Review article

The nuts and bolts of animal emotion

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ABSTRACT

The study of animal emotion, as with its human equivalent, can be confusing due to the complicated and inconsistent use of terminology, and the number of interlinked fields and topics it encompasses. With this review, we aim to provide an up-to-date and, to the best of our knowledge, complete overview of the field of animal emotion, especially intended for new-comers to the field who wish to get a grasp of this field. We start by tackling the terminology and proposing definitions of commonly used terms, and present the different frameworks used for the study of animal emotion. Here, we heavily draw from human literature, as the definitions of animal emotion are derived originally from human research. We follow-up with an overview of current methodologies for the study of animal emotion, in particular the valence dimension of emotion, and include some of the associated limitations linked to these methodologies. We end by pointing out key areas for future research.

1. Introduction

Interest in the emotional lives of non-human animals (hereafter animals) has grown in the past three decades. Some of this interest stems from the increasing public concern for the welfare of captive and domesticated animals (Cornish et al., 2016). Many animal welfare scientists today agree that the 'feelings' of animals, or animal emotions, are at the core of animal welfare science (Dawkins, 1988; Duncan, 1996; Fraser, 2008). Interest in animal emotion has also emerged in many other fields ranging from (evolutionary) zoology (e.g. De Waal, 2008; Soltis et al., 2009), to affective and social neuroscience (e.g. Panksepp, 2004) and psychopharmacology (e.g. Hinchcliffe et al., 2017). Understanding how emotional experiences manifest themselves, how these experiences can be indirectly assessed in non-verbal beings and which animal species are likely to experience emotion is crucial to our understanding of animals, as well as humans. Several reviews on the topic of animal emotion already exist (Bekoff, 2000; Desire et al., 2002; Mendl et al., 2010b; De Waal, 2011; Makowska and Weary, 2013; Anderson and Adolphs, 2014; Murphy et al., 2014; de Vere and Kuczaj, 2016; Perry and Baciadonna, 2017), but most of them focus on specific topics within the field. The aim of the present review is to provide an up-to-date and as complete as possible overview of the current knowledge in the field of animal emotion. With this review we aim to support scientists starting in this field to grasp the basics and efficiently acquire a complete overview of current developments in this area. We start by exploring the terminology and concepts linked to emotion:

what do emotional terms mean, what is the function of emotion, and how can emotion be conceptualised and categorised into various frameworks? Here we draw heavily from human literature because definitions in humans and animals are similar, and animal scientists typically make use of human research. Second, we present promising methodologies for the assessment of animal emotion, based on either behaviour, cognition or physiology. We end by pointing out potential gaps in animal emotion research which warrant future attention.

2. Part 1 – understanding emotion

2.1. Definitions of the terms emotion, mood and affect

Use of the terms 'emotion', 'mood', and 'affect' in both human and animal literature is inconsistent. Definitions are not systematically given by authors and when definitions are provided, these often differ between authors (de Vere and Kuczaj, 2016). Absence of agreement on what these terms refer to has obstructed progress in this field (Paul and Mendl, 2018) and is one reason for the debate regarding which, if any, animal species can be said to experience emotion (de Vere and Kuczaj, 2016).

Hebb (1946) defined emotions as "certain neurophysiological states, inferred from behaviour, about which little is known except that by definition they predispose toward certain specific kinds of action". Other more recent definitions of emotion(s) include "states elicited by rewards and punishments, including changes in rewards and

punishments" (Rolls, 2000), "psychological phenomena that help in behavioural management and control" (Bekoff, 2000), "an intense but short-lived affective response to an event that is materialised in specific body changes" (Desire et al., 2002), "a process that facilitates appropriate responses to a wide range of both internal and environmental situations" (Parr and Waller, 2006), "something that moves one's body and mind" (Veissier et al., 2009), and "a temporary state brought about by biologically relevant external stimuli, marked by specific changes in the organism's body and mind" (De Waal, 2011). Frequently, emotion is simply considered as an internal state which intervenes between perceived stimuli and subsequent responses, resulting in tendencies to engage in certain behaviours (e.g. Hinde, 1985; Waller and Micheletta, 2013). For example, De Waal (2011) states that 'emotions potentiate action'. In human research, the notions of emotion and motivation are intertwined (Berridge, 2018), and some consider emotion as, in part, a goal-achieving motivation that explains the drive for certain behaviours (Fanselow, 2018). However, there is in fact no consensus on the causal direction of the link between emotion and behaviour (see section 2.4). Nevertheless, these definitions do include some common features, as proposed for example by Paul and Mendl (2018) for animals: an emotion is a multicomponent (subjective, physiological, behavioural and cognitive) response to a stimulus or event that is typically of importance to the individual, it is always valenced (pleasant or unpleasant) and can vary in activation/arousal and duration/persistence. The subjective, physiological, behavioural and cognitive components of emotion are described below in section 2.4. The duration of an emotion is somewhat understudied in both humans and animals, but based on human literature may span from seconds to days (Wallbott, 1986; Fitness and Fletcher, 1993; Gilboa and Revelle, 1994).

Berkowitz (2000) wrote of mood: "It is an affective state that typically is fairly long-lasting, often at a relatively low or moderate level of intensity, and generally objectless and free-floating". In contrast to shorter-term emotion, mood has indeed been described as occurring without being directed at a particular object, stimulus or event (Russell, 2003), which explains its frequent characterisation as 'free floating' (Trimmer et al., 2013). According to this view, emotion likely involves more information processing (e.g. appraisal of an object) than mood (Frijda, 1986). Mood, in both humans and animals, has been described as the outcome of the accumulation of short-term emotional experiences, resulting in a 'running mean' of positions occupied across scales of valence and arousal over time (Mendl et al., 2010b; Nettle and Bateson, 2012; Trimmer et al., 2013). If mood is an accumulation of environmentally-triggered emotions, it is also, albeit indirectly, affected by the environment. Mood has furthermore been conceptualised as a background baseline to which individuals fall back in the absence of acute emotion (Nettle and Bateson, 2012), and as a predisposition to act in certain ways (Trimmer et al., 2013). Being in a particular mood can influence cognitive processes and facilitate appropriate behaviour and decision-making, which may in turn influence short-term emotional responses (Russell, 2003). This suggests a bidirectional causal relationship between short-term emotions and longer-term moods (Mendl et al., 2010b). Regarding the duration of mood, authors are generally cautious in providing clear durations of mood, choosing terms such as 'long-lasting' (Berkowitz, 2000) or 'prolonged' (Russell and Barrett, 1999).

The term 'affect' is frequently used synonymously with emotion or mood in animal literature (Paul et al., 2005), yet sometimes these three terms are given distinct meanings. In human research, affective states often refer to mood states (Russell, 2003). Some scientists consider affect to be the basic ability to approach positive stimuli and avoid negative stimuli, which is a behavioural skill many simple organisms such as fruit flies, bacteria and even plants, are capable of (Bliss-Moreau, 2017). Others define affect as the overarching, umbrella term to encompass both emotions and moods (Paul et al., 2005; Quigley et al., 2014; Bethell, 2015). Affect is also sometimes used to refer solely to the subjective experience of emotion (Panksepp, 2005) or to a persistent
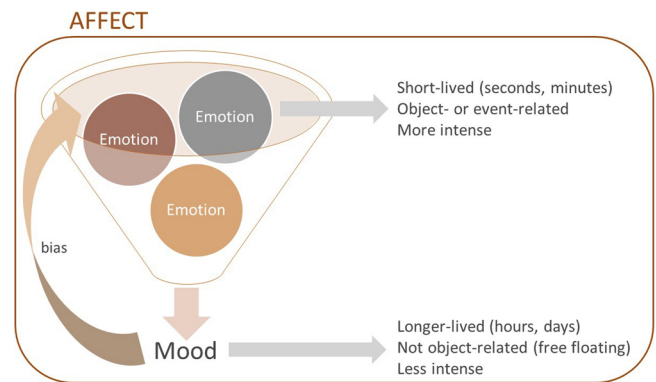

