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Joyful by nature: approaches to investigate the evolution and function of joy in non-human animals

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ABSTRACT

The nature and evolution of positive emotion is a major question remaining unanswered in science and philosophy. The study of feelings and emotions in humans and animals is dominated by discussion of affective states that have negative valence. Given the clinical and social significance of negative affect, such as depression, it is unsurprising that these emotions have received more attention from scientists. Compared to negative emotions, such as fear that leads to fleeing or avoidance, positive emotions are less likely to result in specific, identifiable, behaviours being expressed by an animal. This makes it particularly challenging to quantify and study positive affect. However, bursts of intense positive emotion (joy) are more likely to be accompanied by externally visible markers, like vocalisations or movement patterns, which make it more amenable to scientific study and more resilient to concerns about anthropomorphism. We define joy as intense, brief, and event-driven (i.e. a response to something), which permits investigation into how animals react to a variety of situations that would provoke joy in humans. This means that behavioural correlates of joy are measurable, either through newly discovered 'laughter' vocalisations, increases in play behaviour, or reactions to cognitive bias tests that can be used across species. There are a range of potential situations that cause joy in humans that have not been studied in other animals, such as whether animals feel joy on sunny days, when they accomplish a difficult feat, or when they are reunited with a familiar companion after a prolonged absence. Observations of species-specific calls and play behaviour can be combined with biometric markers and reactions to ambiguous stimuli in order to enable comparisons of affect between phylogenetically distant taxonomic groups. Identifying positive affect is also important for animal welfare because knowledge of positive emotional states would allow us to monitor animal well-being better. Additionally, measuring if phylogenetically and ecologically distant animals play more, laugh more, or act more optimistically after certain kinds of experiences will also provide insight into the mechanisms underlying the evolution of joy and other positive emotions, and potentially even into the evolution of consciousness.

Key words: affective state, animal behaviour, animal emotion, cognitive bias, judgment bias, play, reward-acquisition system.

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I. INTRODUCTION

Work on emotions and phenomenological experience in animals typically centres around fear and affective states that have negative valence. Darwin's *The Expression of the Emotions in Man and Animals* (Darwin, 1872) devotes one chapter each to 'low spirits' and 'high spirits', but then allocates four chapters to considering emotions such as 'ill-temper', sulkiness, disdain, contempt, disgust, guilt, and shame. Ekman & Friesen's (1976) iconic study of human facial expressions recognised six 'basic' or 'universal' emotions: four of them involving negative affect – fear, anger, disgust, and sadness; one whose valence is ambiguous – surprise; and only one positive – happiness.

Given the clinical and social significance of mental states with negative affect – not just emotions, such as depression, but other negative affect states, such as pain and suffering – it is unsurprising that these have received more attention from scientists than positive affective states. The drive to understand and regulate states with negative affect has also motivated a search for appropriate animal models, and thus worries about 'anthropomorphizing' animals have been counterbalanced by the desire to establish the validity of these negative affect states (so-called 'construct validity') for the study of human afflictions.

Positive emotions are sometimes considered to be evolutionary anomalies. Researchers have spent considerable effort explaining why negative emotions are better understood, more evolutionarily important, and/or better differentiated, while positive emotions have only been explored more recently (Fredrickson, 1998; Cohn & Fredrickson, 2009; Nesse & Ellsworth, 2009; Mendl & Paul, 2020). It is relatively well established that, compared with positive emotions, negative emotions are more easily differentiated, either through autonomic responses (Ekman, Levenson & Friesen, 1983; Cacioppo *et al.*, 1993; Levenson, 2014), facial expressions (Ekman, 1992), neurological responses, or self-report in humans (Ellsworth & Smith, 1988*a*,*b*). Indeed, multiple emotions like fear, disgust, anger, and frustration have been definitively operationalised. Some researchers have suggested that this differentiation is closely tied to evolution because each of these emotions requires a differentiated action response: fleeing in response to fear, fighting in response to anger, avoidance in response to disgust, etc. Positive emotions, in some cases, have instead been treated as simply an absence of negative emotions (e.g. Buss, 2000), rather than reinforcers for reward-acquisition systems (see Mendl & Paul, 2020).

Although positive affect has never been completely ignored by psychologists studying humans, when it comes to non-human animals, the balance has typically been firmly tilted towards the charge of anthropomorphism. However, as Balcombe (2009, p. 209) states: 'In the purest sense, human sentience is no more scientifically provable than is non-human sentience. While our sophisticated language likely permits us to share our pain/pleasure experiences more evidently on the psychological plane than for other taxa, the physical privacy of individual experience is as unbridgeable between two humans as it is between a human and a non-human animal. Quite literally, one person cannot actually feel another's pain or pleasure.' A few scientists, notably Jaak Panksepp and Marc Bekoff, have been willing to take a stand on positive emotions in animals, but a science of positive affect in animals is still absent. This deficit in knowledge about positive emotions and feelings in animals represents a ripe target for systematic investigation. Recent special issues in *Current Biology* on the biology of fun (2015) and in the *Philosophical Transactions of the Royal Society B* on the biology of laughter (2022), as well as popular press books like Frans de Waal's *Mama's Last Hug?* (2019), illustrate that there appears to be growing interest in the study of animal positive emotions.

While the 20th century eschewal of the consideration of sentience, consciousness and emotion in non-human animals is now changing (e.g. Seth, Baars & Edelman, 2005; Cabanac, Cabanac & Parent, 2009; Panksepp & Panksepp, 2013), research on non-human animal capacity for pleasure lags far behind research in humans or on negative experiences. This is curious, since pleasure is beneficial to animals in that it rewards individuals for performing adaptive behaviour (Cabanac, 1971) and animal behaviour research is considered almost entirely in an evolutionary framework that posits that behaviour should promote survival and reproduction (Balcombe, 2009). In fact, animal recognition of emotional expressions of other animals enables them to evaluate the intentions and motivations of others, providing important information about how to behave in social situations crucial to survival (Albuquerque *et al.*, 2016).

Positive emotions represent a specific challenge to measure scientifically in animals because the reward or motivation might be distant in time and/or space from the behaviour in question. However, some models treat positive emotions as important on multiple levels. Fredrickson's (1998) 'Broaden and Build' model highlights the potential for observable behaviours that can be accurately measured, as it proposes that positive emotions broaden the contexts, thoughts, and actions associated with an emotion and also allow the individual to build personal resources. For example, she argues that positive emotions build *social resources*, in that the presence of positive emotions serves as a method to enhance social bonds (Fredrickson, 1998). This is certainly true of positive emotions engendered by sexual behaviour, but likely extends to play, humorous interactions/teasing, and physical touch. Additionally, positive emotions should build *physical resources* (Fredrickson, 1998; Byrne, 2015). This is evident in many aspects of play, which tends to be associated with physical activities that are related to species-specific survival skills. Similarly, Nesse & Ellsworth (2009) argue that emotions have evolved to allow individuals to appraise specific contexts to take advantage of them better. Context-specific learning, in this conception, allows for anticipatory actions. For example, classical conditioning means that individuals respond to fear-inducing stimuli before danger becomes imminent. Similarly, operant conditioning would motivate actions associated with specific rewards, and cognitive processes allowing for inferences about potential futures and emotions would enable continued motivation over longer goal pursuit. Specifically, positive emotions 'motivate the organism to take advantage of environmental opportunities and to recognise when it has succeeded in doing so' (Nesse & Ellsworth, 2009, p. 132). Thus, an emotion such as joy would be seen in contexts that are perceived as accomplishments or progress towards one's goals (Izard, 1977; Lazarus, 1991; Fredrickson, 1998).

