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GETTING TO THE HEART OF ANIMAL WELFARE

THE STUDY OF ANIMAL EMOTION

Prof. **MICHAEL MENDL** and Dr. **ELIZABETH PAUL**

Stichting
ANIMALES

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door

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Stichting
ANIMALES

Voorwoord

Voor u ligt de derde uitgave van de Animales-Voordracht, ditmaal gegeven door Professor Michael (Mike) Mendl, hoogleraar Animal Behaviour and Welfare aan de Universiteit van Bristol, Verenigd Koninkrijk, in nauwe samenwerking met zijn collega en partner Dr. Elizabeth Paul.

Professor Mendl is in 1982 afgestudeerd aan de Universiteit van Cambridge in de studierichting natuurwetenschappen om vervolgens promotieonderzoek te doen naar de invloed van de moeder-kind relatie op gedragsontwikkeling. In 1986 ontving hij zijn Doctoraat en zette zijn werk naar gedragsontwikkeling voort aan de Universiteit van Groningen, om via een Postdoc positie aan de Universiteit van Cambridge een vaste aanstelling aan de Scottish Agricultural College in Edinburg te verwerven. In 1997 werd hij benoemd tot lector aan de Universiteit van Bristol, waar hij in 2005 de functie van hoogleraar verkreeg.

Als Stichting Animales zijn wij zeer verheugd dat Professor Mendl heeft toegestemd de Derde Animales-Voordracht te willen houden. Zijn werk naar cognitie, welzijn en gedrag bij dieren heeft in zeer belangrijke mate bijgedragen aan het bevorderen van dierwelzijn. In 2013 ontving Professor Mendl, samen met psycholoog Dr. Elizabeth Paul, de prestigieuze International Society for Applied Ethology Creativity Award voor hun baanbrekende werk naar het kunnen inschatten van emotie bij dieren en met name voor hun theoretische bijdragen op dit gebied en het ontwikkelen van 'cognitive bias' methodes om emotie en cognitie bij dieren te kunnen meten. Deze methodes worden vandaag de dag wereldwijd erkend en toegepast bij onderzoek naar diergedrag en -welzijn om zowel positieve als negatieve gemoedstoestand bij dieren te kunnen identificeren en wordt ook algemeen gebruikt door gedragsbiologen, neurowetenschappers en psychopharmacologen. Professor Mendl en Dr. Paul geven aan dat het begrijpen en het kunnen inschatten van de gemoedstoestand bij dieren van fundamenteel belang is voor het meten en verbeteren van dierwelzijn. Het is hun doel om met de verkregen kennis van dit onderzoek naar emotie, cognitie en gedrag in te zetten ter verbetering van dierwelzijn. Deze visie sluit naadloos aan bij die van de Stichting Animales.

De Stichting Animales heeft tot doel om het dierwelzijn te bevorderen in de breedste zin van het woord. Dit tracht de stichting te bereiken door onderzoek gericht op het gebied van dierwelzijn te stimuleren en financieel te ondersteunen. Door overdracht van kennis, middels bijvoorbeeld de Animales-Voordracht, hopen wij tevens de kennis over dierwelzijn aan dierhouders en beheerders te stimuleren en onder de aandacht te brengen.

Wij willen u hartelijk danken voor uw interesse en hopen dat u met veel genoegen en plezier kennis zult nemen van de inhoud van deze voordracht. Mocht u verder geïnteresseerd zijn in het werk dat de Stichting Animales doet, dan kunt u onze website bezoeken; www.animales.nl.

Dr. Willy H. Metz, voorzitter Stichting Animales

Preface

We are very proud to present the third edition of the Animales lecture, which will be given by Prof. Michael (Mike) Mendl, Professor of Animal Behaviour and Welfare at Bristol University, United Kingdom, in close collaboration with his colleague and partner, psychologist Dr. Elizabeth Paul. Prof. Mendl graduated in 1982 at the University of Cambridge, in the field of natural sciences, to pursue his studies through a PhD on the impact of mother-offspring relationships on behavioural development. In 1986, he received his PhD, and continued his work on behavioural development in animals at the University of Groningen, Netherlands, after which he held a post-doctoral position at the University of Cambridge until moving to a permanent position at the Scottish Agricultural College in Edinburgh. In 1997 he moved to a lectureship at the University of Bristol and has since been promoted to Reader and then, in 2005, to Professor.