Fig. 1. Illustration of the relationship between emotion, mood and affect.

trait characteristic, i.e. a personality trait (Hinde, 1985). In humans, affect and personality are intertwined, leading individuals towards a tendency to experience certain emotions and moods more often and intensely (Watson and Tellegen, 1985). For instance, the human personality dimensions of extraversion and neuroticism have been associated with a tendency towards more frequent positive and negative affect, respectively (Winter and Kuiper, 1997). Note that the term 'emotionality' (sometimes referred to as 'fearfulness') is generally used in human and animal research to indicate a personality trait: propensity to experience (strong) positive or negative emotions (Archer, 1973; Lecorps et al., 2018). The possible occurrence of trait affect or the link between personality and emotion in animals could explain variation in individual affective responses to the same stimuli (de Vere and Kuczaj, 2016). Recently, personality was shown to influence affect in pigs (Asher et al., 2016), calves (Lecorps et al., 2018), dogs (Barnard et al., 2018) and ants (d'Ettorre et al., 2017). In calves and dogs, higher levels of emotionality/fearfulness were linked to negative mood, while in ants and pigs, negative mood was linked to less active personality types in barren environments (here negative mood refers to lower optimism on a judgement bias test; see section 3.2). Following the lead of animal literature on emotional processes, we will hereafter use the term affect as an umbrella term for emotion and mood – unless specified otherwise (Fig. 1).The issue of whether affect requires awareness is addressed in section 2.4.

2.2. Functions of affect

Affect has been described as a super-ordinate mechanism promoting approach towards valuable resources and reward, and avoidance of harm and punishment, thereby facilitating survival and reproductive success (Bethell, 2015). Affect directly enhances fitness by motivating and 'directing' (or 'being linked to' depending on the theory, see section 2.4) relevant behaviour and recruiting appropriate physiological resources (Dawkins, 1990; Duncan, 1996), and is hence commonly perceived as a functional adaptation (Darwin, 1872; Öhman and Mineka, 2001; LeDoux, 2012; Nettle and Bateson, 2012; Trimmer et al., 2013). Affect assists with generalisation from one situation to the next, by providing a form of predictive judgement or expectation in situations that have not been encountered before, or by biasing attention to certain types of stimuli. Negative affect may place a negative veil over future subjective experiences (Grippo and Johnson, 2009), for example leading animals to perceive challenges as more challenging than they are, whereas positive affect may cause an animal to perceive its environment more favourably (Mendl et al., 2010b), creating a buffer against negative events (Van der Harst and Spruijt, 2007; Reefmann et al., 2012).

Affective experiences may also have evolved to facilitate group living in social species by improving the bonds, cooperation and communication between the different group members (Spoor and Kelly,

2004; De Waal, 2008; Špinka, 2012). Affect is indeed not confined to an individual, but instead can spread from one individual to another (Hatfield et al., 1994; Špinka, 2012; Briefer, 2018). In this way, animals may receive signals from conspecifics which are in a negative affective state due to, for instance, the presence of a predator, and via the process of *emotional contagion* (Hatfield et al., 1994), a simple form of empathy (De Waal, 2008), become negatively inclined themselves (chickens: Edgar et al., 2011; pigs: Reimert et al., 2015; rats: Saito et al., 2016; ravens: Adriaense et al., 2019). Animals may also become positively excited by signals from others that are in a positive affective state (Held and Špinka, 2011; Reimert et al., 2013; Saito et al., 2016). The presence of conspecifics (and even the presence of members of other species of social animals such as humans) may moreover 'buffer' the negative affective state of an animal and thereby relieve that animal from its negative state, i.e. a process (in psychology) known as *social facilitation* or more specifically termed *social support* (Rault, 2012; Reimert et al., 2014; Edgar et al., 2015). Social facilitation represents the effect the presence of an individual has on the behaviour of another individual (Zajonc, 1965; Nicol, 1995) and may, for example, reduce fear responses in an individual in the presence of a peer displaying no or little fear (Nicol, 1995). Buffering of negative affective states via the presence of another individual is a process found in a wide range of species including mammals, birds, fish and even invertebrates (Ditzen and Heinrichs, 2014; Oliveira and Faustino, 2017; Kiyokawa and Hennessy, 2018).

2.3. Conceptual frameworks to study affect

Affective experiences in both animals and humans have been studied following different approaches. **First**, affective processes can be studied using two main conceptual frameworks: basic/modular/discrete or continuous/dimensional. In both animals and humans, emotions (and moods, depending on the definition) have, on the one hand, been described as modular or discrete (Darwin, 1872), and this suggests that different types of emotions are processed by different areas of the brain. The discrete emotions approach is challenged because scientists disagree on the number and labels of emotions and because a single label can refer to a number of different states (LeDoux, 2012; Weidman et al., 2017). A recent survey conducted among human emotion scientists showed that there was consensus for the existence (i.e. empirically tested) of five discrete emotions at best; these were anger, fear, disgust, sadness and joy (Ekman, 2016). On the other hand, emotions and moods can be conceptualised as dimensional, and hence classified and quantified along two or more continuous, dimensional scales such as valence (pleasant/unpleasant or positive/negative) and arousal (activation) (Russell, 1980; Wundt, 1896, in Ekman, 2016). For example, whereas people adopting the discrete approach would speak of 'fear', those using the dimensional approach would speak of a negative, high arousal emotion. This two-dimensional framework is also referred to as 'core affect space' (Trimmer et al., 2013), with 'core affect' referring to any experience that varies across the axes of valence and arousal (Russell, 2003)[1] . Dimensions other than valence and arousal have also been proposed to categorise core affect, for example 'persistence in time' (duration) (Anderson and Adolphs, 2014). Others categorise affect in an altogether different space, with for example separate axes for positive and negative affect (Watson and Tellegen, 1985). In human literature, it is still unclear whether positive and negative affect are the two extremes of a single dimension, or whether they can co-occur (Gill et al., 2017). Gill et al. (2017) found negative correlations between positive and negative affect within and between subjects, and therefore support the idea of affective valence bipolarity, that is, a single axis
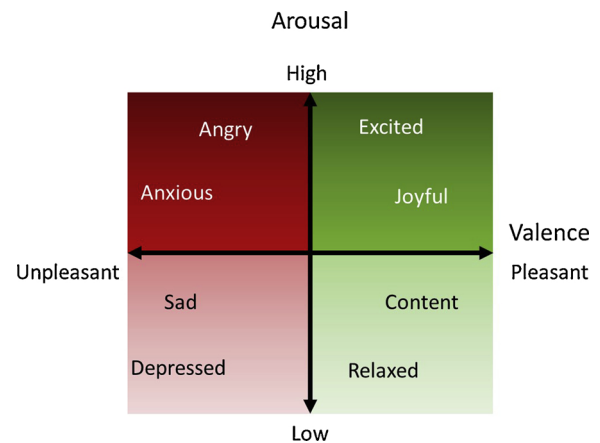

Fig. 2. Core affect represented in two-dimensional space. The words in the four quadrants refer to discrete emotions. Recreated based on Mendl et al. (2010b).

ranging from negative affect to positive affect. Conversely, others consider positive and negative affect as not necessarily mutually exclusive – a claim supported by the existence of mixed-feelings, i.e. two emotions from opposed valences such as joy and sadness occurring simultaneously (Larsen et al., 2001). In their conclusion, Larsen et al. (2001) nonetheless acknowledge that Russel's valence-arousal model of affect in which positive and negative affect are part of one single dimension (Russell, 1980) holds for main emotional experiences, but should be refined with regard to bittersweet experiences. Mendl et al. (2010b) suggested a new framework that combines both discrete and dimensional views, where 'core affect' is continuously experienced (mood) and combined with evaluation of the environment to generate discrete emotions. Mendl's framework is presented in Fig. 2.

Second, theories of emotion (note not mood) generally include different levels of complexity. In human literature, several levels of emotion have been proposed. Some speak of the existence of a number of 'primary' or basic emotion (Izard et al., 1993), the interaction of which can result in more complex, or 'secondary' emotions (Gray, 1990; Ekman, 1992; Izard et al., 1993).