Here we review the current knowledge regarding the relatively poorly understood area of positive affect in non-human animals. Highlighting the benefits and disadvantages of each approach, we outline key behavioural and physiological methods that can be used to investigate positive affect, as well as other practical considerations, including what is known about reward-acquisition pathways in the brains of different taxa. In identifying research gaps, we emphasise the need to take a comparative approach, studying taxonomically diverse species with different life histories, levels of sociality and morphologies, in order to understand the evolution and function of positive emotion. Within positive affect, we highlight the possibility of investigating 'joy', because its characteristics make it particularly amenable to scientific study in a variety of non-human species. The animal welfare and ethical significance of such research is clear (e.g. Williams, 2021), but we argue that the study of positive affect, and more specifically joy, in animals has the potential to open up a broad range of questions, such as why and how humans and other animals maintain curiosity about their surroundings, and are driven to learn. These themes provide new avenues of research focusing on the deeper aspects of animal emotional cognition and the evolution of consciousness, and are thus central to both science and philosophy. As joy is potentially a contentious word to use when referring to non-human animals, we start by defining what we mean.

(1) Defining joy

As a term of ordinary English, 'joy' covers a range of feelings and emotions that typically share three characteristics: (*i*) the affective state is intense and positive; (*ii*) it tends to be event-driven (i.e. a response to some activity, or to the receipt of some news or information); and (*iii*) it tends to be relatively short term, although it may often modulate to a much longer-lasting feeling of pleasure or happiness. As with all ordinary language terms, but especially those attached to mental states, caution about their relationship to psychological and neurological reality is needed: is joy different from delight or ecstasy, is it just a sub-type of happiness, or is it a distinct state? Fortunately, it is neither necessary nor appropriate to answer such questions *a priori*. It is, however, necessary to identify operational criteria for the phenomena studied under the heading of 'joy'. These criteria provide a working definition that aids the selection of cases deserving of further investigation, rather than a conceptual analysis that can be picked apart with counter-examples. If the cases selected turn out to have a range of different psychological or neurological profiles, this may argue against joy as a 'natural kind', or may argue for a more restrictive definition that excludes some of the *prima facie* cases. The outcome of research cannot be predicted in advance.

The three characteristics listed above provide an initial working definition of 'joy'. In application to non-human animals, the second (event-driven) and third (brief) characteristics are the most straightforward to operationalise. Using this definition, we hypothesise that joy might be present in animals that respond in identifiable ways to events like the discovery of high-value food, or to the arrival of a long-unseen companion (e.g. dogs, dolphins, chimpanzees), or to snow (e.g. kea parrots), and who then engage in relatively short bursts of activity (vocalisations, play, etc.) directed towards salient entities in the triggering event.

The first characteristic (intense and positive affect) is more difficult to operationalise in non-human animals because it refers to an internal state. However, we believe it is possible to provide some ways of operationalising this, at least in some species, some of the time. A strategy that seems promising is to relate intense and positive affective states to learning. We hypothesise that joy constitutes an internal reinforcer that drives learning about the conditions that produce it. Building on this, we believe that the contagious nature of joy also has prosocial effects, enhancing bonding within a group, and leading individuals to seek repeated interactions with others. The dynamical aspects of joy are important in these respects insofar as: (*i*) its sudden onset provides a highly salient internal signal that allows for rapid encoding of the episode in memory, around which contextual learning can be structured; (*ii*) its intensity promotes relatively automatic behaviours (such as human laughter, and animal counterparts in kea, mice, and chimpanzees, described below) that are readily recognised by others, thus serving a prosocial function; and (*iii*) because it makes it more likely that the animal transitions to a more subdued state of positive affect (i.e. 'pleasure'), it supports health in the longer term through stress reduction.

Recent research provides strong evidence for various animal calls being analogous to laughter (Palagi, Caruana & de Waal, 2022). Modern phylogenetic analysis has shown that laughter dates back to at least the common ancestor of apes and humans, some 10–16 million years ago (Mya) (Ross, Owren & Zimmermann, 2009). This opens up the possibility that our closest relatives, chimpanzees, bonobos, orangutans and gorillas, may experience joy. Laughter may go back much further than this, given that rats exhibit 50 kHz ultrasonic calls when playing and when tickled by a human (Knutson, Burgdorf & Panksepp, 1998; Panksepp & Burgdorf, 2000, 2003; Panksepp, 2005; Burgdorf *et al.*, 2008; Hinchcliffe, Mendl & Robinson, 2020). They also prefer to spend time with other rats that 'laugh' a lot (Panksepp & Burgdorf, 2003) and these calls induce optimism (Rygula, Pluta & Popik, 2012). Laughter-like vocalisations have also been found in birds: playing the 'warble' call of the New Zealand kea parrot *Nestor notabilis* leads them to play more with each other, start playing with each other even if they are not already playing, and, if alone, start playing on their own (Schwing, Parsons & Nelson, 2012; Schwing *et al.*, 2017). These results have led to the suggestion that the kea warble call might also be analogous to human laughter. Play vocalisations that appear in similar contexts to human laughter are phylogenetically widespread among mammals and some birds (Winkler & Bryant, 2021), raising the possibility that joy might also show the same pattern in nature. Here, we propose concrete strategies for advancing knowledge about other species' experiences with joy, by both looking for observable behavioural correlates (Taylor *et al.*, 2022), and by considering the ways in which experiences may be differently manifested in different bodies and environments.

II. THE STUDY OF JOY IN HUMANS AND AVENUES FOR DIVERSIFYING RESEARCH

One key approach used in human studies of joy has been introspection, where joy is examined through the author's subjective feeling of this emotion (e.g. Close, 1981; Colebrook, 2007; Potkay, 2007; Dennis, 2010; Cottrell, 2016). A more formal way of implementing this process is to ask subjects to remember past episodes of joy (de Rivera *et al.*, 1989; Wilson & Spencer, 1990; Parse, 1997). Others have attempted to generate joy in participants by presenting highly positive stimuli, such as images, video, or music (Aksan & Kochanska, 2004; Wolf *et al.*, 2005; Lee & Lang, 2009; Koelsch & Skouras, 2014). A third approach is to create a series of questions (e.g. 'what is the most joy you felt?') organised into a scale to either measure all emotion (e.g. Fredrickson *et al.*, 2003), or joy specifically (e.g. Tolor, 1978). Researchers have also attempted to measure a large range of physiological correlates of joy, including heart rate, skin conductance, startle responses, facial electromyography and brain activity, as measured using functional magnetic resonance imaging (fMRI) (Wolf *et al.*, 2005; Lee & Lang, 2009; Koelsch & Skouras, 2014).