The board of the Animales Foundation is very pleased that Prof. Mendl has agreed to give the third Animales lecture. His work on cognition, welfare and animal behaviour, which he conducted together with Dr. Paul, has significantly contributed to understanding and promoting animal welfare. In 2013, Prof. Mendl and Dr. Paul, received the prestigious International Society for Applied Ethology Creativity Award for their ground-breaking work on the assessment of animal emotion and, in particular for their theoretical contributions in this area and development of 'cognitive bias' methods for assessing animal affect. Such methods are now commonly used in animal welfare science to identify both positive and negative affective states in animals, and have also been used by behavioural biologists, neuroscientists, and psychopharmacologists. Prof. Mendl and Dr Paul argue that understanding and assessing the affective state of animals is of fundamental importance in measuring and improving animal welfare, and that they would like to continue to use the knowledge gained through his research to help improve animal wellbeing. A vision that seamlessly ties with those of the Animales Foundation.

The Animales Foundation aims to promote animal welfare in the broadest sense of the word. It seeks to achieve this goal by stimulating and financially supporting scientific research aimed at animal welfare. It also hopes to stimulate and raise awareness of animal welfare, by transferring scientific knowledge of animal welfare to the public. The Animales lecture is one of the means to achieve the latter.

We would like to thank you for your interest and hope that you will be pleased with the content of this booklet. Should you be interested in the work of the Animales Foundation, please visit our website; www.animales.nl.

Dr. Willy H. Metz, Chairwoman of the Animales Foundation

Introduction: animal use, animal welfare and animal emotion-like states

We humans use other animals in a multitude of ways. We eat them, study them, watch them, marvel at them, are entertained, inspired and awe-struck by them, battle them as pests and purveyors of disease, strive to save them from extinction, use them as guides and assistants, and live with them as companions. Some of the numbers are phenomenal. In 2014, people across the globe used 21,409,683,000 chickens in food production[1] , and consumed 167,228,959 tonnes of fish.[2] Figures for the other main agricultural species are equally impressive (Figure 1). To achieve all of this requires us to intervene in their lives. Even the simple act of watching from afar can affect the habitats, environments and welfare of charismatic wildlife species (e.g. Moorhouse et al., 2017, Moorhouse et al., 2015). And our impact on animals used for food, research, companionship, and entertainment is even more direct; we keep them captive and manage them in various ways ranging from controlling what and how much they eat, to when and how they die.

Our interactions with other animals are thus multi-faceted, benefitting us in many ways, but also imposing a way of life (and death) on them that may often not be in their best interests. What are the effects of keeping farmed salmon or broiler chickens in tightly stocked groups of many thousands of individuals? How do sows cope with being kept in farrowing crates which prevent them from turning around, nest building, and freely interacting with their piglets? How painful is it for a dairy cow to be lame? How does the shortened muzzle of a brachycephalic dog and its attendant impact on breathing affect its wellbeing? What do the pacing stereotypies of a captive lion tell us about how it is feeling? How stressful is it for a male laboratory mouse to live in close quarters with a dominant cage-mate?

These and many similar questions underlie societal concern about animal welfare. In a 2016 Eurobarometer survey of nearly 28,000 EU citizens, 94% believed that it was important to protect the welfare of

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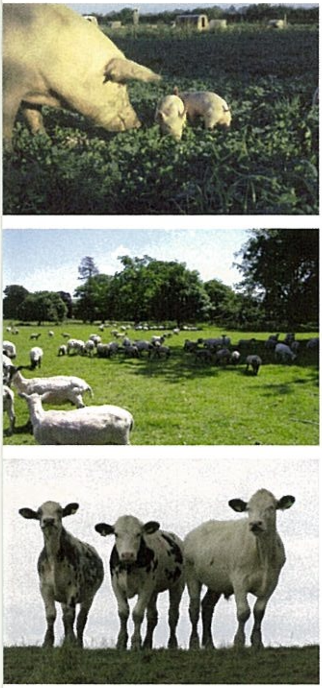
[1] http://www.fao.org/faostat/en/#home

[2] ftp://ftp.fao.org/FI/STAT/summary/a-0a.pdf; http://www.fao.org/3/a-i5555e.pdf



985,673,301 (FAOSTAT 2014)

1,195,624,523 (FAOSTAT 2014)

1,474,526,581 (FAOSTAT 2014)

Figure 1. The number of pigs, sheep and cattle used in agricultural production during 2014 (Food and Agricultural Organisation statistics (FAOSTAT)). Photo credits: pigs, Suzanne Held; sheep, Corinna Clarke; cattle: Oliver Burman.

farmed animals, and 57% said that it was very important to do so (Special Eurobarometer 442, 2016); just one example of the level of concern in some parts of the world. A consequence is that debates on animal usage and animal welfare can be highly charged and emotive affairs, open to the influence of vested interests and biased argument. Whilst political expediency, economic pressures, and societal opinion will inevitably shape the policies and legislation that govern our use of animals and the accompanying welfare standards, there is also an important place for scientific contributions to the debate. Science can provide essential objective information on exactly how different methods of housing and husbandry impact on animal welfare, and hence how imperative it is to do something about them, and what strategies are likely to be successful. However, in order to achieve this, there first needs to be a clear understanding of what we actually mean by animal welfare and therefore how we can study and measure it scientifically.