Damasio et al. (2010)[2] discriminates between three kinds of emotion, given here in the order from least to most complex: *background emotion*, *universal emotion* and *social emotion*: *Background emotion* results from signals from a combination of regulatory systems, such as metabolic and homeostatic processes, and represents one's ongoing 'state of being'; *Universal emotion* refers to commonly expressed discrete emotions such as 'fear', 'anger', 'joy'; and finally *social emotion* emerges from a combination of universal affect influenced by a social context and encompasses more complex emotion such as 'guilt', 'shame', and 'pride'. Another example of emotion classification is proposed by Panksepp (2010)[3], who discriminates between *primary-process emotion*, *secondary-process emotion*, and *tertiary-process emotion* – based on a neurobiological approach. The primary-process (or basic primordial) emotion, which encompasses unconditioned and 'instinctual' emotion action systems, homeostatic emotion and sensory-related emotion with a low level of emotional control, involves sub-neocortical activation. Panksepp distinguishes between at least seven primary-process emotional systems: 'seeking', 'fear', 'rage', 'lust', 'care', 'panic', and 'play' (Panksepp, 2005). *Secondary-process* emotion results from memory and learning processes in the basal ganglia. 'Wanting' – as defined by Berridge (1999) - for instance has been proposed as secondary-process emotion derived from the primary-process emotion 'seeking' (Panksepp

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[1] Russell (2003) defines core affect as "a neurophysiological state that is consciously accessible as a simple, nonreflective feeling that is an integral blend of hedonic (please-displeasure) and arousal (sleepy-activated) values".

[2] Damasio et al. (2010) define emotions as evolved 'automated programs of actions', that are not necessarily felt.

[3] Panksepp (2005) defines emotions as the 'umbrella concept that includes affective, cognitive, behavioral expressive, and a host of physiological changes'.

et al., 2017). Finally, *tertiary-process emotional systems*, such as rumination and contemplation, requires higher cognitive abilities, allows an individual to act with intention, and emerges from the activation of neo-cortical structures (Panksepp, 2010). Of note, Panksepp (2010) supports the theory that the 'feeling', or subjective component of emotion arises from ancient subcortical structures of the brain. Panksepp hence defends the idea that at least all mammals are able to experience primary emotions. This is in contrast with other authors who differentiate/separate the behavioural and neurophysiological changes from the feelings (Kringelbach and Berridge, 2017). Berridge and Kringelbach (2008) for example discriminate 'wanting', an incentive salience emerging mostly from subcortical activation that can occur without conscious awareness, from wanting – a conscious desire emerging from cortical structures.

Regardless of the classification adopted, authors tend to distinguish between a set of 'raw', possibly innate, emotional states, from which more complex, learned emotion is derived. In animals, differentiating between different levels of emotion is less common than in humans, although it is clear that different species will likely be capable of different levels of complexity in their emotional experiences.

Third, there are several distinct theories regarding the causation and processing of emotion (Moors, 2009; Scherer, 2009a; b)[4]. Note that we here focus on emotion, which is a response to specific internal or external stimuli, as opposed to mood which is possibly free-floating. Appraisal theories, for example, suggest that a cognitive process (not necessarily conscious) that evaluates the importance of events for fitness, referred to as *appraisal*, precedes and causes an emotion (Scherer, 1999; Moors et al., 2013). Appraisal might additionally be an ingredient for emotion rather than only a cause per se (Ellsworth, 2013). Thus, appraisal theories suggest that the emotion elicited by a specific stimulus or event does not depend on the situation itself, but is based on the appraisal of the situation and hence may differ between individuals, or within individuals over time (Ellsworth, 2013). Appraisal theories suggest several appraisal variables, also called criteria, that are important in differentiating between emotions (valence, goal relevance, coping potential, agency and novelty). The combination of appraisal variables can lead to a wide range of potential emotions (Ellsworth, 2013). Appraisal and emotion, moreover, constantly evolve in time in a dynamic process (Scherer, 2009b; Ellsworth, 2013).

Another popular theory regarding causation and processing of emotion is Barrett's theory of constructed emotions (Barrett, 2017), following the conceptual act theory (Barrett, 2006) and building on Russell's (2003) theory of core affect. In Barrett's theory, emotions are seen as constructions of the world based on experience, not as reactions to the world, and different emotions are suggested to be labelled as a result of knowledge and experience. In other words, emotions are not direct, more or less automated responses to stimuli, but rather the outcome of learning through experience. Thus, here the categorisation of emotion is seen as something that helps to shape experience (Moors, 2009).

The causal link between emotion and behaviour is discussed in Section 2.4 below.

2.4. Components of affect

In most theories of affect, different components of an affective episode are distinguished, but the specific components and their labels may differ from one author to the next. Most authors, however, refer to

the following components of affect: feeling/subjective, motor/behavioural, cognitive, and somatic/physiological (e.g. Scherer, 2001; Desire et al., 2002). We focus here on emotion, as opposed to affect, as more is known about acute emotion in this context than longer term mood, except for the cognitive component which is often linked to background affective states, hence mood-like states, and except for the composite-indicators in the physiological part, which most likely also reflect mood rather than short-term emotion. This means that the term emotion is deliberately used here throughout, except in the section about the cognitive component of affect.

2.4.1. Feeling or subjective component

Several terminologies are used to refer to the feeling component, including 'the subjective component', 'the conscious component', 'the experiential component' as well as simply the term 'feeling'. Some researchers argue that emotion inherently involves subjective experiences (Clore et al., 1994; Dawkins, 2006), consciousness having emerged from primordial emotion itself (Denton et al., 2009). Others question the feeling component of emotion in both animals and humans (Winkielman et al., 2007). However, even if empirical evidence of unconscious elicitation of emotions exists (Öhman and Soares, 1994), the presence of non-conscious emotion itself is still debatable (Winkielman et al., 2007). One study nonetheless showed that subliminal positive and negative emotional visual stimuli could elicit distinct behavioural responses among participants without them reporting any difference in terms of emotional valence and arousal before and after the subliminal exposure (Winkielman et al., 2005). These authors concluded that the emotional stimuli were able to alter participants' behaviour and emotional state, without them being aware of it (Winkielman et al., 2005).

As explained by LeDoux and Hofmann (2018), who focus on fear, some simply consider the subjective component of emotion as a psychological construct, and hence not an inherent part of emotional experience. Adherents to this theory consider individual subjective reports of emotion as an invalid indicator of emotion based on the lack of correlation between individual brain activation and subjective reports (LeDoux and Hofmann, 2018).

Others propose that the 'richness' of a species' subjective experience depends on its level of consciousness (Damasio et al., 2010), and that different levels of animal consciousness are associated with different levels of complexity in the emotional repertoire (Le Neindre et al., 2017), although no consensus has yet been reached on the different existing levels of consciousness (de Vere and Kuczaj, 2016).

Addressing all positions on the subject, some authors carefully conclude that animal "emotional processes […] may or may not have subjective components, depending on the species and circumstances involved" (Paul et al., 2005). Where in phylogeny the subjective experience of emotion emerges is not known. Although subjective life is often thought to be restricted to species with high levels of brain organization, neuro-ethological data show that animals can also have forms of subjectivity, emerging from activity in evolutionarily 'old' brain areas (Panksepp, 2004; Fabbro et al., 2015; Panksepp, 2016). Subjective experience of emotion in invertebrates, but also many vertebrates, is subject to intense debate (Duncan, 2006). In any case, whether it exists or not in particular species, the experiential component of emotion remains difficult to assess in all animals as they cannot verbalise it. Most animal researchers nonetheless assume that it can be inferred from other components of emotion, i.e. the behavioural, cognitive and physiological ones (Mendl et al., 2010b), which are described later on in this review.