Research shows that joy in humans can be identified by high levels of self-reported positivity, specifically positive emotion that is short in duration, experienced as a spontaneous, involuntary event, and sometimes involving a momentary loss of self (Close, 1981; Colebrook, 2007; Potkay, 2007; Dennis, 2010; McEntee, Dy-Liaco & Haskins, 2013; Cottrell, 2016). This type of research may be replicable, for example in ape species that can be tested using both linguistic and non-linguistic methods. Fully linguistic apes (i.e. humans) can be tested using non-verbal experimental paradigms and observational coding of naturalistic behaviour. These non-verbal measures can then be compared to self-report of emotional experience. Non-linguistic apes, such as those living in zoos, sanctuaries, or the wild, can be studied non-verbally, using both observational and experimental methods. Additionally, semi-linguistic apes (language-trained apes in captivity) represent an opportunity to compare performance on non-verbal tasks and language-based tasks. Of course, the language-based tasks within the capabilities of these apes do not involve interviews or self-report, but they do raise the possibility of comparing humans to non-human apes on experimental paradigms that require simple linguistic instruction or interaction (Lyn, 2017).

Physiologically, joy in humans can be identified by increased orbicularis oculi activity (Wolf *et al.*, 2005; Lee & Lang, 2009). This muscle group encircles the eye and its activation represents a sign of positive emotion which cannot be faked (Ekman, Davidson & Friesen, 1990). The zygomaticus major muscle and depressor anguli oris muscle also appear to be activated when humans feel joy (Wolf *et al.*, 2005). However, other physiological measures, such as heart rate, skin conductance, and startle responses do not appear to be strong predictors of joy (Lee & Lang, 2009). A promising avenue comes from recent fMRI work on musically induced joy in humans (Ekman *et al.*, 1990; Koelsch, 2014; Koelsch, Skouras & Lohmann, 2018). Here, musical stimuli used for the 'fear' and 'joy' conditions led subjects to report experiencing joy or fear. They also activated different areas of the human brain, specifically the involvement of a neural network with computational hubs in the superficial group (SF) and laterobasal group of the amygdala, hypothalamus, and the striatum, with the SF appearing to play the most central role (Koelsch & Skouras, 2014). Even among non-primates, many of these areas have functional homologues (e.g. Cheng *et al.*, 1999; Reiner *et al.*, 2004; Oelschläger *et al.*, 2008), and detailed correspondence mapping of brain connectivity in humans and in other primates, currently being developed (e.g. Hayashi *et al.*, 2021), will better enable this line of research to go forward. The main challenge here is to understand what kind of musical stimuli would elicit joy or fear in animals, as has recently been done on pigs (Zapata Cardona *et al.*, 2022). This seems like a promising avenue of research.

In addition to music, other external stimuli might influence or modulate joy. Human joy can be influenced by weather, season, and temperature. Abiotic factors such as these may impact the mood and behaviour of humans and non-human animals alike. In humans, there is evidence that mood can be significantly improved by bright light (Kripke *et al.*, 1992; Kripke, 1998; Leppämäki *et al.*, 2003), or good weather (Keller *et al.*, 2005; Bayliss *et al.*, 2018), although results have at times been inconsistent (e.g. Denissen *et al.*, 2008; Klimstra *et al.*, 2011; Lucas & Lawless, 2013). Bright sunlight appears to increase the intensity of both positive and negative affect (Kööts, Realo & Allik, 2011), and appears to promote selfless behaviour (Guéguen & Lamy, 2013). Similarly, bright light improves human perception of mood and sociability and there is an inverse relationship between daily illumination and depressed mood (Jean-Louis *et al.*, 2005; Turner, Van Someren & Mainster, 2010). However, the abiotic effects on shorter-term bursts of positive emotion such as joy are undetermined.

The effect of weather on affect in animals appears to have been completely overlooked. This is all the more surprising given that light is the key abiotic signal regulating circadian patterns of behaviour and physiology (Dunlap, 1999; Turner *et al.*, 2010). A few studies have investigated the impact of artificial lighting on animal welfare, including play behaviour. Strong artificial light reduces play in nocturnal wistar rats (Vanderschuren *et al.*, 1995), most likely because a bright environment would be deemed unsafe in this species. Similarly, bright light induces anxiety-related behaviours in laboratory mice (Kapogiannatou *et al.*, 2016). This suggests there are conditions more conducive to animal joy, or at least play, and these can vary depending on season. Seasonal effects on observable behavioural indicators of pleasure in animals, like play, are frequently reported in the literature and are associated with periods of nutritional stress (low habitat quality). This is believed to be because play is expected to occur only when animals have enough energy due to high levels of nutrition (surplus energy theory). For example, in vervet monkeys *Chlorocebus pygerythrus* (Lee, 1984), gelada baboons *Theropithecus gelada* (Barrett, Dunbar & Dunbar, 1992) and squirrel monkeys *Saimiri sciureus* (Stone, 2008), play is reduced during the dry season with patchy and nutritionally poor food. There are also seasons where play is reduced due to a need to focus on higher priority behaviours, such as mating [e.g. harbour seals *Phoca vitulina* (Renouf, 1993); wolves *Canis lupus* (Cordoni, 2009)]. However, animals also pursue rewarding sensations that help maintain homeostasis (Cabanac, 1971), such as sun-basking in lizards, and this in turn also affects their activity budgets. For example, Columbian ground squirrels *Spermophilus columbianus columbianus* spend more time playing rather than feeding at midday, when temperatures are highest (Betts, 1976).

There are also apparently more 'frivolous' examples of animal play related to abiotic factors. Here, the reward for play is play itself, stimulating reward centres in the brain (Held & Špinka, 2011). For example, river otters *Lontra canadensis* play by sliding, not only down smooth rocks in rivers, but also on snow (Stevens & Serfass, 2005). Sliding in the snow has also been observed in corvids. Similarly, we have observed kea sliding down a steep snow-covered roof (X. J. N., personal observations). Indeed, the parrots flew to the top of the roof, lay on their backs, and slid down the snow compacted from the previous attempt, suggesting that they preferred the increased speed of the already-compacted snow. Similarly, Japanese macaques *Macaca fuscata* living in semi-natural conditions have been observed to construct and roll snowballs (Eaton, 1972).

III. MEASURING POSITIVE AFFECT IN NON-HUMAN ANIMALS

Although theorists hold different views about the ontological and definitional relationships between cognition and affective states – such as whether emotions have a cognitive component, or whether cognition merely informs and is informed by emotional responses – those wishing to pursue the kind of research advocated here can remain initially neutral between these theoretical stances. Despite differences among these theoretical stances, they agree on the idea that emotions and cognition are somehow connected. Thus, *empirical* relationships between cognition and joy are important to consider. For example, humans can feel joy upon the completion of a task, particularly when that task has been very challenging, and such joy clearly depends causally on recognising that the goal has been accomplished. In non-human animals, captive bottlenose dolphins *Tursiops truncatus* produce a vocalisation upon completion of a task and associated with the expectation of reward (Ridgway & Carder, 1998; Ridgway *et al.*, 2014; Dibble, Van Alstyne & Ridgway, 2016). This opens up new avenues of empirical investigation: can humans design cognitively challenging tasks that animals are motivated to complete, and thus manufacture situations in which they will experience and express joy? The field is ready for a serious science of positive emotion in animals, and we suggest that, being brief, intense, and event-driven, joy is an especially amenable expression of positive affect that is more likely to be measurable than, for example, a longer-lasting 'positive mood'. Below we outline four types of data that could provide empirical evidence for the presence of positive emotions in non-human animals: optimism, subjective well-being, behavioural indicators, and physiological indicators.