Our aim in this booklet is to explore this key issue, arguing that ultimately what motivates many people's concerns about animal welfare is the assumption that animals are capable of suffering; that is experiencing negative emotional states – the animal equivalent of feelings that we label with words like 'fear', 'anxiety', 'sadness' and 'depression'. Accordingly, good animal welfare should be characterised by positive emotional states – feelings that we call, for example, 'happiness', 'pleasure' and 'contentment'. But if this is the case, and emotional states lie at the heart of what we mean by animal welfare, then it is imperative that we study and devise methods for assessing them, despite the significant challenges that this presents. As humans, we are able to tell each other about what we are feeling, providing as direct an insight into our experiences as is currently possible, though not of course infallible – we can lie and ultimately we cannot know for certain what any other person is experiencing. However, other species cannot use language to report their conscious experiences. In fact, we don't know for certain which species actually have conscious feelings – some have argued that only humans do (Macphail, 1998). And, if other species do have such experiences, how can we assess them?

The mystery of how consciousness – our first person subjective experience of the world through perceptions, thoughts and feelings – is linked to the activity of our brains, and whether similar associations between brains and consciousness occur in other species, are 'big questions' at the cutting edge of modern biological science and philosophy. We will not presume to be able to provide answers to these hugely challenging puzzles. Rather, we will present a framework for the study of emotion-like states in animals which side-steps the consciousness question, but makes them accessible to scientific investigation. We will discuss new methods that we and others have developed that are designed to help us understand and measure these states, and hence to assess animal welfare. As you may have noticed, we will also use the term 'emotion-like' as a short-hand reminder that, although our ultimate interests in animal welfare are driven by our own subjective experience of emotions such as happiness, sadness and anxiety, we are currently unable to know whether other animals share such conscious feelings, or some species equivalent, and therefore we should cautiously refer to the phenomena that we study as 'emotion-like'.

Figure 2. Are you worried about the welfare of any of the sources that gave rise to the ingredients of this beefburger? If so, which sources and why? And why aren't you worried about the other sources? See text for more information. (source: http://pikachakula.com/recipe/beef-burger/#!prettyPhoto)

The heart of concerns about animal welfare: feelings and emotion-like states

Our argument that emotion-like states lie at the heart of concerns about animal welfare is simple, and perhaps simplistic. If we ask you whether you are worried about the welfare of any source components of the beef burger shown in Figure 2, we would imagine that those of you who do have concerns will have them about the provenance of the beef and cheese parts, but would be surprised if you told us that you were troubled about the past welfare of the lettuce, tomato or bread. Why should that be? All the source ingredients are likely to have been reared in ways that are somewhat unnatural, for example being exposed to specially formulated food, housed or planted at high stocking densities, kept on unusual substrates such as concrete floors or without soil in hydroponic systems, and treated with growth promoting chemicals, fertilisers, and pesticides. However, these things only appear to bother us from a welfare perspective if they happen to animals and not when they happen to plants. Our guess is that this difference arises from an assumption that the animal progenitors of the beef burger's ingredients are capable of experiencing some form of suffering due to the way that they are housed and husbanded, but the plant progenitors are not. In other words, it is the assumption that this ability to suffer exists that defines our animal welfare concerns.

This view is encapsulated in Jeremy Bentham's (1879) famous quote: 'The question is not, Can they reason? nor, Can they talk? but, Can they suffer?' In considering animal welfare, the capacity for suffering – the experience of negative emotional states – is key, and seen by many as being morally relevant (Brambell, 1965, Rollin, 2006). Other animal welfare scientists have made the same point (e.g. Dawkins, 1990, Duncan, 1993), and 'sentience' – the ability to have subjective experiences – is recognised in legislation as a fundamental driver of our animal welfare obligations (Box 1). Moreover, research shows that perceptions of the intelligence of other species and whether they can be considered to have a 'mind' seems to be related to concerns about their welfare (Davis and Cheeke, 1998). There are differing views, however. Some welfare scientists argue that the animal's physical health and physiological functioning are the major determinants of its welfare, whilst others have posited that living a natural life with the freedom to perform 'normal' behaviour is critical (e.g. Kiley-Worthington, 1989, McGlone, 1993; Box 1).

