', 'jealousy' or 'anger', and (ii) as states that vary along two or more underlying dimensional characteristics, including the key property of *valence*. Next, we describe different temporal categories of affective state, spanning short-term 'emotions', longer-term 'moods' and 'affective disorders' that may last for many months to years, and overall 'cumulative affective experience'. We also briefly consider that different individuals may have different 'affective personalities'. It is important to note that these perspectives and categories are all *constructs*: conceptual ways of thinking about the organisation and structure of affective states, rather than hard-and-fast biological entities, and they may overlap with each other.

We end this chapter by outlining why these states are so challenging to investigate in animals, and why their subjective components are, at present, essentially unmeasurable. Nevertheless, by developing and using a logical inference framework, measurable indicators of affect can be identified and validated as tools for assessing welfare. In Chapter 2, we introduce such a framework.

## Affective states: their natures, temporal characteristics, functions and long-term consequences

In this section, we give more detail about the constructs identified earlier and also consider their potential functions and long-term consequences.

### Affective state concepts: discrete and dimensional views

Because affective states are human constructs derived from our own subjective experience of emotions, moods and other valenced feelings, much of what we know about them comes from research with humans, where linguistic self-report is used as the gold standard indicator

of felt experience (e.g. Russell 2003; Mauss and Robinson 2009; Mendl et al. 2022). This research often identifies two distinct ways of conceptualising affective states: either as discrete entities (such as 'fear', 'sadness' or 'joy'), or as states that vary continuously along a few simple dimensions (such as *valence* – the positive or negative nature of a state). The merits and demerits of these two views attract much discussion in human emotion science, and understanding them is helpful for welfare scientists too (e.g. Izard 2007; Panksepp 2007; Adolphs 2017; Barrett 2017; van Heijst et al. 2023).

### Discrete emotion theories

Discrete or 'basic' emotion theories propose that distinct emotions are elicited by different situations and characterised by fundamentally different responses (e.g. facial expressions) and unique 'feels' (Ekman 1992; Panksepp 1998). Furthermore, many of these theories propose that such states are universal across humans and have their origins in adaptive suites of behaviours, underpinned by distinct neurobiological circuits or systems (e.g. those located in the amygdala, LeDoux 1996), that can also be seen in many other (especially mammalian) species. For animal welfare researchers, this has an obvious intuitive appeal since it allows direct mapping of human and non-human states, and captures how different discrete emotions have different causes. But it has some disadvantages too. One is that the emotional and mood labels used in our own culture may limit what we think to look for and assess in other animals. English speakers, for example, may simply overlook the possibilities of *uitbuiken*, the Dutch concept of feeling pleasantly full after a meal, or the Japanese *shinrin-yoku*, the calming experience of being in a forest. More worryingly, it risks unjustified anthropomorphism: assumptions that other species are like us even when they have evolved in sensory or social worlds very different from our own. It is probably absurd to look for 'jealousy' or 'grief' in non-social species, for example, while conversely some species may have states so dissimilar from our own that we cannot imagine them. What does it feel like to be a lion who has just killed and eaten a rival's cubs, for example, some affectively positive combination of uitbuiken and lust as he waits for the lioness to come into oestrous? As Wittgenstein (1953) put it, "*if a lion could talk*, *we would not understand him*". And this challenge is even greater for animals whose sensory worlds and abilities diverge even more considerably from our own. Thomas Nagel famously asked "*What is it like to be a bat*?", in the title of his paper discussing the unknowability of alien minds (Nagel 1974). Perhaps bats lack some of the specific emotions that we have (such as guilt) but feel their own unique negative emotions if their sonars are bombarded with very strong ultrasound, or their own unique positive emotions if they capture a particularly agile insect.

### Affective dimensions

The second, alternative conception of affective states sidesteps this issue by treating them as varying continuously along some simple, underlying dimensions. The prominent 'core affect' model, resulting from statistical analyses (e.g. principal components analysis [PCA]) of perceived differences, similarities and temporal associations between human emotion words and expressions, identifies two key dimensions: (i) *valence*, the degree to which a state is positive or negative, and (ii) *arousal* – how activating or arousing the state is, from soporific to frenetic (e.g. Russell 2003). The 'location' of different emotional states in this two-dimensional *core affect space* thus depends on their valence and arousal characteristics. In Figure 1.2, we show examples of (human) discrete emotions arranged according to the levels of arousal and valance that are likely associated with them. Their distribution in our figure differs from the

classic 'circumplex' in which they are arranged, according to PCA statistical models, in a circle around the *edge* of core affect space (e.g. Russell and Pratt 1980; Russell and Barrett 1999). However, our figure follows the recognition that, at any one time, an individual's affective state reflects their current combination of valence and arousal and can occupy *any* area of the space. Additionally, it is suggested that the further away the current state is from the centre of core affect space, the more *intense* the accompanying emotional feeling (Russell 2003; Russell and Barrett 1999). Hence, 'fearful' is further from the centre than 'distressed', as is 'depressed' relative to 'sad', and 'elated' compared to 'happy'. Figure 1.2 thus implies that arousal and valence vary independently from each other; they are orthogonal. Nevertheless, as we will see in later chapters (e.g. vocalisations in Chapter 4 and cortisol in Chapter 5), changes in some indicators of affective state appear to reveal an underlying correlation between arousal and valence. For example, increases in the release of stress hormones (e.g. cortisol, see Chapter 5) as a situation becomes more challenging or dangerous reflect elevations in arousal plus a strengthening of valence and, in humans at least, an increasingly intense emotional feeling (e.g. increasing fear). So, for some markers and affective states, arousal, valence and emotional intensity may covary. In these cases, levels of arousal may be a useful proxy marker of valence strength.