2.4.2. Behavioural component

Emotion involves behavioural changes, but there is no consensus on the causal direction for this link: while most state that emotion causes behaviour, others hold that behaviour is part of emotion, and others yet believe that behaviour in fact causes emotion (see Anderson and

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[4] The term emotion is used here in reference to an 'emotional episode' Moors et al., 2013. Appraisal theories of emotion: State of the art and future development. Emot. Rev. 5, 119-124. An emotion episode is pluri-component, and involves changes at the appraisal, motivational, somatic, motor and subjective levels. According to Moors et al. (2013), appraisal can be seen as *one* determinant or *the* core determinant of the emotional feeling.
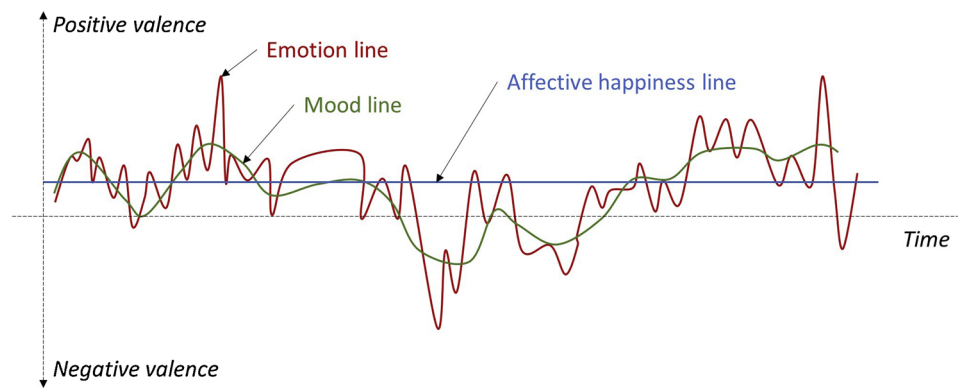
Fig. 3. Rough illustration of the relationship between short-term emotions, longer-term moods and affective happiness; source: Webb et al. (2018).

Adolphs, 2014 for a detailed review). In addition, behavioural responses themselves may feed back to the brain and lead to an adjustment in the current emotional state, a principle termed 'interoception' (Anderson and Adolphs, 2014). Some researchers, therefore, prefer to use the term 'emotional episode' (Moors, 2009; Scherer, 2009b) or 'emotional process' (Ellsworth, 2013) to refer to anything from the stimulus to the consequences of an emotion. An emotional episode or process is thus broader than the emotion per se. Despite this lack in consensus regarding the direction or nature of the relationship between emotion and behaviour, behavioural changes, such as facial expressions, can be used as an important indicator of emotion in non-verbal species (see section 3.1).

2.4.3. Cognitive component

Affect and cognition are closely interwoven (Hinde, 1985). It is suggested that affect evolved earlier than several intellectual abilities, arising from ancient subcortical brain structures, in turn suggesting that affect is more widespread across species than intellect is (Dawkins, 2000; Panksepp et al., 2017). Supporters of this theory nonetheless acknowledge the fact that higher cortical structures are involved in affect regulation and inhibition processes (e.g. Damasio and Carvalho, 2013). Some scientists view affective processes as dependent upon cognitive processes and vice versa (Lazarus, 1999), while others see affective and cognitive processes as independent systems. For instance, Panksepp (2003) views the affective system as subcortical and the cognitive system as cortical and hence more recent in evolutionary terms. In humans, cognitive processes can trigger, or be affected by, particular emotions and moods (Hinde, 1985; Mathews and MacLeod, 2002), and this is most likely true in animals too. This bidirectional link between affect and cognition can hence be used to indirectly assess animal affect (see section 3.2). In humans, emotions and moods are known to cause *cognitive biases*: manipulation of information processing by the brain, affecting judgement, attention and memory (Mathews and MacLeod, 1994; Mineka et al., 1998; Lerner and Keltner, 2000; Schwarz, 2000; Mathews and MacLeod, 2002). Recently cognitive bias testing has been applied to a variety of animal species, including invertebrates (see section 3.2.1). Emotions and moods seem to also influence sensitivity to reward loss (Burman et al., 2008) (see section 3.2.2), which can more or less be seen as a type of cognitive bias in terms of evaluation of current/past negative events (as opposed to ambiguous future events in judgement bias).

2.4.4. Physiological component

Traditionally, psychophysiology focused on univariate physiological parameters as measures of emotional arousal (Cacioppo et al., 2007). Subsequent work on multivariate analysis of autonomic measures later revealed emotion-specific physiological responses (Kragel and LaBar, 2013). Human research also established promising links between emotion and physiological changes at the neuroendocrine and immune

levels (Steptoe et al., 2005). An approach integrating the different physiological systems (neuroendocrine, immune and autonomic) has also been promoted to further clarify psychophysiological relationships (Cacioppo et al., 2007). These findings open up an avenue of research for animal welfare scientists (see section 3.3), especially with mammalian species – which share sub-neocortical limbic systems structures with humans (Panksepp, 2005).

2.5. A brief note on animal satisfaction with life

Satisfaction with life in humans, also referred to as happiness, is defined as the 'subjective enjoyment of one's life as a whole' (Veenhoven, 2000). When evaluating how happy they are, humans draw from two sources of information: how well they feel most of the time (affective/hedonic happiness) and how their life-as-it-is compares with standards of how they believe their life should be (cognitive happiness) (Diener, 2000; Kringelbach and Berridge, 2009). Overall, little attention has specifically been given to the topic of animal happiness but Boissy et al. (2007) proposed that frequent positive affective experiences could lead to frequent positive moods, which could then lead to an overall state of satisfaction with life or 'happiness': a persistent, positive background state.

Affective happiness as described in humans is likely to define animal happiness, since there is currently no evidence that animals are capable of cognitive happiness. Affective happiness, and thus animal happiness, is a separate concept from the transient affective experiences that are emotions and moods, as it represents the balance in the frequency of all positive and negative affective experiences over time. This balance tends to be stable under stable conditions and represents how one feels *most of the time* (Fig. 3). Similarly to humans, happiness in animals could be assessed using the frequency of positive and negative affect over a set period of time and computing the ratio of positive to negative affective experiences, that is, the affect balance (Webb et al., 2018). Affect balance is an indicator used in human happiness research since the 1960s (Glatzer and Gulyas, 2014) which correlates well with self-reports of happiness but to our knowledge has not yet been applied in animals. Indicators of short-term emotions, which could be used to compute affect balance, are described below in part 2 of this review.

3. Part 2 - assessing affect in non-verbal beings

How exactly subjective experiences arise and what we should be looking for when searching for evidence of subjectivity is called 'the hard problem' by Chalmers (1995). It is even called the 'hardest problem in the whole of biology' by Dawkins (2006). Although many people are confident in their belief of affective capacities in at least some animal species, it remains a mere assumption. We simply cannot know what it is like to be a different individual than ourselves, and essentially, this is also true for fellow human beings (De Waal, 2011).

Human verbal reports of emotions and moods are accepted as the 'gold standard' indicator of affect (Paul et al., 2005), assuming humans can accurately perceive, interpret and report their own affective experiences. Since animals are not capable of verbal speech to communicate how they feel, we must rely on other methods to indirectly assess their affective experiences. These different methods, which focus on the behavioural, cognitive, and physiological components of affect, aim to identify similarities with humans and get some indication of affective experiences in animals. The currently known methods will be discussed below, grouped by the component they are based on. We focus here on valence, because: 1) affect is always valenced (Paul and Mendl, 2018), 2) arousal seems less relevant to overall wellbeing (based on findings in human happiness research, Diener et al., 2009; Webb et al., 2018), and 3) discussing indicators of arousal in addition to indicators of valence would make this review impossibly long. As this review aims to cover all topics in the field of animal affect, we introduce below all known methods to assess affect in animals but we do not cover these methods in-depth. Instead we provide an extensive literature list for further in-depth reading. Finally, we do not specifically address whether these methods assess short-term emotions or moods as this is not always clear/known and would again make this review too long, but rather combine these into the umbrella term of affect.