(1) Optimism (cognitive bias)

Humans can view the same stimulus as either positive or negative depending on their mental state – the classic glass half-full *versus* half-empty perspective (e.g. Eysenck *et al.*, 1991). Many animals do the same, interpreting the same stimulus as either more positive or more negative depending on how optimistic they are feeling (Harding, Paul & Mendl, 2004). Optimism and pessimism about future events are not equivalent to emotions like joy or fear, but studies with human participants have found relationships between emotion and optimism/pessimism using both traditional language-based measures (Sharot, 2011) and non-verbal designs used with animals (Aylward *et al.*, 2020). These relationships are found in both long-term mood disorders like depression (Roiser, Elliott & Sahakian, 2012), and short-term emotions (Paul *et al.*, 2011). More studies are needed to explore fully the relationship between emotion and expectations about the valence of future events, particularly the potential relationship between joy and optimism. Most human studies on future judgements are biased towards negative moods and focus on the relationships between emotional disorders like depression and pessimism (e.g. Strunk & Adler, 2009). But a relationship between positive mood and optimism has been reported in humans (Segerstrom *et al.*, 1998).

To measure optimism (and pessimism), animal researchers use a paradigm called the cognitive bias test, also called the ambiguous judgement task or judgement bias test. In this design, animals are trained on two anchor stimuli, one of which is always positive and one of which is always negative (or neutral). Researchers then measure what the animals do when presented with an ambiguous stimulus – do they respond as if the stimulus is positive or negative? For example, rats might be trained that when a box is placed on the right side of a table it always contains food, but when the box is placed on the left it contains nothing. The rats learn to approach the box quickly when it appears on the right of the table, and to approach more slowly or not at all when it is on the left. After the rats have formed these strong positive and negative associations, the box is placed in an intermediate location, halfway between the right and left sides, and the researchers record whether the rats approach and how quickly they approach. A more optimistic animal will approach faster because it will judge the box to be more similar to the positive stimulus (right-hand box), while a more pessimistic animal will approach slower because it will judge the box to be more similar to the negative stimulus (left-hand box).

This flexible categorisation of ambiguous stimuli as more positive or negative has been used across a large range of animals, paradigms, and contexts. Manipulation of an animal's environment, or the animal itself, leads to predictable positive or negative biases in judgements of ambiguous stimuli. Rats (Brydges *et al.*, 2011; Richter *et al.*, 2012), starlings *Sturnus vulgaris* (Bateson & Matheson, 2007; Matheson, Asher & Bateson, 2008) and pigs (Douglas *et al.*, 2012) approach ambiguous stimuli more quickly after having their home environments enriched, and more slowly when housed without enrichment. Similarly, when animals rather than their environments are negatively manipulated – such as when piglets are handled roughly (Brajon *et al.*, 2015), calves are separated from their mothers (Daros *et al.*, 2014), honeybees are shaken (Bateson *et al.*, 2011), or chicks are socially isolated (Salmeto *et al.*, 2011) – they are slower to approach ambiguous stimuli. Positive manipulations, such as the tickling of rats, or tool use in New Caledonian crows *Corvus moneduloides*, lead animals to approach ambiguous stimuli more quickly (Rygula *et al.*, 2012; McCoy *et al.*, 2019). In rats, greater positive bias in the categorisation of ambiguous stimuli is also associated with laughter-like vocalisations: optimistic individuals 'laughed' more (Rygula *et al.*, 2012).

These findings establish the cognitive bias test as one that can determine the degree of optimism (expectation of a positive *versus* negative outcome) that an animal feels after experiencing an external stimulus. Importantly, the relationship between positive emotion and positive bias on the cognitive bias test has also been seem in humans. In a task involving lines presented at various angles, human participants in more positive moods responded to ambiguous stimuli as if they were more similar to the positive stimuli than the negative stimuli they had been trained on (Segerstrom *et al.*, 1998). The relationship of joy to performance on the cognitive bias test is currently unknown. But, asking whether experiences that spark joy in humans lead to animal subjects approaching ambiguous stimuli more quickly could deepen our understanding of animal joy.

(2) Subjective well-being

Joy has been considered part of positive affect that is associated with subjective well-being (Chen, Lehto & Cai, 2013; Gana, Saada & Amieva, 2015), with Martela (2017) describing joy as a sub-dimension of well-being. Subjective well-being has been used for comparative research between humans (as reviewed by Diener *et al.*, 1985; Diener & Ryan, 2009) and non-human animals (King & Landau, 2003; Weiss *et al.*, 2009; Schaefer & Steklis, 2014; Gartner, Powell & Weiss, 2016). Well-being is assessed in humans using questions relating to an individual's life satisfaction and balance of positive and negative affective states (Diener *et al.*, 1999) and in non-human animals through questionnaires to the human caregivers of the animals (King & Landau, 2003). This method of assessing animals' well-being has been used with several primate and felid species and has been shown to be a reliable measure (e.g. King & Landau, 2003; Weiss *et al.*, 2011), with questions interpreting the animals' moods, social interactions, and personal control, as well as an item asking how happy the human would be to be that particular animal.

Subjective well-being can be used as a short- or long-term measure (Eid & Diener, 2004) and has been shown to be stable over time in humans (Sandvik, Diener & Seidlitz, 2009) and non-human primates (Weiss *et al.*, 2011). However, given that these measures depend on humans interpreting animals' mental states through their behaviours, such work is open to the criticism of being overly anthropomorphic. Recent work has begun to address this difficulty, by correlating measures of subjective well-being with short-term physiological responses, such as cortisol levels (Inoue-Murayama *et al.*, 2018). These kinds of correlations would be the most useful for exploring joy, specifically, since our definition would predict an intense, short-term burst of emotion which could be correlated with similar physiological responses.

Alternatively, a study on captive chimpanzees *Pan troglodytes* suggested that higher well-being was associated with reduced play behaviour, such that chimpanzees that played less were counterintuitively rated as having higher subjective well-being (Robinson *et al.*, 2017), possibly because play can sometimes also be associated with stress (Held & Špinka, 2011). Since play may be one possible indicator of animal joy (see Section III.3.*b*), this suggests either a potentially complex relationship between animal subjective well-being and joy, or issues with the anthropomorphic basis of this method.

(3) Behavioural indicators of joy and positive contexts

One reason why the study of positive affect in non-human animals has been largely scientifically intractable is because it is not trivial to measure internal experiences in the absence of language. However, there are several types of behaviour that are likely correlated with strong positive affect. Expressions of play, emotion-related vocalisations (Burgdorf & Panksepp, 2006; Winkler & Bryant, 2021), and facial expressions are all possible markers of joyful states, particularly in mammals. While play can occur as a result of a positive affective state or elicit it, there are a number of contexts that are positive and likely cause joy. Examples are receiving preferred food or social attention as well as access to preferred social or mating partners and mating itself. Animals often produce specific signals in such contexts (McComb *et al.*, 2000; Pradhan *et al.*, 2006; Slocombe & Zuberbuehler, 2006; Serrapica *et al.*, 2017) and studying these can lead to indicators of joy.