Some argue that the core affect model best represents the structure of and relationships between different human affective states; Mauss and Robinson (2009), for instance, said "*it is quite clear that dimensions such as valence and arousal … capture the lion's share of variance*" (see also Lindquist et al. 2012; although for counters, see Kragel and Labar 2016; Vytal and Hamann 2010). Others further argue that the combination of core affect with sensory, perceptual and interoceptive information enables humans to construct a potentially limitless set of feelings (e.g. Barrett 2017). This so-called 'constructionist' perspective is in marked

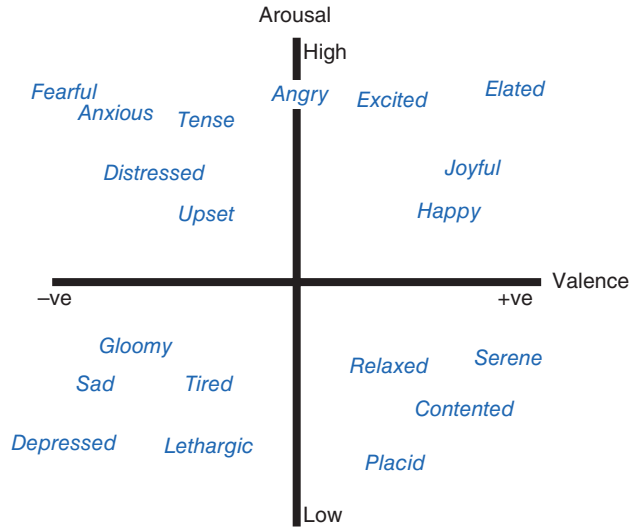


**Figure 1.2** A dimensional core affect model. According to this model, valence and arousal, or activation, are the two main dimensions along which affective states can be separated. Human emotion words in italics illustrate where different types of affective state might lie in this 'core affect' space depending on the level of arousal and strength of valence that characterise them. Source: Adapted from Russell (2003).

contrast to the idea of a limited set of discrete emotions that is experienced by all members of a species and supports a view of affective states as primarily culturally determined, and having 'fuzzy' boundaries (Russell 2003), with gradual transitions between related states.

Other statistically-generated dimensional models, whilst yielding the same basic affective space, emphasise the importance of two dimensions lying at roughly 45° from the valence and arousal axes (Russell and Barrett 1999; Watson et al. 1999; Yik et al. 1999; Carver and Harmon-Jones 2009; see also Burgdorf and Panksepp 2006; Knutson and Greer 2008). These have been given labels such as *Positive Activation* and *Negative Activation* (Watson et al. 1999) or *Promotion* and *Prevention* (Higgins 1998), and linked to neurobehavioural systems underpinning two evolutionarily ancient imperatives – the need to acquire resources for survival (*reward acquisition*), and the need to avoid harm (*punishment avoidance*; Gray 1987; Carver 2001; Corr 2008; Norris et al. 2010; Norman et al. 2011). Neurobiological substrates of reward acquisition systems in mammals include mesolimbic dopaminergic, opioidergic and endocannabinoid systems acting at various brain locations (e.g. nucleus accumbens, ventral striatum, insular and orbitofrontal cortices) during anticipation or presence of reward, and are associated with high-arousal positive affect (e.g. Schultz et al. 1997; Knutson and Cooper 2005; Nguyen et al. 2021). Reduced activation of these systems has also been associated with low-arousal negative states such as depression (e.g. Forbes et al. 2009). Similarly, associations have been found, again at least in mammals, between anticipation or presence of punishment and activity in amygdala insula and anterior cingulate cortex, and between anticipation of relief and activation in the amygdala and substantia nigra (Seymour et al. 2005 2007; Carlson et al. 2011).

The activity of reward acquisition systems thus appears to vary according to presence/anticipation and absence/loss of reward and is associated with, respectively, high-arousal positive affect and low-arousal negative affect. Likewise, the activity of punishment avoidance systems varies with presence/anticipation and absence/avoidance of punishment, and is associated with, respectively, high-arousal negative affect and low-arousal positive affect (Watson et al. 1999). This is illustrated in Figure 1.3 which shows how the presence or absence of rewarding and punishing events can be mapped to locations in core affect space. Importantly, these neurobiologically-focused views also illustrate hypothesised links between affective arousal and valence on the one hand, and the evolutionarily important activities of acquiring resources and avoiding harm on the other. They may also underlie the positive associations between arousal and valence observed for some affective states and indicators as discussed earlier.

The link between reward, punishment and location in core affect space also maps to Rolls' (2014) definition of emotional states as "*states elicited by rewards and punishers*", where rewards are things for which an animal will work and punishers are things that it will work to escape or avoid (see also Mendl and Paul 2020). This is an example of an *operational definition* in which a concept (emotional state) is defined in terms of how it can be identified and/or measured, thus rendering it open to experimental investigation. This operational definition allows rewards and punishers to be identified empirically according to the behavioural work that animals do to, respectively, access or avoid them. Rewards and punishers identified in this way can then be used to induce emotional states as defined: delivery of rewards *and* removal of punishers gives rise to positive affective states, while delivery of punishers *and* removal of rewards gives rise to negative states. Anticipating such events can also elicit affective states (Rolls 2014; Mendl and Paul 2020; see Figure 1.3). Later in the book, we will see how this dovetails with two tests (Tests 2 and 3 in Chapter 2) that can be used to validate indicators of animal affective states.