3.1. Methods based on the behavioural component of affect

The valence of affective experiences in animals can be studied by observing their behaviour in their home environments (Fureix and Meagher, 2015; Reimert et al., 2017) or in specific test situations (Forkman et al., 2007; Murphy et al., 2014). The particular behaviour studied can range from 'whole animal behaviour' to only observing specific body parts of the animal. Examples of 'whole animal behaviour' are approach and avoidance behaviour (Paul et al., 2018), freezing and play behaviour (Paul et al., 2005; Boissy et al., 2007; Held and Špinka, 2011). Freezing and play behaviours are thought to be markers of negative and positive affective experience, respectively (Paul et al., 2005; Held and Špinka, 2011), but see Ahloy-Dallaire et al. (2018) for a critical review of play as an indicator of positive affect. Other behaviours that have been associated with affect and more or less involve the whole body are: 1. anticipatory behaviours - i.e. behaviours displayed in anticipation of a reward or punishment, e.g. increased locomotion and frequent behavioural transitions (Spruijt et al., 2001); 2. consumptive behaviours – i.e. eating or drinking behaviours (Paul et al., 2005); 3. affiliative behaviour – i.e. social behaviour such as allo-grooming (Boissy et al., 2007; Proctor and Carder, 2015); 4. aggressive behaviours such as attacking or threatening another individual (Kudryavtseva, 2000; Wingfield et al., 2006) and defensive behaviour such as seen in horses starting to kick upon being approached (Sankey et al., 2010); and 5. displacement behaviours indicative of (heightened) anxiety such as destructive behaviour and hyperactivity in dogs (Ohl et al., 2008) or scratching in primates (Baker and Aureli, 1997; Coleman and Pierre, 2014). The behaviour of the 'whole animal' is also observed in the Qualitative Behaviour Assessment (QBA) method (Wemelsfelder et al., 2001; Temple et al., 2011). In this method, the way an animal behaves is evaluated via scores on, among others, affective words such as 'nervous' and 'calm'.

Specific body parts of the animal that have received attention in relation to affect are head and tail postures and movements (Briefer et al., 2015; Reimert et al., 2015). Facial expressions - recently reviewed by Descovich et al. (2017) - have been studied as indicators of affective experiences for a while in primates (Andrew, 1963; Van Hooff, 1967) and are now also under investigation in other animals. An elegant and objective system has been development to aid the analysis of facial expressions, called the Facial Action Coding System (FACS) (e.g. primates: Vick et al., 2007; Parr et al., 2010; dogs: Waller and Micheletta, 2013; horses: Wathan et al., 2015). Based on the FACS, another system has been developed to specifically study pain in the

faces of animals, called the Grimace Scale (e.g. mice: Langford et al., 2010; horses: Dalla Costa et al., 2014; pigs: Di Giminiani et al., 2016; sheep: McLennan et al., 2016; ferrets: Reijgwart et al., 2017). In these aforementioned studies the entire face is taken into account. There are also studies that only looked at one aspect of the face in relation to affect, such as the percentage of visible eye white (Sandem et al., 2006; Lambert and Carder, 2017) and type of ear posture and frequency of change between different ear postures (Reefmann et al., 2009a; Boissy et al., 2011; Reimert et al., 2013; Goumon and Špinka, 2016). Frequent ear posture changes in sheep, for example, seem associated with negative affect, whereas passive ear postures (ears hanging down loosely) seem associated with low arousal positive affect (Reefmann et al., 2009a).

Furthermore, specific vocalisations have also been linked to affect (Briefer, 2012; Leliveld et al., 2017). Rats, for example, emit a specific type of 22 kHz ultrasonic vocalisations in putatively negative contexts (Portfors, 2007; Burgdorf et al., 2008) and a group of high frequency vocalisations referred to as '50 kHz' ultrasonic vocalisations in putatively positive contexts (Panksepp and Burgdorf, 2000; Brudzynski and Pniak, 2002; Burgdorf et al., 2011; Rygula et al., 2012).

Lateralized behaviours associated with brain function asymmetries have been shown in numerous species (Vallortigara, 2000): the right hemisphere appears dominant in processing negative affect while the left hemisphere appears dominant in processing positive affect (Leliveld et al., 2013). As a consequence, interest in the affective meaning of specific lateralized behaviours has recently increased (Leliveld et al., 2013). In summary, it seems that animals exhibit a behavioural lateralization according to their perception of the pleasantness/aversiveness of an external stimulus (Siniscalchi et al., 2018). For example, dogs have been shown to display a right-biased head orientating response to recordings of joyful humans, probably as a result of left-brain-hemisphere activation (Siniscalchi et al., 2018). In addition, mares were found to mainly use their left eye to explore a negatively valenced stimulus, but their right eye to investigate a neutral stimulus, while no difference in eye lateralization was found for a positively regarded stimulus (Des Roches et al., 2008). However, the influence of specific types of affect (e.g. fear versus anger) on lateralised behaviour remains to be elucidated. To our knowledge, only one study in dairy cattle looked into this matter, without conclusive results (Kappel et al., 2017).

Behaviour, hence, is an important component of affective experiences in animals. Caution is however required as interpretation of behaviour is not always straightforward and the relationship between affect and behaviour complex (Hinde, 1985; Faragó et al., 2017). For instance, a specific behaviour can be observed in various affective contexts and vice versa (Hebb, 1946; Paul et al., 2005). Species-specific behaviour as well as subject-related and environment-related contexts need to be taken into account (Hebb, 1946; Hinde, 1985; Paul et al., 2005). It is moreover likely that high arousal behavioural indicators are easier to detect than low arousal ones. And finally, it is not always easy to distinguish affective behaviour from non-affective behaviour (Hinde, 1985; Maestripieri et al., 1992). Therefore, we would like to end this section by emphasising that making inferences about affective experiences based on the behavioural component should always be done with care.

3.2. Methods based on the cognitive component of affect

3.2.1. Cognitive biases

Affect-congruent cognitive biases are inclinations to process information in particular ways due to affective states. These cognitive biases include judgement, attention and memory biases, and are described in more detail below.

3.2.1.1. Judgement bias.
Affect-congruent judgement bias is the propensity to judge ambiguous cues or situations more or less optimistically. This type of cognitive bias is usually tested in animals

by training them to respond in a certain way to a positively- and a negatively-associated cue (Harding et al., 2004). For example, animals are trained to go to a positive cue to receive a reward, and not go to a negative cue to avoid a punisher – this type of test is referred to as a *go/ no-go* paradigm. Once trained, animals are exposed to intermediate, ambiguous, novel cues. The hypothesis is that, as in humans, negative affective states incline animals to respond to ambiguous cues as if they predict a negative event and vice versa (Harding et al., 2004). This test was first designed in animals for rats (Harding et al., 2004), and has since then been adjusted and applied to numerous other species – from chimpanzees (Bateson and Nettle, 2015) to bumblebees (Perry et al., 2016). Generally the test varies to suit the needs of the particular species being studied. Recently, however, a promising (spatial) test design that can suit two very different mammalian groups: horses and rodents, was proposed (Hintze et al., 2018).

Judgement bias tests have been criticised on several accounts: many studies find opposite results to those initially expected (Doyle et al., 2010a; Burman et al., 2011; Baciadonna and McElligott, 2015); the activity of an individual animal may influence results (Mendl et al., 2009, 2010a); ambiguity can be lost after repetitive presentations of the ambiguous cues (Doyle et al., 2010b; Roelofs et al., 2016), training is time-consuming (Roelofs et al., 2016) and judgement bias testing might provide cognitive enrichment which may impact affect in itself (Roelofs et al., 2016). Several strategies to counteract the undesirable loss in ambiguity following repeated exposure to ambiguous cues have already been suggested, i.e. partial reinforcement of ambiguous cues (Neave et al., 2013) or rewarding ambiguous cues according to expectations (Hintze et al., 2018). Another important consideration for this cognitive test is that the 'reward' and 'punisher' in go/no-go paradigms should be perceived as having equal strength on the motivation of the test animal. As mentioned by Mendl et al. (2009), if this is not the case, and the punisher is for example stronger than the reward, the animal is likely to choose not to respond (no-go) to all ambiguous cues because the cost of making a mistake in this case is simply too high. A final important consideration linked to judgement bias testing is that motivation level across successive sessions may vary, for example with animals reaching satiety where food rewards are used, and this is generally only tested posteriori (e.g. Henry et al., 2017).