Play and emotion, particularly joy, pleasure, happiness, and contentment, are interwoven – indeed, by generating positive affective states, play is self-rewarding (Burgdorf & Panksepp, 2006; Held & Špinka, 2011; Ahloy-Dallaire, Espinosa & Mason, 2018). Consequently, play is generally considered a strong indicator of positive affect (e.g. Boissy *et al.*, 2007; Held & Špinka, 2011; Palagi *et al.*, 2016), although in some cases it may serve as a coping mechanism to deal with unexpected situations (Špinka, Newberry & Bekoff, 2001). Additionally, human laughter and certain facial expressions are well known to convey positive affect, and in some animals, vocalisations akin to laughter have been found [rats (Panksepp & Burgdorf, 2003); parrots (Schwing *et al.*, 2017)]. Similar findings suggest that mammalian facial expressions can convey emotional information (e.g. Lansade *et al.*, 2018). As detailed below, research to date suggests that play behaviour and acoustic signals are likely the most reliable indicators of positive affect in non-human animals.

(*a*) *Facial expressions and other behavioural/postural indicators*

Facial behaviours are most often termed 'facial expressions', as they are so regularly seen as expressive of internal emotion in humans (Waller, Julle-Daniere & Micheletta, 2020). In animals, facial behaviours have most often been studied as indicators of negative emotions in mammals, such as fear or pain (see Descovich *et al.*, 2017). However, recent studies have begun to explore mammalian facial behaviours as indicators of positive emotion. For example, Vick *et al.* (2007) created the first non-human version of the Facial Action Coding system (FACS) showing that, in chimpanzees, facial behaviours showed many homologues with human expressions. For example, the muscles that contracted in humans during laughter were the same muscles that contracted in chimpanzee play faces (Parr & Gothard, 2007). Other researchers have detailed behaviours associated with positive emotion in other animals, including changes in features, such as ear posture and eye shape (Proctor & Carder, 2014; Finlayson *et al.*, 2016; Lambert & Carder, 2017). However, in at least one case (domestic horses), neither ear nor neck posture were reliable indicators of positive affect, and some expressions (eye size, lip contraction) were more reliably correlated with negative affect (Lansade *et al.*, 2018).

Perhaps the most promising facial behavioural indicators of positive affect are found in studies using pleasant- and unpleasant-tasting stimuli. Several studies have found that stereotyped facial expressions that convey emotional information in humans are mirrored in closely related primate species (Steiner *et al.*, 2001; Parr & Waller, 2006). Overall similarities in the facial responses between rodents and primates (including humans) to tastants, whereby sweet flavours elicit licking responses and bitter flavours elicit gaping and head shaking, suggest shared evolutionary origins (Balcombe, 2009). However, other taxa, like birds, do not have the complex facial musculature of mammals, and as such cannot produce facial expressions associated with emotion (Emery & Clayton, 2015), but they do have the ability to erect feathers in localised body parts, which may be homologous. Nevertheless, further problems with facial expressions during tasting events arise: aside from the clear 'disgust' and 'liking' facial expressions associated with bitter and sweet tastants, facial expressions generally are more reliably associated with positive affect than other behavioural indicators, but they are potentially open to misinterpretation as facial expressions can be used in different contexts (see Descovich *et al.*, 2017). For example, the communicative function of the grimace (or bared-teeth display) common to mammalian species ranging from canids to primates, differs dramatically depending on species and social context (Parr & Waller, 2006).

Misinterpretation is a pervasive problem when using behavioural indicators of emotion. For example, inactivity can be construed as a negative state (poor health, boredom), or as a positive state (sun-basking, post-consummatory inactivity). Without full context, it is difficult to discern one from another (Fureix & Meagher, 2015). Additionally, most studies in this area do not address the specific mechanisms underlying the behaviours, making the utility of the findings somewhat limited. For example, in goats, ear position correlates with several other behaviours and with 'arousal', described as bodily excitation (i.e. movement), which, unsurprisingly, also correlates with several other motion-based behaviours (Briefer, Tettamanti, McElligott, 2015). Similarly, lambs anticipating a toy or food reward behave differently than control lambs, as measured by the number of transitions from one behaviour to another and the time spent still (Anderson *et al*., 2015). Clearly, if a comparative control group is needed every time a positive or negative emotion can be reliably inferred (akin to requiring morose people to stand alongside happy people in order to evaluate happiness), this method is of limited use. What is needed, like a human Duchenne smile (Ekman *et al*., 1990), is a reliable and reproducible expression of positive affect. Unfortunately, behavioural markers do not yet meet the bar as reliable indicators of positive emotion, but research in this area is promising (Davila-Ross & Palagi, 2022). With a better understanding of the species-specific nuances of posture and facial expression, aided by techniques like machine learning to code fine-grained behaviour, these sorts of indicators may be more useful in the future. For example, facial behaviours have been codified in several species through the use of FACS – making homologues easier to analyse (Waller *et al*., 2020) and machine-learning vocal categorisation systems like DeepSqueak (Coffey, Marx & Neumaier, 2019) have been used to automate the analysis of vocal behaviour that had been previously difficult or impossible. Additionally, there is now considerable use of machine learning to classify postures and other behaviours, particularly among farm animals (e.g. Hansen *et al*., 2018; Neethirajan, 2020; Balasso *et al*., 2021; Price *et al*., 2022).

(*b*) *Play*

Animals explore their environments and manipulate objects in many different ways. Many species interact with their environments in ways that appear to be driven by pleasure and excitement, rather than necessity. For example, rats have been shown to play hide-and-seek with humans, taking on the roles of both 'seeker' and 'hider' (Reinhold *et al*., 2019). The adaptive functions of play may differ depending on species, sex and age, and are often temporally disassociated from the occurrence of the play behaviour (i.e. the adaptive function of childhood play may not be observable until adulthood). By its very nature, play is difficult to define precisely, and may involve a mixture of social play, solitary (often locomotor) play, and object play.

Playful interactions with the physical environment are found across many species, and these playful contexts may elicit or encourage the expression of joy. Because pleasure can act as a reinforcer for play (Anderson *et al*., 2015), it can act as the proximate mechanism that causes animals to behave adaptively – by playing (Balcombe, 2009). Pleasure is associated with positive emotional states (e.g. Trezza, Baarendse & Vanderschuren, 2010), which suggests that play may assist animals to interpret and respond correctly to a play partner's emotions (Kuczaj & Horback, 2013). Thus, social play may require high-level cognitive architecture, and it may be notable that, aside from domesticated species, social play is found at particularly high levels in primates and cetaceans (Palagi, 2011; Janik, 2015).

Physical play typically involves unusual ways of moving the body in relation to the environment (e.g. sliding, swinging, rolling, inverting, bouncing), moving an object in relation to the body (e.g. waving, shaking, juggling), or moving the body and a substrate to connect with one another (e.g. squishing, splashing). These types of play may provide opportunities for animals to rehearse problem-solving by placing them in scenarios where they lose partial control over their locomotion, balance, or senses and must regain that control or quickly adapt to its loss (Špinka *et al*., 2001). By handicapping themselves in various ways in a safe environment, play provides a safe context for animals to train for the unexpected (Špinka *et al*., 2001). This environmentally targeted play can occur in solitary individuals (there is some evidence for play in octopus *Octopus vulgaris*; Zylinksi, 2015), or in social groupings, and is widespread across animal taxa [e.g. marsupials, placental mammals, birds, reptiles, and fish (Bekoff & Byers, 1998; Burghardt, 2005)].