These three different perspectives have been labelled the *feelings, function* and *freedom* approaches to conceptualising animal welfare (Fraser et al., 1997) and each has its own proponents. Our own view is that both (mal)*function* and (lack of) *freedom* influence welfare by altering *feelings*. A disease that impedes an animal's functioning is also likely to generate pain and malaise. Preventing an animal performing a highly motivated behaviour is likely to lead to a frustration-like state. If so, both would impact on the animal's welfare. On the other hand, if a plant is riddled with a fungal infection that severely limits its function, or its freedom to grow or move towards sunlight is impeded by a dense overhead canopy, we may say that it is diseased, or constrained from achieving a survival goal, but we are unlikely to say that its welfare or well-being is poor. Our assumption that plants do not feel or have emotion-like states prevents us from extending the concept of welfare to them.

Box 1. Feelings, function, and freedom as key determinants of animal welfare

Feelings are paramount

"Let us not mince words: Animal welfare involves the subjective feelings of animals"

Dawkins 1990

"Neither health nor lack of stress nor fitness is necessary and/or sufficient to conclude that an animal has good welfare. Welfare is dependent on what animals feel"

Duncan 1993

"Desiring to ensure improved protection and respect for the welfare of animals as *sentient* beings, have agreed upon the following provision"

Treaty of Amsterdam amending the Treaty of European Union 1997, p.110.
Protocol on protection and welfare of animals (italics added)

"An Act—
(a) to reform the law relating to the welfare of animals and the prevention of their ill-treatment; and, in particular,
(i) to recognise that animals are *sentient…*"

New Zealand Animal Welfare Act 1999 (italics added)
(amended to recognise animals as sentient in 2015)

Function is paramount

"an animal is in a poor state of welfare only when physiological systems are disturbed to the point that survival or reproduction are impaired"

McGlone 1993

Freedom is paramount

"If we believe in evolution… then in order to avoid suffering, it is necessary over a period of time for the animal to perform all the behaviours in its repertoire"

Kiley-Worthington 1989

Can we study animal feelings?

By choosing to adopt the *feelings* approach to animal welfare, you could argue that we are setting ourselves an unnecessarily difficult challenge. Indeed this is one pragmatic reason for favouring the *functions* approach. It is relatively easy to measure aspects of functioning such as growth rate, disease and injury levels, metabolic status and so on, although deciding when these metrics are sufficiently different from 'normal' that a welfare problem exists is not straightforward (e.g. Mendl, 1991, Rushen, 1991). By contrast, attempting to measure emotional feelings, even indirectly, is a much more difficult undertaking. Nevertheless, our view is that there is space in animal welfare science for this endeavour purely because, as we have argued, feelings are so central to our concerns about animal welfare in the first place. Furthermore, a deeper understanding of animal emotion-like states will help provide information on the necessity for, and utility of, current animal models in understanding and treating human emotional disorders, such as depression and generalised anxiety, and other pathological feeling states such as chronic pain (see Cryan and Mombereau, 2004).

So, how can we attempt to measure the subjective feelings of animals? One approach taken by the ethologist Francoise Wemelsfelder (Wemelsfelder, 1997) is to adopt a stance similar to that of philosopher Gilbert Ryle (Ryle, 1949) and argue that animal subjectivity is indeed accessible to observation. This perspective has led Wemelsfelder and colleagues (Wemelsfelder et al., 2001) to develop a method for assessing the expressive quality of animal behaviour (Qualitative Behavioural Assessment) which, she has argued, reveals animal subjectivity directly. Observer ratings produced by this method have been correlated with conventional behavioural and physiological indicators of animal welfare (Camerlink et al., 2016), and the method has been used in on-farm welfare assessment schemes (EU Welfare Quality®). In this view, animal subjectivity can indeed be studied directly.

A different and more common approach is to assume that we cannot directly measure mental experiences in other species, and to rely instead on the argument by analogy that similarities in behaviour, physiology and neural function between ourselves and other animals may be accompanied by similar subjective experiences (e.g. Griffin and Speck, 2004, Dawkins, 2006, 2017). A group of neuroscientists and consciousness researchers drew up a statement to this effect in 2012 declaring that possession of a neocortex is not necessary for conscious experience and therefore that, in addition to humans, all mammals and birds, and some other species such as octopuses, possess the neural substrates of consciousness, may show the capacity for intentional behaviours, and hence, in principle, have conscious experiences too.[3]

However, there are dissenting voices. Some argue that a neocortex *is* essential for the emergence of consciousness (Key, 2016), and others propose that the capacity for higher-order cognition including syntactic manipulation (language) is likely to be a pre-requisite for consciousness. Hence, they conclude that many and perhaps all non-human species are not conscious (e.g. Macphail, 1998, Rolls, 2014).