3.2.1.2. Attention bias. Affect-congruent attention bias is the propensity for heightened awareness of, or attention towards, novel or negative aspects of the environment in individuals experiencing a negative affective state, such as fear or depression. Attention biases can hence be assessed in animals by testing how attentive individuals are to a visual cue that is presented in a location associated with a threatening stimulus (Paul et al., 2005) or to novel auditory cues (Rochais et al., 2016). Attention bias can also be assessed by testing how attention-demanding tasks are interrupted by threatening stimuli, hypothesizing that animals in negative affective states would be distracted more (Paul et al., 2005). Attention biases linked with anxiety have been studied in various species, including rhesus macaques (Bethell et al., 2012), starlings (Brilot and Bateson, 2012), sheep (Lee et al., 2016; Monk et al., 2018), and cattle (Lee et al., 2017). In horses, decreased attention towards novel auditory stimuli was linked to depressive-like states (Rochais et al., 2016) and in pigs attention biases have been studied to test the impact of housing conditions (Luo et al., 2019).

Attention bias studies in animals are relatively recent and the validity of the developed methodologies is still under investigation. Compared to judgement bias tests, attention bias tests require shorter (Monk et al., 2018) to no training time (Brilot and Bateson, 2012). Attention bias, similarly to other cognitive biases, is influenced by personality (Cussen and Mench, 2014; Luo et al., 2019) and social rank (Bethell et al., 2012), which is not surprising since personality and social rank are likely to influence affective state. Validation of attention bias as a potential marker of positive affect – by opposition to negative affect – is still required (Lee et al., 2017; Monk et al., 2018).

Furthermore, the influence of arousal on attention bias needs to be investigated (Monk et al., 2018). Monk et al. (2018) suggest that sensors or physiological measurements could help disentangle the impacts of valence and arousal on attention bias.

3.2.1.3. Memory bias. Affect-congruent memory bias is the propensity to remember specific objects or events that are in line with one's current affective state (Klaassen et al., 2002; Burman and Mendl, 2018). Depressed humans, for example, have been shown to recall negative experiences better than non-depressed people (e.g. Mineka and Nugent, 1995). To the authors' knowledge, animal studies on this subject have only been conducted in rodents (mice: Takatsu-Coleman et al., 2013; rats: Burman and Mendl, 2018). An example of such a test was training rats with different social statuses, that is, rats assumed to be in different affective states, to receive one pellet of food in each arm of a radial arm maze (Burman and Mendl, 2018). Following this rats were exposed to either a positive, neutral or negative event: letting them walk down one arm of the maze with either 12 food pellets, 1 food pellet or quinine soaked pellets, respectively. It is hypothesized that rats in a more positive affective state, i.e. high social status, will remember arms associated to positive events better than arms associated to negative events, and vice versa. Memory is based on approach and avoidance behaviours. In this example with rats, social status did not seem to create a memory bias (Burman and Mendl, 2018). Takatsu-Coleman et al. (2013), however, observed that mice exposed to 12h-social isolation displayed a memory bias for the arms paired with the aversive event (higher avoidance), compared to control mice which had experienced no social isolation. Memory bias may also be influenced by affective arousal (Paul et al., 2005), and remains a time-consuming tool to investigate animal affective states because animals must first be trained (Burman and Mendl, 2018).

Affective bias is slightly different from memory bias yet related as it refers to a bias in preference, which is linked with memory and learning processes (Stuart et al., 2013): in brief, one's preference for particular resources are based on one's affective state at the time of first encounter with the resources. Affective bias tests have been applied to rats (Stuart et al., 2013, 2015; Hinchcliffe et al., 2017) and mice (Graulich et al., 2016). In practice, the rodents are exposed to two rewards of equal value. The first reward is presented with no manipulation of affect, while the second is presented following or directly preceding either a positive treatment (e.g. social play) to induce positive affect or a negative treatment (e.g. social isolation) to induce negative affect. Once trained, the preference of the rodents for the two rewards is tested. It is hypothesized that rodents will prefer the second reward when it is associated with the positive treatment, and avoid the second reward when it is associated with the negative treatment (Stuart et al., 2013; Hinchcliffe et al., 2017). Affective bias tests would thus offer the possibility to discriminate between affective states of different valence; but some suggest that their implementation should be restricted to studies of short-term affective manipulations (Graulich et al., 2016).

3.2.2. Reward loss sensitivity

Another indicator of affect that more or less relies on cognition and may be viewed as a bias in evaluation, is one's sensitivity to reward and punishment (or reward loss). Typically, individuals are more sensitive to reward losses than gains, but when in a negative affective state, individuals show an increased sensitivity to such losses (Burman et al., 2008). To assess sensitivity to reward loss, a successive negative contrast technique can be used (Flaherty, 1999). With this technique, reward loss can, for instance, be simulated by unexpectedly decreasing the size of a food reward in an operant or runway paradigm (Rosas et al., 2007; Burman et al., 2008). The expectation is that, following an unexpected and maintained decrease in reward, animals will work less, or run slower for this decreased reward in comparison to animals that have been trained to work or run for the same reward size from the beginning. Furthermore, animals in a negative affective state are

expected to work even less or run even slower for this new smaller reward for an extended period of time (Flaherty, 1999; Burman et al., 2008). The latter is thought to reflect higher sensitivity to reward loss, hence higher and/or more persistent negative affect following a loss. As with some other cognitive bias tests, sensitivity to reward loss requires training, may depend on individual differences and its interpretation may be complicated by differences in reward sensitivity per se (Luo et al., 2018).

3.3. Methods based on the physiological component of affect

The papers referred to below are restricted to those in literature investigating a direct link between affective valence (hence not arousal) and physiological changes in animals.

3.3.1. Neuroendocrine biomarkers of affect

Animal researchers have shown increased interest towards neuroendocrine markers as potential indicators of positive or negative affect. Interestingly, these biomarker candidates have often been investigated in parallel with a judgement bias paradigm.

3.3.1.1. Dopamine. Central dopamine (DA) is known to assign a motivational value to rewarding behaviours, i.e. to be involved in positive (anticipatory) behaviours (Berridge and Robinson, 1998; Berridge, 1996). Recently, its role in reward processes has been investigated using the judgement bias test: bumblebees treated with a DA antagonist were more pessimistic than their control counterparts (Perry et al., 2016). Furthermore, in rats, knock-out of DA transporter in the nucleus accumbens has been found to increase anxiety- and depression-like behaviour (Bahi and Dreyer, 2019). These results support the role of central DA in affective processes. Nonetheless, it is worth noting that in monkeys, only a subset of midbrain DA neurons were inhibited by aversive stimuli and excited by rewarding ones; while most neurons were excited by both aversive and rewarding stimuli (Matsumoto and Hikosaka, 2009). Different groups of DA neurons would thus have distinct functions, e.g. motivational or action-oriented (Matsumoto and Hikosaka, 2009). Animal researchers should thus focus on motivational-related dopaminergic system to investigate DA as a marker of affective valence. Peripheral measures of DA as markers of mood-disorders have also been recently investigated in humans, and DA levels in peripheral blood mononuclear cells have been shown to be lower in depressed individuals (Zheng et al., 2016).