Play behaviour is especially widespread among mammals, and is found in about half of all avian families (Ortega & Bekoff, 1987). Burghardt (2005) suggested five criteria that are critical to the definition of play across animal species. These are: (*i*) an incompletely functional behaviour that is (*ii*) voluntary and spontaneous, (*iii*) initiated under stress-free conditions, (*iv*) repeated but not stereotypic, and (*v*) modified or exaggerated from its regular pattern. For our goal of identifying reliable markers of positive affect, the key question is how we recognise play in other species. For many, the answer is that it is simply obvious and intrinsically recognisable to humans. Indeed, as a playful species ourselves, we do appear to be able to assess rapidly the criteria suggested by Burghardt (2005), but what is particularly apparent to us is that, at the time of its occurrence, play is utterly pointless. This is because, in play, there is limited immediate function (i.e. the actions are not instrumental to a goal, like acquiring food; Burghardt, 2005). In play, the actions are typically repeated. This criterion is very useful for scientists when attempting to distinguish play from instrumental actions. Sliding provides a good example of this. If a raven *Corvus corax* slides down a snowbank on its stomach, we might see it as an effective mode of descent that did not require taking flight. However, if it flies back up to the top of the hill and repeats the sliding several times, it is clear that it is not trying to descend efficiently, but more likely that it simply enjoys the activity (e.g. Heinrich & Smolker, 1998).

While environmental play can occur either with or without others, there are some types of play that require a partner. Common forms of social play include chasing, wrestling, play biting, and other forms of 'rough-and-tumble' play. These can resemble fighting, but are accompanied by communicative signals marking them as playful (reviewed in Palagi *et al.*, 2016). Signals include a range of forms and modalities: facial expressions (e.g. play faces in primates; Waller & Dunbar, 2005), whole-body movements (e.g. play bows in dogs; Bekoff & Allen, 1998), or vocalisations (e.g. warble calls in kea; Schwing *et al.*, 2017). Some signals are given during invitations to play or at the start of a play bout, while others may emerge as a result of the increased excitement during play (e.g. laughter in apes; Ross *et al.*, 2009). Play signals help researchers to identify play, yet it is the signals that result from animals experiencing pleasure during play that may be especially useful in identifying interactions in which animals are more likely to experience joy.

In some species (notably apes and rats), social play may result in 'laughter' (Panksepp & Burgdorf, 1999; Ross *et al.*, 2009; see Section III.3.*c*). The function of laughter in animal play is debated, but it is likely to be used to strengthen or signal social bonds. In chimpanzees, laughter extends play sessions (Matsusaka, 2004). Chimpanzees also laugh differently when they are responding to others' laughter, perhaps signalling alignment or social closeness (Davila-Ross *et al.*, 2011). In humans, laughter is often a marker of joy, so it is not far-fetched to believe that it could serve a similar role in other animals, particularly other apes. Across cultures, people associate laughter with joy (Sauter *et al.*, 2010). This raises exciting possibilities of a deep link between humour and joy, as connected by laughter and play. In their book on humour and cognitive science, Hurley *et al.* (2011) argue that some forms of play, such as tickling and chasing, may be the earliest manifestations of (proto) humour and that social play is likely the 'birthplace' of laughter. Laughter, whether human or animal, may thus be a particularly useful external signal of the internal experience of joy.

Across species, juveniles typically engage in more play behaviours than adults do, although some kinds of play frequently persist into adulthood (Fagen, 1981; Ortega & Bekoff, 1987; Brown, 1988; Mendoza-Granados & Sommer, 1995; Smith *et al.*, 1996; Dolhinow, 1999; Lee & Moss, 2014). Even within the juvenile period, age can affect the type and amount of play. For example, in chimpanzees, 3 to 6-year-olds play longer with novel objects than 7 and 8-year-olds. Older juveniles are initially as interested in novel objects as younger juveniles are, but the novelty appears to wear off more quickly (Welker, 1956). Despite higher levels of play in immature individuals, and the greater frequency of expressions of joy during play, we know little about whether proclivity towards experiencing joy is also higher in younger individuals. Increased activity levels and expressiveness in juveniles may mean that their external expressions of emotion are more readily detectable by human observers. This further complicates the ability to compare subjective experiences of joy across age classes. If a younger individual is more likely to express joy on its face or in its 'body language' than an older individual experiencing the same intensity of emotion, then measures of joyful behaviour will be skewed towards the young. This cannot be avoided in studies that use behavioural measures to study species that cannot provide self-reports of emotional states, but is important to keep in mind when studying age effects in expression of emotion.

(*c*) *Acoustic signals in positive contexts*

Acoustic communication is widespread in birds and mammals, and may be the most common form of communication in these taxa (e.g. McComb *et al.*, 2000; Pradhan *et al.*, 2006; Slocombe & Zuberbuehler, 2006; Wilson *et al.*, 2008). Therefore, if non-human joy or other measures of event-driven positive affect are communicated to others, vocalisations emitted exclusively during pleasurable experiences would be a clear path to investigate. Indeed, research across different animal species suggests that vocalisations may be reliable indicators of positive emotion. For example, snorts in domestic horses appear to be reliable indicators of positive emotions of low intensity, such as when feeding (Stomp *et al.*, 2018), while, based on contexts such as affiliative interactions and anticipation of food, in Przewalski's horses *Equus ferus przewalskii*, positive affect is vocalised using a 'nicker' call (Maigrot *et al.*, 2017).

Many animals produce vocalisations during play behaviour (Palagi *et al.*, 2016; Winkler & Bryant, 2021), indicating likely positive affect. For example, the rate of play vocalisations of dwarf mongoose *Helogale undulata rufula* juveniles increases with arousal, or motivation to play (Rasa, 1984). In rats, individual variation in the positive valence associated with tickling is reflected in the rate of their 50 kHz 'laughter' vocalisations (Hinchcliffe *et al.*, 2020). Laughter vocalisations in some animals are very similar to human laughter. All ape species laugh (Davila-Ross, Owren & Zimmermann, 2009), but we know relatively little about the conditions in which laughter naturally occurs across individuals, age classes, and species. Exploring the contexts in which apes naturally laugh and identifying other behaviours that frequently co-occur with laughter in apes would build a strong foundation for work on joy in primates.

Human laughter is contagious, in that people are more likely to laugh after hearing someone else laugh (so-called laugh tracks during television sitcoms are built on this premise). Contagious behaviour, like laughter or yawning, may indicate contagion of the underlying motivational/emotional states. Emotional contagion is thought to occur in situations where one individual is emotionally moved by perceiving the emotional state of another (Špinka, 2012) and results in emotional state-matching. Anyone who has observed cows being corralled into a slaughterhouse will have seen negative emotional contagion in non-human animals, but this has also been shown to occur in positive situations using vocalisations. Audio playback of the 'warble' call of kea parrots results in kea spontaneously playing (Schwing *et al.*, 2017). This suggests that the kea warble call is analogous to human laughter, in that it is an emotionally contagious social call that is produced during play, and provokes play in and of itself.

As the warble call is also performed during solitary play, this also suggests that excitement level may be the instigator of play vocalisations in kea.