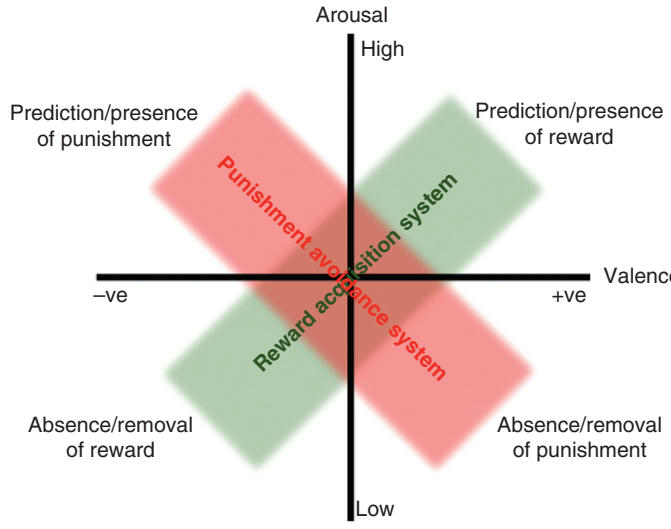


**Figure 1.3** Presence/absence of reward/punishment and location in core affect space. The green and red bars represent axes along which affective states change according to the activity of neurobehavioural systems underpinning evolutionarily ancient imperatives: acquiring resources and avoiding harm.

Dimensional views have distinct advantages for animal welfare researchers, not least because they avoid the risks of anthropomorphism inherent in translating human-specific discrete emotion terms to other species (LeDoux 2017). They acknowledge that animal affective states are influenced by their sensory and perceptual worlds, and hence may be very different from our own (e.g. Bliss-Moreau 2017). And they also focus our attention on the attribute most likely to matter to animals themselves: the extent of positive or negative valence (e.g. Duncan 2006). However, these views have disadvantages too, including that states like pain and fear might be treated as similar, since their locations in two-dimensional 'core affect space' may overlap, when of course their causes and outcomes are very different.

In this book, we will use the dimensional approach, and particularly the concept of valence, to build a framework for validating animal affective states. But first we consider how affective states can also be distinguished according to their temporal characteristics. In doing so, we identify putative functions and consequences of these different affective categories.

## Affective state concepts: temporal categories of affect

Affective states change across time, as illustrated in Figure 1.4, for core affect. An additional issue in the categorisation of affective states therefore relates to their duration. Here we consider the distinction between short-term emotions, longer-term moods, affective disorders, affective personality and cumulative affective experience across time. In doing so, we identify causes and putative functions of these different temporal categories.

### *Short-term emotions, their causes and functions*

The terms 'emotion' and 'emotional state' are often used colloquially to denote a range of affective phenomena. However, 'emotion' also has a specific, narrower meaning in affective science, referring to short-term affective states that are closely tied to rewarding or punishing external or internal events that human subjects can typically pinpoint, the latter including

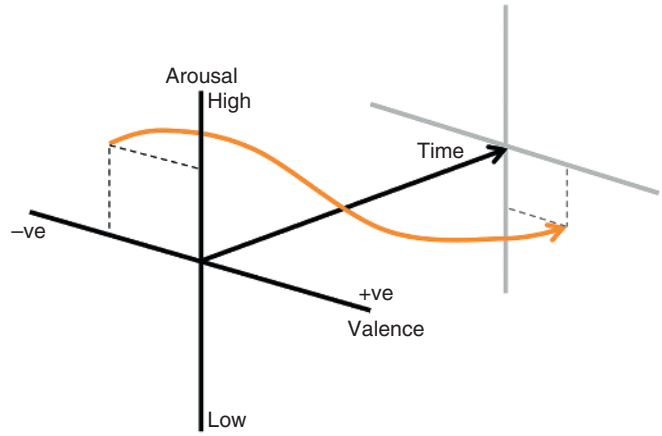


**Figure 1.4** Affective states have a temporal component. The figure shows a hypothetical trajectory of core affect for an individual moving from a high-arousal, negatively valenced state to a low-arousal, positively valenced state, for example, as a result of the successful avoidance of a predator.

bodily signals and recall of previous experiences. 'Emotions' are thus often said to be 'about' something – to have a specific cause or focus (e.g. *I am delighted by X*, *scared of Y*, *thrilled about Z* or *pained by this burn*) – and are consequently fairly short-lived. Their duration is typically considered to be seconds to minutes and, occasionally, hours (Oatley and Johnson-Laird 2014).

The generation of emotions usually involves some interpretation or *appraisal* of the causal event (Schachter and Singer 1962; Scherer 1999). Some rewards and punishers are stimuli that would have been reliably good or bad for ancestral fitness (e.g. attractive mates or dangerous predators, respectively; e.g. Rolls 2014). For these, it is likely that all members of a species will undertake similar appraisals and show similar emotional responses. They will likely also experience similar homeostatic or 'primordial emotions': affective components of sensations (e.g. pain caused by injury, nausea caused by sickness) or motivations (e.g. intense thirst caused by disruptions to homeostasis). But some stimuli can be rewards to some individuals and punishers to others (e.g. licorice, Marmite or the Japanese food natto), or rewards in one situation and punishers in another (e.g. iced tea on a hot day or a cold day). New punishers and threats can also be learned, for instance by classical conditioning or social transmission. Human examples might include joy when your team scores a goal, replaced by eye-rolling disappointment or anger when the opposition equalises minutes later, or excitement when you hear fireworks, replaced by fear as you realise they are gunshots. Learning from individual experience can result in the same event generating quite different emotions in different people. And again, thanks to learning, emotions in humans can also be elicited by simply hearing good or bad news, or remembering past negative or positive events.

Ekman and Cordaro (2011) argued that "*Each … emotion prompts us in a direction that, in the course of our evolution, has done better than other solutions in recurring circumstances that are relevant to our goals*". But what *are* the adaptive functions of emotions? Emotions that involve facial expressions can be important for enhancing or minimizing the acquisition of sensory information; for example, the eyes and nostrils are widened in fear and narrowed in disgust (e.g. Susskind et al. 2008). They can also function for communicating with

conspecifics (something returned to in Chapter 4 on vocal signals). But more broadly, *all* emotions appear to be involved in appropriate decisions to approach or avoid, choose between diverse options and drive reinforcement learning that shapes future behavioural responses (Mendl and Paul 2020). These three functions are described next.