3.3.1.2. Serotonin. Serotonin (5-HT: 5-hydroxytryptamine) depletion in humans has been linked to vulnerability to depression (Ruhé et al., 2007). Similarly, 5-HT depletion has been associated to a pessimistic bias in judgement bias tests - i.e. linked with negative affective states - in both sheep and pigs (Doyle et al., 2011; Stracke et al., 2017a) – supporting the role of 5-HT in negative affective processes. However, tryptophan supplementation in pigs – which is a precursor of 5-HT – failed to induce the expected optimistic bias in a judgement bias test (Stracke et al., 2017b). More recently, the link between 5-HT and putative positive affect induced by enrichment in pigs was also investigated (Rius et al., 2018), without conclusive results. There are limitations to studying 5-HT functioning in the brain, and therefore peripheral (blood) 5-HT measurements have been explored. 5-HT uptake, storage and release in blood platelets shows some similarity with that in brain 5-HT (Stahl, 1977; for review see Mück-Šeler and Pivac, 2011) and were found to be altered by depression in humans (Barton et al., 2008). Ursinus et al. (2013) reported correlations between pigs' fear-related behaviours in an open field test and both brain and peripheral (platelet) 5-HT levels and platelet 5-HT uptake but concluded that these relationships might reflect personality differences rather than variations in affective state. Further research is hence needed to understand the potential of central and peripheral 5-HT as marker of negative affect.

3.3.1.3. Oxytocin. The potential of oxytocin (OT) as an indicator of animal affect has been investigated in several species, with a bias towards the study of positive affect - for a critical review, see Rault et al. (2017). Results remain inconsistent between species: neither straw provision in pigs or positive tactile stimuli in horses induced expected rises in plasma OT levels (Lansade et al., 2018; Rius et al., 2018). The role of the oxytocinergic system in affective processes remains poorly understood and different theories have been put forward. Rault et al. (2017) hypothesised that higher OT levels may reflect positive animal affect in stable social contexts, and negative affect in socially challenging situations. Kemp and Guastella (2011) proposed that, in humans at least, OT enhances approach related-behaviours while reducing withdrawal-related ones. OT might hence in social contexts facilitate positive affect linked to approach behaviour, such as trust, but also facilitate negative affect linked to approach behaviour, such as anger and jealousy (Kemp and Guastella, 2011). Conversely, OT might inhibit affect like fear - a theory consistent with the anxiolytic properties of the hormone (Neumann and Landgraf, 2012). The potential of OT as a biomarker of affect has been investigated in various matrices. In dogs, in particular, urinary and plasma OT have been showed to increase in response to positive stimuli (Handlin et al., 2011; Mitsui et al., 2011). Synchrony of OT levels may also be an indicator of social positive affect: strongly bonded dyads of marmosets have been shown to exhibit synchronised OT fluctuation (Finkenwirth et al., 2015). Note that the use of peripheral OT level has been questioned, as well as the validity of current assays (McCullough et al., 2013).

3.3.1.4. Opioids. In humans, the role of the opioid system in the regulation of positive and negative affect has been acknowledged (for a review see Nummenmaa and Tuominen, 2017). However, in animals, research on the subject is scarce and appears to mainly focus on animal models of depression (Boissy et al., 2007; Robinson et al., 2017). Yet one study by Kalbe and Puppe (2010) found that long-term food-rewarding cognitive enrichment, likely promoting positive affect, modified the opioid receptor mRNA expression in the brains of pigs. It has recently been suggested that opioids would facilitate approach-orientated affect (including positive and negative affect), while modulating withdrawal-oriented affect (Nummenmaa and Tuominen, 2017). This suggests that opioids cannot be used to discriminate between affective states of different valence (Nummenmaa and Tuominen, 2017), as their concentrations are affected by both positive and negative affect in the same direction.

3.3.2. Immune biomarkers of affect

In humans, several classes of immune biomarkers linked to affect have been brought to light: acute phase proteins (e.g. fibrinogen and positive affect: Steptoe et al., 2005; c-reactive protein and positive affect: Steptoe et al., 2007), cytokines (e.g. interleukin 6 and positive affect in women: Steptoe et al., 2007; seven peripheral cytokines and negative affect: Graham-Engeland et al., 2018), and immunoglobulins (e.g. salivary immunoglobin A and both positive and negative affect: Hucklebridge et al., 2000). Consequently, some researchers have encouraged animal scientists to conduct studies on the link between animal affect and the immune system (Tuchscherer et al., 1998; Boissy et al., 2007). Saliva protein composition, for instance, could potentially be used as an indicator of animal affect (Grigoriev et al., 2003). In particular, salivary alpha amylase and salivary immunoglobulin A have been suggested as promising indicators of positive affect in animals (Boissy et al., 2007). The latter hypothesis seems to be confirmed by a recent study conducted in calves that found higher salivary immunoglobulin A levels in calves exposed to a positive affective stimulus compared to those exposed to a negative one (Lv et al., 2018).

3.3.3. Autonomic biomarkers of affect

Animal researchers often investigate profiles of autonomic

responses to affective stimuli rather than univariate indicators of affective response. For conceptual purposes, the indicators are nevertheless presented separately below.

3.3.3.1. Heart rate variability. Some indices of heart rate variability (HRV) are thought to reflect affective valence. HRV can be assessed by non-linear, frequency domain or time domain indices, for which the root mean square of successive inter heartbeat interval differences (rMSSD) reflecting the vagal cardiac influence in an example (Von Borell et al., 2007). HRV (e.g. rMMSD) is lower in depressed humans (van der Kooy et al., 2006; Patron et al., 2014; Schiweck et al., 2019), and HRV (SDNN: SD of normal-to-normal interval) has also been shown to increase in response to a pleasant tactile stimulus (Triscoli et al., 2017). In humans, six out of nine HRV indices (but not rMSSD) were found to differ between joy and sadness (Shi et al., 2017). In dogs, negative affective states following isolation have been associated with a decrease in rMSSD (Katayama et al., 2016). In horses, regular 'relaxing' massages have been associated with higher HRV (rMMSD, among others) (Kowalik et al., 2017). Similarly, in sheep, rMSSD was higher when animals were in a putative positive affective state (being groomed) than when they were in a putative negative affective state (being isolated) (Reefmann et al., 2009b). Nonetheless, Briefer et al. (2015) found no relationship between rMMSD and affective valence when controlling for arousal in goats.

3.3.3.2. Respiratory rate. Respiratory rate has also been investigated as a potential indicator of affective valence in animals. In sheep, respiration rate increased in response to feed-related negative affective stimuli and decreased in response to feed-related positive affective stimuli (Reefmann et al., 2009a). In goats, however, respiration rates have only been linked to affective arousal, not valence (Briefer et al., 2015).

3.3.3.3. Peripheral temperature. Affect can be accompanied by a drop in peripheral temperatures, subsequently followed by a rise in core body temperatures – a phenomenon called *emotional fever* (Cabanac and Gosselin, 1993; Proctor and Carder, 2015). Vasoconstriction caused by stress causes blood to be diverted away from the periphery and towards centrally located, vital organs (Oka et al., 2001). Afterwards, post-stressor vasodilatation occurs to dissipate the accumulated heat, and peripheral temperatures consequently rise. Primates exposed to a threatening stimulus show a decrease in nasal temperature – which does not occur in response to a neutral stimulus (Kuraoka and Nakamura, 2011). Conversely, the withers and nasal temperature of sheep increased after a putative pleasant experience, i.e. brushing (Tamioso et al., 2017). Another study suggests that a significant drop in nasal temperature in cows reflects a change in affect in terms of valence (from positive to negative or vice versa) regardless of arousal (Proctor and Carder, 2016).

3.3.4. Other candidates for physiological indicators of affect

So far, despite promising research into the physiological facet of affect, no single indicators has yet been identified as a reliable indicator of affective valence. Research on the subject is still in its infancy and new indicators are currently being investigated and put forward, including composite indicators.

3.3.4.1. Telomere attrition. A telomere is a repetitive DNA segment at the extremities of a chromosome, which maintains the genome integrity and naturally shortens during mitosis (Stewart et al., 2012). In humans, affective experiences have been shown to influence telomere attrition: for instance, depression has been linked with shorter peripheral telomere length (Ridout et al., 2016), while a personality profile linked to higher optimism has been linked with longer telomeres (Schutte et al., 2016). Recently, telomere attrition has also been proposed as a marker of animal welfare (Bateson, 2016). Consistent

with this hypothesis, roe deer in poor environmental conditions have shorter peripheral telomeres than those experiencing better conditions (Wilbourn et al., 2017). In line with Webb et al. (2018), we encourage animal welfare researchers to investigate links between telomere length and animal welfare, with a particular focus on long-term affective states such as mood or happiness.