In rats, 50 kHz calls emitted during rough-and-tumble play (Burke *et al.*, 2018) can be elicited through tickling and are inhibited by aversive stimuli (reviewed in Wöhr, 2018). This led Burgdorf & Panksepp (2006) to hypothesise that these calls reflect a positive affective state akin to human joy and laughter. These calls are socially important. They are used to promote and maintain playful behaviour, both when produced spontaneously during social interactions and when experimentally presented in playback studies (reviewed in Wöhr, 2018). They also induce optimism in the cognitive bias test (Rygula *et al.*, 2012) and are thought to be emotionally contagious (Saito *et al.*, 2016), with rats also choosing to associate with other rats that produce these vocalisations (Panksepp & Burgdorf, 2003).

The calls of rats have been extensively studied in terms of their physiological effects, the pathways of which are described in more detail in Section III.4. Ultrasonic calls are initiated by the activation of dopamine (pleasure) receptors within the dopaminergic reward subsystem of the brain (Simola & Brudzynski, 2018). Consistent with this, in addition to social and sexual contact-calling and social play, 50 kHz calls are produced in reward-based appetitive contexts, such as sweet tastants, drugs of abuse, and food, particularly after periods of deprivation (Mulvihill & Brudzynski, 2018). Intriguingly, recent work suggests that high levels of these calls may be indicative of high-arousal and mania-like elevated moods: sleep-deprived rats call more frequently, but this is reversed by administration of the antimanic drug lithium carbonate (Wendler *et al.*, 2019).

(4) Physiological indicators of joy

Whilst our particular cognitive architecture may support different subjective experiences than other animals or may permit us to derive pleasure from more abstract concepts, the fact that subcortical regions of the brain are involved in emotions (Burgdorf & Panksepp, 2006) suggests that conceptual thought is not necessary for the experience of emotion. Indeed, some argue that emotion must, in fact, be a trait conserved at a basal level well before the divergence of mammalian groups (Berridge & Kringlebach, 2008; Cabanac *et al.*, 2009; Albuquerque *et al.*, 2016), as the ability of animals (especially social animals) to 'read' the emotional situation of another animal (whether this be through mirroring/sharing the affective state of the other animal, or more simply through increased attention towards the other; see Schneider *et al.*, 2020) is bound to have significant impacts on fitness. A misread cue may result in missed opportunities for reproduction, or even cost an animal its life. Because of this, models of positive emotions are largely based on observations of successful approach and consummatory behaviours.

Berridge & Kringlebach (2008) argue that hedonic valence acts as the interface turning sensation into goal-directed behaviour. This behaviour is often adaptive, with the classic examples being food and sex. For social animals, the pleasure of social interactions, like grooming, facilitates adaptive outcomes such as parasite removal and social bonding. Similarly, negative experiences, like pain, contribute to adaptive goal-directed behaviour – avoidance. Following this logic, the common survival function of hedonic responses, coupled with neural conservation (see Section III.4.*b*), suggests that both humans and non-human animals experience pleasurable responses (Berridge & Kringlebach, 2008; Berridge, 2018). This view is corroborated by facial expressions produced in response to different tastants described in Section III.3.*a*.

Emotions can be classified in three dimensions: approach/avoidance, arousal or bodily excitation (Cabanac, 1979; Burgdorf & Panksepp, 2006), and a dimension incorporating the strength of the feeling. Viewed in terms of neurobiology (an area now referred to as affective neuroscience; Berridge & Kringlebach, 2008), the approach/avoidance dimension might be mediated in large part by amines (especially dopamine), while the arousal dimension could be primarily influenced by opiate receptors (Burgdorf & Panksepp, 2006). Under this conceptualisation, joy could be seen as approach coupled with high arousal (Burgdorf & Panksepp, 2006), but could vary in intensity. However, the hedonic dimension is invariably affected by rewards, which are altered, in turn, by motivation and learned associations (Berridge & Kringlebach, 2008; Berridge, 2018), all of which are also affected by hormones. This leads to a well-known, and somewhat simpler model presented by Russell, Weiss & Mendelsohn (1989) with only two dimensions: arousal indicating intensity, and valence which has fitness effects (Briefer *et al.*, 2015; Crump *et al.*, 2020; Mendl & Paul, 2020). Under this conceptualisation, joy would have positive valence and high arousal, and is part of a theorised reward acquisition system (Fig. 1), while states such

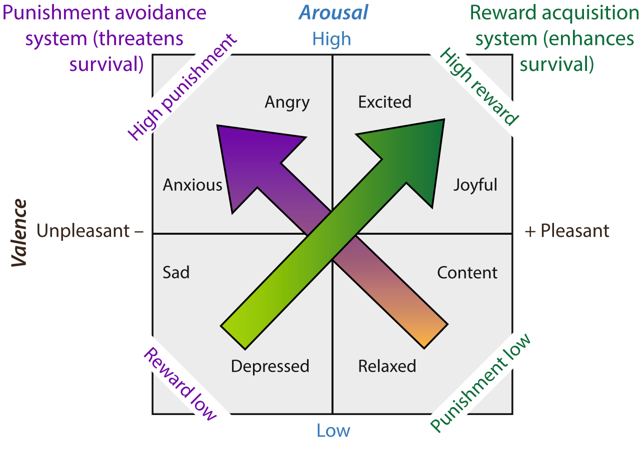

Fig. 1. Proposed model of emotional states. Valence coupled with arousal produces specific affective states (indicative words in quadrants) relating to emotions. The purple arrow indicates the punishment avoidance system and the green arrow indicates the reward acquisition system, with the upper quadrants indicating strong arousal or intensity of emotion. Modified from Crump *et al.* (2020) and Mendl & Paul (2020).

as anxiety, which have negative valence, would form part of a punishment avoidance system (i.e. avoid risk).

Vertebrates respond to noxious stimuli both behaviourally and physiologically (de Bruijn & Romero, 2011), falling under the remit of the punishment avoidance system (Fig. 1). Under the premise that neuroendocrine systems are about regulation and have antagonistic processes, we should also expect corollaries for positive stimuli. Negative physiological responses, known as the 'stress response', consist of two pathways. One is mediated through amine-based neurotransmitters/neurohormones and is quickly regulated by the central nervous system and glands (the sympathetic–adrenal–medulla axis), while the other, slower, endocrine pathway (which releases glucocorticoids) is regulated by the hypothalamic–pituitary–adrenal (HPA) axis. Thus, neuroendocrine aspects of joy cannot be approached in isolation, and a brief outline of the effect of both hormonal and neuronal regulation of pleasure is needed to understand the physiological complexities underlying positive emotions, which may have evolved to facilitate the seeking of rewards (e.g. food, mates, social grouping).

(*a*) *Hormones*

Vertebrate glucocorticoids, such as corticosterone in birds, amphibians and reptiles, and cortisol in fish and mammals (the latter sometimes have a mixture of corticosterone and cortisol), are hormones whose secretion increases in stressful scenarios, leading to a variety of metabolic changes, including energy increases and improved capacity for memory formation (Boonstra, 2004; Reeder & Kramer, 2005). In birds, adverse weather can cause measurable stress responses (Romero, Reed & Wingfield, 2000; Bize *et al*., 2010; de Bruin & Romero, 2011), and this is especially true during periods when animals may be physiologically challenged and vulnerable, such as during feather moulting (Romero *et al*., 2000), although 'tolerable' weather (and associated lack of stress) is highly dependent on species and its natural habitat (e.g. Romero *et al*., 2000).