"*Some argue that approach and avoidance are more or less synonymous with positive and negative emotional states*", proposed Mauss and Robinson (2009). This chimes with the views of those who emphasise the role of homeostatic or primordial emotions such as hunger, thirst and pain in motivating homeostatic responses including searching for food or water and avoiding noxious stimuli (Craig 2003). Looking first at positive emotions, humans have a tendency to view even objectively neutral stimuli as mildly positive and to expect positive things to happen (Ito and Cacioppo 2005; Sharot 2011), perhaps because we are a naturally curious, exploratory species. However, stimuli that are *strongly* liked (as opposed to only weakly liked) typically attract the fastest approach, most attention, greatest consumption and greatest willingness to bear costs to obtain access (e.g. Cabanac 1992; Pessiglione et al. 2007; Anderson and Adolphs 2014). That such effects are adaptive is nicely illustrated by the way that emotional responses to certain stimuli change with the body's homeostatic need for them. Thus, warmth is judged as more emotionally positive when we are cold, motivating us to seek shelter when needed (Cabanac 1992). Similarly, food, water and salt are judged as more delicious and pleasurable when our bodies are deprived of them, again helping motivate the restoration of homeostasis (Robinson and Berridge 2013; Rolls 2014; Saker et al. 2014). To paraphrase Cabanac (1992), "*What's pleasant is useful*".

Negative emotions, and the avoidance behaviour they trigger, are also adaptive. The affective component of pain, for instance, helps us avoid damaging tissue injury (Eccleston and Crombez 1999), while warmth is judged as negative and unpleasant when we are already too hot, promoting adaptive avoidance that helps with thermoregulation (Cabanac 1992; see Chapters 2 and 5). Ancestrally important signs of danger (e.g. spiders or snakes) are also highly motivating, often with very negative affective impacts, including potent abilities to attract our attention and generate revulsion. This can even occur despite little modern-day relevance: as Nettle (2009) and many others have pointed out, today people still tend to fear things like snakes and spiders even though electric shocks and road accidents are now a much bigger threat for most modern humans. The evolutionary imperative of avoiding harm is likely why, at least in humans, negative emotions are often more rapidly triggered, stronger, longer-lasting and more diverse than positive ones (Baumeister et al. 2001; Ito and Cacioppo 2005). Such motivational correlates of emotion are also what makes assessing preference and avoidance such a valuable tool in animal welfare research (see Chapters 2 and 3), and when inferring positive or negative states during the construct validation of indicators (as discussed in the next chapter).

Cabanac (1992) proposed that valence, as a scalable sense of pleasure or displeasure, functions as a "common currency" for decision-making. This would operate when obtaining a resource comes with a cost (such that approach only occurs when the positive affect offered by a resource outweighs the negative affect involved in obtaining it). It would also enable adaptive choices between diverse options offering different costs and benefits such as deciding whether to risk cold and predation in order to eat, versus staying safe and warm but unnourished at home (Mendl and Paul 2020). Some human data support this hypothesis: emotional 'gut feel' choices between options appear to reflect an internal weighing up of their diverse pros and cons. Complex decisions – such as which apartment to rent or which roommate to choose – thus can operate particularly efficiently when rapid, feelings-based choices are made (e.g. Mikels et al. 2011; Dijksterhuis 2004).

As a final, and perhaps most important, function, emotions influence learning and hence future actions. Maximising long-term rewards over punishments, and hence positive over negative states, is at the heart of reinforcement learning and decision-making (Mendl and Paul 2020). Associative learning thus occurs rapidly when it results in acquisition of very pleasant *outcomes* – powerful rewards – or avoidance of very unpleasant, punishing ones (Panksepp 2005; Rolls 2013), especially if these are surprising and/or unexpectedly pleasant or unpleasant. Similarly, ancestrally important *cues*, such as the shape of snakes, are particularly efficient at promoting learning about the negative consequences that can follow them (e.g. Tomarken et al. 1989; so-called *pre-prepared* fear learning: Öhman and Mineka 2001). These cues and outcomes do not even need to be close together in time for learning to occur. For example, the adaptive avoidance of contaminated food can be learnt with just one single pairing of a novel food/flavour with the later punishing experience of nausea (Garcia et al. 1955).

### *Long-term moods, their causes and functions*

Moods are longer-lasting affective states that often do not, from the human subject's perspective, have an obvious immediate cause – they seem unattached to a specific event and are sometimes described as 'free-floating' (Beedie et al. 2005; Mendl et al. 2010, 2022; Nettle and Bateson 2012;). Examples include feelings of contentment that are not linked with any one particular event, or senses of doom, gloom or sadness. Lingering sickness-related malaise, or lassitude, is also a mood-like state that appears to be related to immune responses to infection (Schrock et al. 2020; Bucks et al. 2008) and hence is an example of a homeostatic emotional feeling linked to interoceptive evaluation of bodily function. Moods are usually considered to last from hours to days, sometimes weeks (Oatley and Johnson-Laird 2014), thus forming fuzzy temporal boundaries with the concepts of 'Emotions' (above) and 'Affective Disorders' (below), and illustrating the overlapping nature of these constructs.