3.3.4.2. Allostatic load index. The allostatic load index is a composite indicator that reflects the overall physiological dysregulations occurring in response to cumulative, long-term chronic stress at the neuroendocrine, immune, autonomic and metabolic levels (Juster et al., 2010). These physiological responses to stress are known to be sensitive to one's evaluation of a threat (i.e. one's subjective perception) (McEwen and Gianaros, 2010). Consistent with this idea, the allostatic load index has recently been associated with human affective experiences: the allostatic load has been positively correlated with frequent negative affect (Dich et al., 2014) and inversely correlated with frequent positive affect (Schenk et al., 2018). We hence suggest that the allostatic load could also be a promising indicator of long-term affect in animals.

3.3.4.3. -Omics techniques. Exploratory research on physiological components of affect is expected to flourish in the future. In particular, the use of –omics techniques (i.e. metabolomics, proteomics, ...) may allow researchers to obtain a more comprehensive insight into the different physiological pathways related to affective states. Years ago, metabolomics were proposed as a valuable tool to study neuropsychiatric disorders in humans (Quinones and Kaddurah-Daouk, 2009), but this application in animals is still limited (Goldansaz et al., 2017).

3.3.5. Comparative neuroscience

Other options to learn more about animal affect include neuroscientific approaches. As LeDoux (1996) suggested, the most reliable and objective way to measure an individual's current affective state is by directly looking at the ongoing processes in the brain. Techniques in affective neuroscience indeed make it possible to study animal (and human) brains. This has yielded several types of neuroscientific evidence for the existence of animal affect. Comparison of human and animal brain structure has revealed similarities in neural circuits and parts of the brain that are important for affective experience and processing. Primary affect is wired into subcortical structures that are anatomically and neurochemically homologous in all mammals, suggesting that at least these types of affect are fairly widespread among mammals (Gray, 1987; LeDoux, 1995; Panksepp, 2011). Primates also share important cortical structures that are necessary for 'secondary affect', with humans (Damasio and Carvalho, 2013).

Positron emission tomography (PET) scanning and functional magnetic resonance imaging (fMRI) procedures can be used to compare brain activity in humans and non-humans and to map affective systems (Andersen et al., 2002; Takamatsu et al., 2003). For example, by using PET imaging, the separation distress system in animal brains has been shown to be strikingly similar to human sadness systems (Damasio et al., 2000). By means of electrical and chemical stimulation of homologous subcortical regions of mammalian brains, evidence has also been found for other distinct affective systems such as lust, fear, rage, panic/grief and play (Panksepp, 2010).

3.3.6. Limitations of physiological markers of affect

Using physiological measurements as indicators of affect entails some general methodological issues. First, the time course of responses in relation to the trigger should be accounted for, as well as circadian and individual effects on baseline levels (von Borell and Ladewig, 1992; Ruis et al., 1997; Schrader and Ladewig, 1999). Second, the collection of invasive samples may induce confounding reactions (Broom and Johnson, 1993), though there is a growing number of assays for non-

invasive biofluids, such as saliva and urine (Mormède et al., 2007). Third, some physiological changes may not necessarily accompany affective change, as is known in humans (Lane et al., 1997; Stone and Nielson, 2001). Fourth, certain single biomarker measures may not be able to distinguish the subtleties of affect (Dawkins, 2000) and are said to potentially mask the richness of animal affective experiences (Bekoff, 2000). Fifth, limitations of measurements of brain activity as described here include the need for immobility, which involves either training animals or anesthetising them, or the need for less intrusive wearable devices. Sixth, studies must also ensure that they take arousal into account, as arousal may have a confounding effect on physiology, possibly pointing to inexistent valence effects, in particular where negative and positive cues/events/contexts differ in arousal levels. And finally, it is important that researchers give attention to discriminating trait biomarkers linked to individual differences/personality and state biomarkers linked to affect.

4. General discussion, conclusions and future research

The aim of this review was to provide an overview of current knowledge in the area of animal affect, starting with an explanation of what affect is thought to be and following with a description of current methods to assess affect in non-verbal beings. Given the inconsistent use of the affective terminology in both animal and human literature, and ensuing confusion, it is essential that authors define the words they use and consistently use them throughout their articles. Recently, a definition of affect was provided by Paul and Mendl (2018), who discuss the benefits of descriptive versus prescriptive definitions, which will hopefully help bridge the gap between the different disciplines and researchers and thereby support this field of research in moving forwards more rapidly. This may also reconcile human and animal affect research, with both fields having much to learn from each other.

Another important question is how do methodologies to assess emotion and mood differ? Should they differ? And can these two affective processes be disentangled in practice? As an example, since optimism is likely impacted by both short-term emotion and baseline mood (as well as personality), it is not completely clear what the judgement bias test assesses exactly. So far it seems that this test assesses a combination of both mood and emotion, because long-term environmental conditions affect optimism in animals (Harding et al., 2004; Douglas et al., 2012), but acute events preceding the test also impact the outcome (Sanger et al., 2011). With these two affective systems being heavily dependent on one another, it may be difficult to attempt to disentangle them with certain methodologies. Moreover, affective systems depend heavily on individual differences, also referred to as trait affect, and it is crucial therefore that researchers take into account these personality variables when investigating state affect. For example, cognitive biases may be the result of individual personalities rather than transient affect (Paul et al., 2005; Mendl et al., 2009; Luo et al., 2019).

As previously mentioned by others (e.g. Boissy et al., 2007), positive animal affect has in the past received less attention than negative affect, and this gap in research is now encouragingly being addressed (e.g. Finlayson et al., 2016; Ahloy-Dallaire et al., 2018) and should hopefully continue to be in the future. Low arousal positive affect may however have been less studied due to practical limitations in assessment. Low arousal is sometimes incompatible with test situations, such as exposure to play pens (Reimert et al., 2013), which create high arousal states. Low arousal behavioural indicators may moreover be more subtle or more difficult to disentangle from low arousal neutral or negative states, e.g. inactivity (Fureix and Meagher, 2015). The added complexity of separating low arousal positive emotion from low arousal positive mood, may also come into play here. However, if animal welfare is the focus of the study, the question of whether it matters what kind of positive affective state is under study, is also relevant. In human happiness for example, it is the frequency of positive affect,

regardless of whether it is emotion or mood and regardless of intensity, that seems of importance (Diener et al., 2009). So if the aim of a study is simply to assess animal welfare, maybe the exact nature of the affective state that is recorded is less important than capturing the average frequency of positive affect over time.

As seen above, none of the current methods to assess affect in animals is perfect; they each have their own advantages and disadvantages. Any one measure is still an indirect measure and cannot unequivocally prove subjective affective experience(s) in animals (Mendl et al., 2009). Since all methods have limited value on their own, it has been proposed – and we agree – that coupling results of different techniques will yield the best interpretation of animal affect (Broom and Johnson, 1993; Paul et al., 2005; de Vere and Kuczaj, 2016). Physiology may be key here. There have recently been several promising physiological markers of animal affect put forward. Though in the past physiology was used more often as an indication of activation/arousal, interesting links with affective valence are now apparent, especially for mood or happiness, hence long-term affect.

Finally, some researchers emphasize that combining "hard" and "soft" (anecdotal) research is needed to improve our understanding of animal affect (Bekoff, 2000; Morris et al., 2008). They argue we should not confine attention to quantitative data that is based on abstract measures, but also include qualitative, narrative data, for example QBA, or simply a detailed description of observations. It is often argued that this approach inherently involves unscientific anthropomorphic assumptions, but others would argue that critical anthropomorphism (Burghardt, 1991) could have valuable contributions to the study of animal affect in addition to conventional experimental approaches (Konok et al., 2015; Spunt et al., 2017; Veissier et al., 2009; de Waal, 1999; Hebb, 1946; Morris et al., 2008; Wemelsfelder, 1999).

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at https://doi.org/10.1016/j.neubiorev.2020.01.028.

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