Oxytocin (OT) is often considered an indicator of positive state; as such, in contrast to most research on animal well-being, OT research is biased towards positive valence and is studied primarily in social mammals, such as primates, marine mammals, canids and rodents (Rault, van den Munkhof, Buisman-Pijlman, 2017; Robinson *et al*., 2017; Rossi *et al*., 2018). In these cases, OT has typically been found to increase in response to social interactions, although non-social or negative situational controls are often lacking (Rault *et al*., 2017). Its avian counterpart, mesotocin, has also been found to promote pro-social behaviour, but has not been found to influence bond formation (Duque *et al*., 2018, 2020). As this research is still in its infancy and methodology among studies differs greatly, little is known about the precise mechanisms of action of the 'feel good' OT hormone in mammals, and less so for mesotocin in birds. Thus, it is premature to conclude that increased OT or mesotocin is as good an indicator of positive emotion as is often purported (Rault *et al*., 2017); indeed, a recent study on horses suggests that lower OT baseline levels might be associated with improved well-being, but is not a good measure of a discrete positive emotional change like joy (Lansade *et al*., 2018). Due to its role in mother–offspring relationships, it is also often permanently elevated in dependent offspring (Robinson *et al*., 2020).

For both stress hormones and positive social hormones, results are highly variable and dependent on, among other things, sampling method, species, age, population, photoperiod (circadian patterns affect circulating hormone levels), and season in which animals are sampled (Romero, 2002; Boonstra, 2004; Reeder & Kramer, 2005; Rault *et al*., 2017; Duque *et al*., 2020). Any research in these areas should minimise these confounding variables.

(*b*) *Neurocircuitry and neurotransmitters*

A systematic review of the human literature (Machado & Cantilino, 2017) identified neural correlates of positive emotions in reduced right prefrontal activation, enhanced left prefrontal activation, and bilateral reductions in temporoparietal cortex, along with increased activity in cingulate gyrus, inferior and middle temporal gyri, amygdala, and ventral striatum. These findings have not yet been mapped to animal models, although homologous areas exist in many species of mammal (Esperidião-Antonio *et al*., 2017) and possibly birds (Emery, 2006; Emery & Clayton, 2015; Medina, Abellán & Desfilis, 2019).

Two primary methods have traditionally been used to investigate the role of neurotransmitters in the expression of behaviour. Pharmacological studies typically block or facilitate the release or receptivity of neurons towards neurotransmitters (receptor agonist and antagonist studies), while behavioural studies often use drug-based paradigms (e.g. Buck *et al*., 2014; Grant *et al*., 2018), typically involving animals seeking a reward, such as a drug that increases dopamine levels in the mammalian brain. Some of the work in this area is informed by self-stimulation studies in which rats and many other species will perform behaviours to stimulate the expression of neurotransmitters in specific areas of the brain (Olds, 2010; Berridge & Kringelbach, 2015). Although the relationship between dopamine, reward, and pleasure is complicated (Berridge & Robinson, 1995, 2016), further investigation of the dopamine system (along with the role of endocannabinoids; discussed below) is undoubtedly important for future understanding of joy.

Based on these types of studies, we know that, in mammals, positive affect is largely mediated by the limbic system, pathways of which notably extend into the very ancient upper brainstem, common to all vertebrates, and in sub-limbic systems within sub-neocortical regions of the brain (Burgdorf & Panksepp, 2006; Berridge & Kringelbach, 2008). Birds have a functionally homologous brain area to the limbic system (Atoji & Wild, 2007) and dopamine pathways appear to be essential to the avian brain reward system (Emery & Clayton, 2015), yet comparative studies on the pathways involved in behaviours resulting or emerging from positive affect in birds and other taxonomic groups are needed. To date, most research has been done on laboratory mammals (typically rats) using the paradigms of anticipatory eagerness and gustatory pleasure, which appear relatively conserved across mammals (Burgdorf & Panksepp, 2006).

Dopamine systems have a major role in regulating play behaviour in rats (probably because of dopamine's effect on the brain's reward system), and studies suggest that basal control of play behaviour in rats is subcortical (Siviy & Panksepp, 2011). Other important neurotransmitters (or their receptors) which appear to affect play are opioids and endocannabinoids. Although their role is as yet unclear, endocannabinoids may affect the pleasure experienced during play, rather than the motivation to play (Berridge & Kringelbach, 2008; Trezza *et al*., 2010). Noradrenergic receptors (those responding to noradrenaline) also seem to regulate play, although again their role is unclear, possibly because noradrenaline is involved in the modulation of a wide range of neurobiological processes. This is also true for the neuromodulator serotonin, which plays an important role in the regulation of mood, emotion, and social behaviour (Wöhr, van Gaalen & Schwarting, 2015). That these neurotransmitters are involved in many different neurobiological processes complicates research specifically on joy. However, although much is left to learn about how they may specifically mediate positive affect and its behavioural outcomes, this avenue of research is ultimately likely to yield important insights in this area.

IV. CONCLUSIONS

(1) Positive emotions are relatively less well-studied than negative ones, in part because positive emotions are less likely to result in specific, identifiable, behaviours being expressed by an animal. While fear can be readily identified through behaviours such as fleeing, positive emotions can have many potential behavioural correlates: in addition to its role in thermoregulation, an animal may bask in the sun because this behaviour makes it feel good, or because it is bored.

(2) The characteristics of joy, however, make this emotion particularly amenable to scientific study in a variety of non-human species. Joy is intense, brief, and event-driven (i.e. a response to something), which permits investigation into how animals react to a variety of situations that would provoke joy in humans, as many behavioural correlates of joy are measurable.

(3) The discovery of vocalisations that are specific to positive contexts, most notably those appearing analogous to laughter, opens up the possibility of joy having a direct behavioural marker that can be measured while an animal experiences different scenarios. Play behaviour is another potentially useful marker of joy. Play in humans is interwoven with joy, pleasure, and happiness. Indeed, by generating positive states, play is self-rewarding. Play behaviour produced when experiencing pleasurable situations offers an excellent avenue to search for analogues of human joy. Another promising avenue for research on joy involves using novel paradigms that can be tailored to species which are now available to researchers to measure animal emotion, such as the cognitive bias test. This provides a powerful method for research focused on deepening our understanding of animal joy.

(4) Research on play in social species may be a productive way to study positive emotions in non-human animals because social behaviour often requires bond formation, which could be facilitated by positive affect. While bond formation need not require play behaviour, several social species are known for playful behaviour and have vocalisations which may indicate positive affect.

(5) Many of the potential markers of positive affect outlined here could be applied to species with highly different ecologies, life histories, and morphologies. Key to understanding the ancestral origin of phenotypes is a comparative approach, which will provide a deeper understanding of the commonalities in the expression of joy in human and non-human animals. Looking for similarities among taxonomically diverse species will be useful, especially if functional homologies in the brain are established, aiding in interpretation of results and proximate causes of behaviour. Given the improved understanding of the mental capacities of non-human animals is contributing to the development of better animal models for clinically significant conditions, such as memory decline, the study of joy/positive effect in animals could have similar translational value.

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