Many moods seem to result from the accumulation and integration of previous shorter-term emotional experiences. For example, minor and major s*tressful life events* (e.g. job loss, bereavement) can give rise to negative emotions of varying intensities and durations (e.g. Anderson and Adolphs 2014), which at some point seem to accumulate, fuse and persist as longer-term moods that are detached from their original causes (Beedie et al. 2005). Moods can also change emotion dispositions. For example, negative affective states may increase the likelihood of experiencing negative or less positive emotions by, for example, lowering thresholds to experience negative affect or biasing attention to negative stimuli (e.g. Mathews and Macleod 1994; Benning and Oumeziane 2017, Clarkson et al. 2020; see also Larsen and Ketelaar 1991). Moods also alter the appraisal of events (and thus the short-term emotions that arise from these events), such that there can be bidirectional, mutually potentiating relationships between short-term emotions and longer-term mood states (Mendl et al. 2010; Mendl and Paul 2020).

The mechanisms by which emotional experiences shape long-term moods are far from elucidated. However, positive and negative moods may be influenced differentially (e.g. Watson et al. 1999). For example, Clark and Watson (1988) found that self-reported positive moods were associated with pleasant social interactions and other positive daily life events, while negative, anxious moods were instead more often predicted by health problems (e.g. headaches, gastrointestinal problems, sickness such as colds or flu). In a similar study of people in the workplace, Miner et al. (2005) found that, while positive events were more common, negative events had a considerably stronger influence on ongoing mood. Further evidence that experiencing negative emotions predicts the emergence of negative moods

comes from research on the mood disorders discussed in the next section (e.g. Tennant 2002), although the picture here is complex – factors like personality, socio-economic status and gender can moderate the link between stressful life events, emotions, moods and mood disorders (Hankin and Abramson 2001; Hyde et al. 2008; Sullivan et al. 2000).

Figure 1.5 (adapted from Mendl and Paul 2017; see also Webb et al. 2019) shows a simple conceptual model of affective valence incorporating emotion, mood and also affective disorder. The length of the *x*-axis represents minutes to hours. Rewarding or punishing events generate short-term emotions indicated by spikes in affective valence (black line) which return to a longer-term underlying mood state (wide grey line). The size and duration of spikes reflect the impact of the affective events. Mood is influenced by cumulative experience of short-term emotions, becoming more positive after positive emotional responses and more negative after negative responses, but with a tendency to regress towards a 'baseline' state (dashed horizontal line). This state may vary between, and be characteristic of, individuals but, at population level, it tends to be slightly positive (Sharot 2011). The grey mood line interpolates mood trajectory between emotional event spikes. As discussed later, negatively-valenced affective disorders may start to develop after repeated or particularly intense negative experiences. These may reflect qualitative changes in the relationship between experience and emotions – such that, for example, there is decreased sensitivity to reward and/or increased sensitivity to punishment, leading to a downward trajectory of mood. The wide blue line indicates the onset of such changes. Whether there is an absolute neutral valence point on the *y*-axis, above which states are qualitatively positive and below which they are negative, or whether the *y*-axis represents relative valence, has received little discussion in the animal literature. Some human psychology researchers argue that neutral affect does exist, is qualitatively distinct from positive and negative affect, and may function to promote inactivity (Gasper 2023). For simplicity, Figure 1.5 does not show any difference between the impact of strongly rewarding or strongly punishing events on mood. And effects of mood on appraisal of and reactivity to rewarding or punishing events are illustrated only for the blue affective disorder line; in this example of a negatively valenced affective disorder, negative events generate relatively stronger emotions than do positive events (e.g. anhedonia during depression).

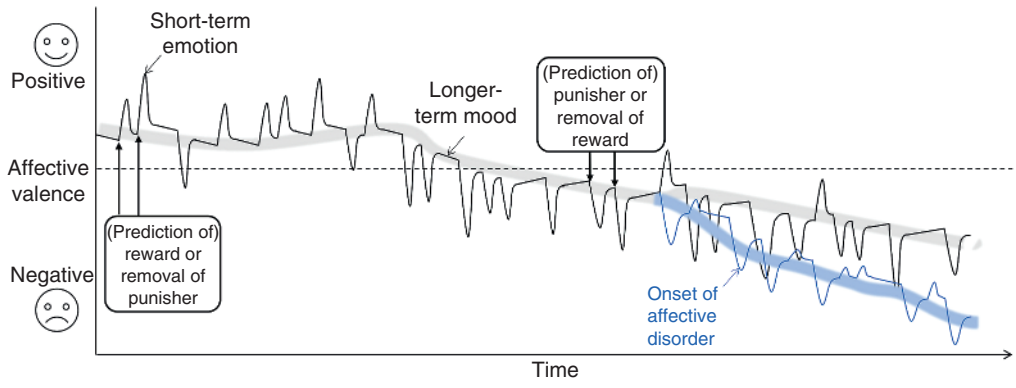


**Figure 1.5** A simple conceptual model of temporal changes in affective valence resulting from the interplay between emotions and moods and including the onset of negatively-valenced affective disorder (see text for details).

Functionally, moods play a role in many aspects of cognition and decision-making, but unlike those associated with object-focused emotions, these effects mostly concern broad classes of stimuli rather than specific ones. The positive or negative nature of a mood can influence decisions made about a whole range of daily events (e.g. Schwarz and Clore 1983; Forgas 1995; Loewenstein et al. 2001; Mendl and Paul 2020). For example, people in negative moods show increased attention to threatening stimuli (Bar-Haim et al. 2007), make more pessimistic judgements about the future (Strunk et al. 2006) and more negative judgements about a range of ambiguous stimuli (for reviews, see Blanchette and Richards 2010; Paul et al. 2005). Unpleasant though they are to experience, such negative moods almost certainly have (and/or have had in the past) greater evolutionary significance than positive ones, helping us to avoid threats and minimise energetic costs (Nettle and Bateson 2012). For example, anxious moods, which involve great behavioural activation and rapid shifts of attention towards potentially threatening stimuli, may have evolved because being both fast and decisive is important to successfully avoid dangers such as predator attack (Nesse 2000, 2005). Moods seem to mediate these effects via a variety of cognitive processes including altered attention, memory and decision-making (Paul et al. 2005; Mendl and Paul, 2020), as considered further in Chapter 7 on judgement biases.

### *Affective disorders, their causes and possible functions*

People suffering from *affective disorders* such as generalised anxiety disorder, panic disorders, post-traumatic stress disorder and major depression experience prolonged, disproportionately negative affective states. These states are longer lasting, and tougher-to-reverse, than everyday negative moods; in fact, they can last several weeks, months or even years (e.g. Oatley and Johnson-Laird 2014). In many cases, they co-occur (e.g. clinical anxiety and depression are particularly likely to be comorbid; Saha et al. 2021) and may also involve many non-affective elements which contribute to their debilitating nature (e.g. in depression or anxiety: insomnia or hypersomnia, problems concentrating, weight loss or weight gain, cognitive impairments and 'fight or flight' physiological responses like racing hearts: MacLellan et al. 2021). In humans, depression and anxiety appear to be associated with changes in the processing of rewards and punishments. A recent meta-analysis (Katz et al. 2020) for example indicates increased sensitivity to punishment in both depression and anxiety, and decreased reactivity to reward (i.e. anhedonia – see *Diagnostic and Statistical Manual of Mental Disorders,* American Psychiatric Association 2013]) in depression. Relatedly, Bishop and Gagne (2018) argued that reduced estimation of the likelihood and value of rewarding events and increased estimation of the likelihood and value of punishment are key components of depression and anxiety respectively which, in turn, impact on decision-making. As briefly mentioned earlier, we attempt to illustrate these changes in reward and punishment processing in Figure 1.5 (blue lines). This shows that during (the onset of) negatively valenced affective disorders, rewarding events may generate a smaller positive emotion peak whilst punishing events generate a larger negative peak, leading to a downward trajectory of mood (see Chapter 9 on reactivity to reward).

Affective disorders in humans are generally more likely in individuals who have faced childhood adversity (Brown et al. 1999; Heim et al. 2008; Colman and Ataullahjan 2010; Nanni et al. 2012) and also dealt with numerous unpleasant challenges throughout their lives (Tennant 2002; Hammen 2005). Thus, as well as involving current negative affect, they provide indirect evidence of past poor well-being. It is therefore not surprising that, according to many medical perspectives, these affective disorders are counter-productive,

non-functional and pathological (e.g. Drevets et al. 2008). However, an alternative view is that these disorders are functional in some way, or were to our ancestors, at least for those individuals experiencing milder (non-lethal) forms (e.g. McNamara and Buchanan 2005). For example, a recent meta-analysis has shown that depressive disorders are associated with enhanced learning about punishment (Pike and Robinson 2022), supporting ideas that depression can function to enhance focus on the analysis of challenging problems (Andrews and Thomson 2009). Another possibility is that depression functions to inhibit potentially risky actions in a dangerous environment and to encourage inactivity that may allow the individual to 'ride out' difficult times (Nesse 2000). So, while often pathological in the modern human context, depression could have helped our ancestors survive in social or physical environments where punishments were common and severe. Likewise, temporary extreme anxiety or panic, although highly unpleasant to the sufferer, could be a small price to pay if the 'fight or flight' responses typifying them help protect an individual from danger (Nesse 2005).

### *Affective personality*

We briefly note here that many human and animal personality characteristics (e.g. 'shyness', 'boldness', 'neuroticism', 'optimism', 'fearfulness', 'aggressiveness' and 'emotionality' itself) appear to have an affective basis and may reflect underlying genetic or epigenetic predispositions to exhibit particular affective behaviours and states (e.g. Larsen and Ketelaar 1991; Gosling and John 1999; Diener et al. 2003). From a dimensional perspective, the propensities to show stable differences in approach and withdrawal tendencies, or to be more or less sensitive to rewards and punishments, have been identified as important personality traits underlying vulnerability to disorders such as anxiety and depression (Davidson 1998; Corr 2008). These traits likely last for years or are lifelong (Oatley and Johnson-Laird 2014), and may equate to a 'baseline' (e.g. dashed horizontal line in Figure 1.5), towards which an animal's affective state will drift when not experiencing short-term emotion-inducing events or longer-term affective disorders. We will not dwell on this large topic area, but suffice to say that such predispositions can act alongside the impact of experience to influence an individual's affective states, disorders and hence their welfare (e.g. Diener et al. 2003).

### *Cumulative affective experience across time*

Cumulative affective experience can be thought of as the summed experience of emotions, moods and affective disorders across a whole lifespan, or a specified timescale; and they manifest in the way that affective states of all kinds can have long-lasting consequences on behaviour, cognition and physiology. These effects have been most extensively studied in humans experiencing negative emotional states, in research focusing on what is variously termed *cumulative adversity*, *lifetime stress exposure* or *cumulative stress*: the combination of chronic difficulties and acute challenges that plague everyone to greater or lesser extents. These studies find that early, repeated or prolonged negative affect often accelerates the processes of ageing (e.g. Shields and Slavich 2017; Acer et al. 2020), reflecting underlying autonomic and cellular changes (e.g. reduced telomere length: see Chapter 12) that are collectively often called *allostatic load* (McEwen and Stellar 1993; McEwen 1998). These changes can also have harmful effects on ongoing physical health, including the increased likelihood and severity of cancer, stroke and cardiovascular disease, plus elevated all-cause mortality (increased chances of dying from a wide range of causes; e.g. Lampert et al. 2016; Shields and Slavich 2017; Cohen et al. 2019): effects that are mirrored in other animal species (e.g. Cavigelli

and Mcclintock 2003; Walker et al. 2012; Cait et al. 2022). Early, repeated or prolonged negative affect can have harmful effects on *mental* health too, exacerbating not only the affective disorders already discussed (see e.g. Coelho et al. 2021; Foubert et al. 2021), but also conditions characterised by abnormal repetitive actions such as obsessive-compulsive disorder (e.g. Cromer et al. 2007) and trichotillomania (a hair-plucking disorder; e.g. Özten et al. 2015). And as we will discover in Chapter 11, this has important implications for understanding repetitive stereotypic behaviours in animals.

In humans, many of the lasting consequences of negative affect are believed to be mediated via three processes that are not mutually exclusive (e.g. Shields and Slavich 2017; Cohen et al. 2019; Yarrington et al. 2023). The first involves changes in *appraisal* (as described earlier), with people exposed to aversive events altering their anticipation, valuation and processing of rewarding and punishing events such that successive stressors become increasingly impactful. The second involves exposure to, or responses to, one type of adversity making other stressors more likely (e.g. divorce precipitating financial problems or loneliness). The third involves structural and functional consequences (such as alterations in skin, hair, blood vessels, endocrine systems and brain) that are relatively slow to reverse, such that progressive changes accumulate over time. Poirier illustrates this in her chapter on hippocampal changes within the brain (see Chapter 13), and we can sometimes see such effects visually too, as in the case of stress-induced grey hairs in mice or in humans above a certain age (Zhang et al. 2020; Rosenberg et al. 2021). Such somatic damage may in turn cause further declines in affective state (see Chapter 12).

So far, we have focused on cumulative negative states only. But what of net cumulative affective experience, taking positive states into account? For animals, any indicator that could track cumulative affective experience would be enormously useful for assessing their lifetime welfare or overall quality of life. It might allow the net cumulative impacts of entire husbandry systems to be evaluated, and be used to inform decisions about when to euthanise pets or retire research animals (see Yeates 2011; Bateson and Poirier 2019; Poirier et al. 2019). For some outcomes in humans (e.g. aspects of self-reported depressed mood), positive experiences seem to have rather little impact (e.g. Frank et al. 1996; Coelho et al. 2021). Other studies are less downbeat, finding that affectively positive events can mitigate the effects of negative ones (e.g. on self-reported general distress, albeit not anhedonia; Yarrington et al. 2023), and that mental attitudes and physical activities that may not be affective *per se* (e.g. healthy diets, exercise, positive appraisals; Puterman et al. 2015; Riepenhausen et al. 2022; see also Chapter 12) can have similar effects. Unfortunately, effects of cumulative affective experience are far less well-studied than the effects of cumulative adversity alone, particularly for variables that can be measured in animals. However, Chapters 12 and 13 present promising evidence that telomere length and certain hippocampal biomarkers have potential here.

## Summary

In this chapter, we have seen that affective states can be conceptualised according to their structure and temporal characteristics and that different categories (emotions, moods, affective disorders, cumulative affective experience) have different causes and putative functions. When considering cumulative affective experience, we also touched on the issue of how we might assess these states and saw that a range of measures (e.g. behavioural, physical, cognitive, neurophysiological, physical) can be used. These indicators are considered to be 'components' of affective states which, unlike the conscious subjective component, are amenable to direct measurement (Scherer 1984). Figure 1.6 brings this all together and illustrates how short- and longer-term affective states (valence) are related and how

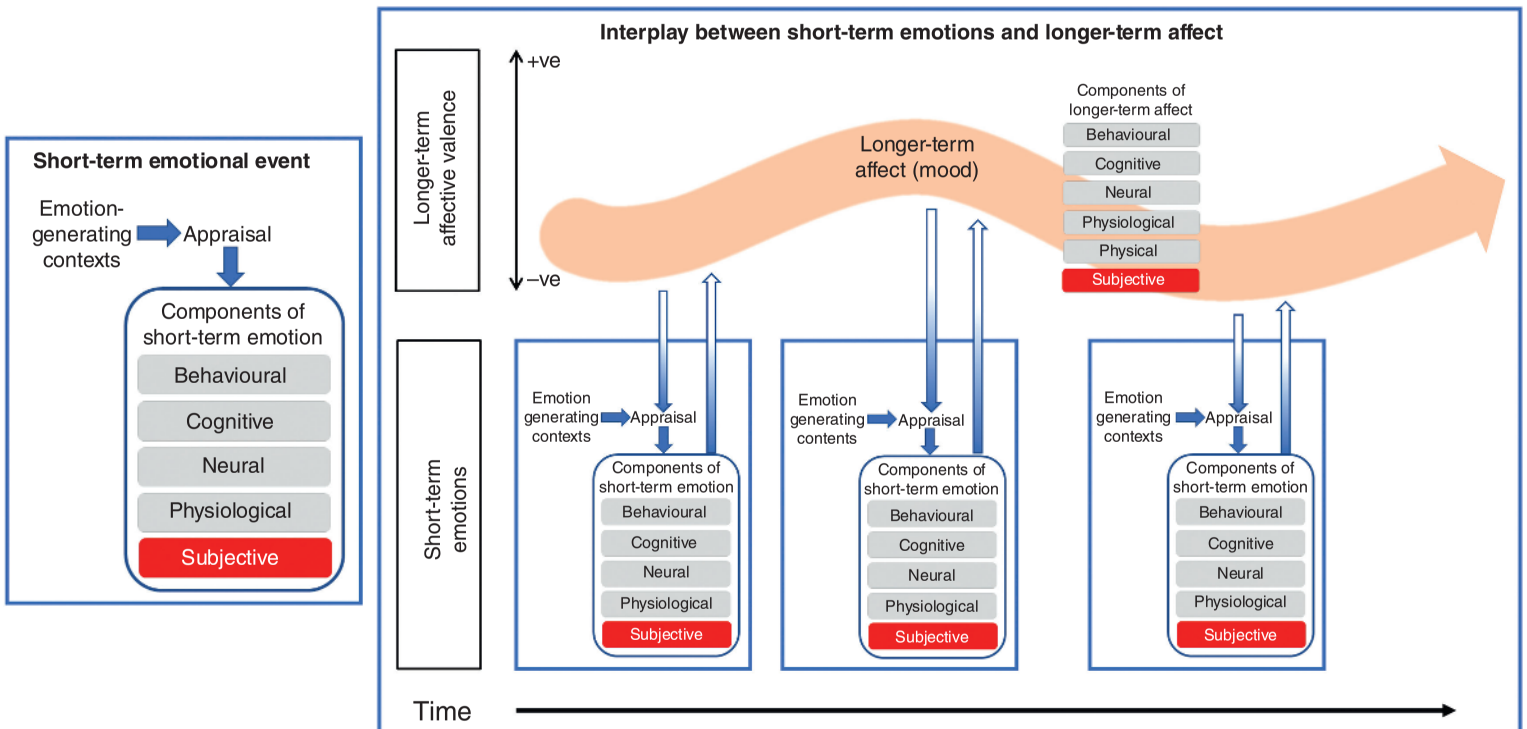


**Figure 1.6** Short-term emotion, longer-term affect and the componential view of affective states. Left-hand panel: emotion-generating contexts elicit appraisal and interpretation of the situation and lead to the resulting short-term emotion including, in sentient species, a subjective affective experience. This is what we are interested in from an animal welfare perspective, but it needs to be inferred from changes in other measurable components (also known as 'welfare indicators'; see Chapter 2) of the affective state, including behavioural, cognitive, neural and physiological markers. Right-hand panel: cumulative experience of short-term emotions leads to fluctuating 'background' mood states (and, in some cases, longer-term affective disorders) which in turn influence appraisal processes. The lower half of the panel shows a sequence of three emotion-generating events across time, appraisal of each of which is influenced by background mood (upper half of panel) which in turn is then influenced by the resulting short-term emotion. Longer-term affective states comprise similar components to emotions but may also include physical indicators that change more slowly such as morbidity and mortality.

they can be assessed by measuring these components. The final section of this chapter briefly introduces the challenges inherent in trying to use these measurable changes to make inferences about what matters most from a welfare perspective, an animal's subjective experience of their affective state: how positively or negatively they feel. It is these challenges that this book aims to tackle.

## Assessing animal affective states: the other minds problem and challenges faced by welfare scientists

In this chapter, we have seen that concerns about subjective affective states are at the heart of animal welfare (e.g. Mendl and Paul 2017). To better understand welfare, we therefore need to better understand and assess these states. This makes welfare science not only a fascinating field, but also a very challenging one.

That such internal, subjective experiences are private and inaccessible to measurement in others – the 'Other Minds' problem (e.g. Dennett 1996; Dawkins 2000; Farah 2008; Godfrey-Smith 2017; Avramides 2023) – is perhaps the biggest challenge facing any scientist interested in animal affective states (Paul et al. 2020). Historically, it explains why studying animal emotion has sometimes been regarded as "taboo" and not a proper topic for scientific research (e.g. Midgley 1984; LeDoux 1996; De Waal 2011). And today, it means that we still do not know where the boundaries of sentience are (Birch 2024) – that is, which non-human species (or developmental stages) *consciously* experience affective states. With our current knowledge, we just have to assume that these states are present in a variety of animals. This assumption makes biological sense given evolutionary homologies, and behavioural and cognitive similarities, between us and many other species. For example, in 2012, a group of consciousness researchers, including cognitive and neuroscientists, signed the Cambridge Declaration on Consciousness (Low et al. 2012), concluding that "…*the weight of evidence indicates that humans are not unique in possessing the neurological substrates that generate consciousness. Nonhuman animals*, *including all mammals and birds*, *and many other creatures*, *including octopuses*, *also possess these neurological substrates*". And in 2024, scientists, philosophers and other signatories of the New York Declaration on Animal Consciousness (Andrews et al. 2024) contended that "*empirical evidence indicates at least a realistic possibility of conscious experience in all vertebrates* (*including reptiles*, *amphibians*, *and fishes*) *and many invertebrates*". Such proposals make ethical sense as a 'precautionary principle', since to mistakenly treat sentient beings as unfeeling could cause great harm (e.g. Bradshaw 1998; Birch 2024). Nevertheless, they are not yet proven facts, which is why this book largely focuses on the postnatal birds and mammals for whom sentience assumptions are currently least controversial.

But the distribution of sentience is not the only challenge raised by the Other Minds problem. A second is that, as we noted earlier, even when we are comfortable assuming that sentience is present, we cannot know what different animals' specific affective experiences are like. As in our imagined examples of bats and lions, some animals' affective states may well be very different from our own: species a long way from us evolutionarily, or very different from us in their social or sensory worlds, are likely to have types of subjective experience that we lack, and to lack ones that we have. This is one key reason why this book largely takes a simple, dimensional view of affect, focusing on valence as a broad reference point for emotions in general: how positive or negative an affective state is, and therefore, how good or bad an animal's welfare can be said to be.

The third challenge arising from the Other Minds problem is that our job as welfare scientists is therefore to measure the unmeasurable! We can, however, measure in animals the changes in behaviour, cognition, physiology and health that, as we have seen in the preceding sections, accompany valenced subjective experiences (feelings). The challenge then is to infer reasonable conclusions from these measures about animals' subjective affective states. The next chapter covers how to do this logically and well.

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