Whatever our stance on whether and which other species have the capacity for consciousness, it is still valuable to develop measures that can give us an insight into what state an animal may be experiencing at any one time (the *contents* of its putative conscious experience). From an animal welfare perspective, the states of interest are emotion-like ones, and the challenge is to develop objective and observable markers of these states even if, in contrast to the philosophical assumptions of Wemelsfelder's approach, we cannot know for certain whether they are accompanied by conscious experiences.

Emotion concepts: discrete and dimensional models

Since the concept of emotion comes from our own subjective experiences, we inevitably need to rely on humans as a model for animals in guiding our choice of indicators of animal emotion-like states. Contemporary theories view human emotions as composed of a number of components – subjective experience (emotional feelings) and accompanying behavioural, physiological and neural changes (e.g. Scherer, 2005, see Paul et al., 2005). Whilst, as we have discussed, we are unable to measure the subjective, conscious component in non-human animals, or to know for certain that it is there, we can objectively measure the other components. So, taking humans as a model, we need to ask what changes in which components reflect which emotional feelings?

Psychologists have developed two main ways of conceptualising human emotions. The *discrete emotions* model posits that there are a number of

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[3] http://fcmconference.org/img/CambridgeDeclarationOnConsciousness.pdf

Figure 3. Masks of the facial expressions of the six basic emotions identified by Paul Ekman and colleagues (Ekman 1992). From top left to bottom right: sadness, surprise, happiness, disgust, anger and fear. (source: http://2fobbek4ecv2jhzw7qruit1c.wpengine.netdna-cdn.com/wp-content/uploads/2011/04/Emotional-Trading.jpg)

so-called 'basic emotions', for example 'happiness', 'sadness', 'fear', 'anger', 'disgust', 'surprise' (Ekman, 1992) that reflect the activity of distinct underlying neurobehavioural systems which have evolved to mediate suites of responses to the array of challenging situations that animals encounter. Some argue that these discrete emotional feelings are reported in all cultures and are identifiable by distinctive patterns of behaviour and physiology – for example the facial expression of Ekman's six basic emotions (Figure 3). This is in line with Darwin's notion that man and animals display species-specific characteristic emotional expressions (Darwin, 1872). If this were the case, it would be possible to search for specific behavioural, physiological and neural signatures in other species as indicators of these states.

However, there are a number of reasons why this may not be so simple. For example, there are different discrete emotion models which assume different fundamental human emotional states (see Izard, 2007). Similarly, some cultures have words for certain emotions that others do not, thus indicating a potential lack of universality (e.g. age-otori – the feeling of having had a bad haircut (Japan)). Reviews of the literature sometimes indicate consistent clusters of behavioural, physiological and neural changes associated with reported discrete emotions (e.g. Kreibig, 2010, Vytal and Hamann, 2010, Kragel and Labar, 2016), but in other cases do not (e.g. Mauss and Robinson, 2009, Lindquist et al., 2012). And there are theoretical arguments against the idea that discrete modular emotion systems are 'natural kinds' triggered by specific stimuli, and generating characteristic response profiles and associated feelings (Barrett, 2006). Notably, the theory of constructed emotion argues that discrete emotions such as 'anger' are actually categories of similar emergent states induced by a combination of fundamental interoceptive feelings of positivity or negativity (core affect, see below), evaluation of incoming sensory information and categorisation of that information in the light of previous experiences. In this view, emotions are 'constructed', variable, and categorised post-hoc into groupings of similar states that are given labels such as 'anger', rather than being 'triggered', uniform, and the product of discrete emotional systems (Barrett, 2017).

An alternative view is the *dimensional model* of human emotion. This was originally based on studies which used factor analyses of the clustering in time of reported emotional experiences, or the categorisation of discrete emotion words, and detected two or three key underlying dimensions that accounted for much of the variation in the data. A ubiquitous dimension is that of *valence* (positivity or negativity), which can be thought of as the defining characteristic of emotions – the key thing that makes a subjective experience emotional is whether it is pleasant or unpleasant, rewarding or punishing, positive or negative (e.g. Cacioppo and Berntson, 1999, Watson et al., 1999, Carver, 2001, Russell, 2003, Anderson and Adolphs, 2014). Another common dimension is *arousal*, the degree of activation experienced. Both these dimensions characterise the prominent *core affect* model of emotion (Russell, 2003); see Figure 4.

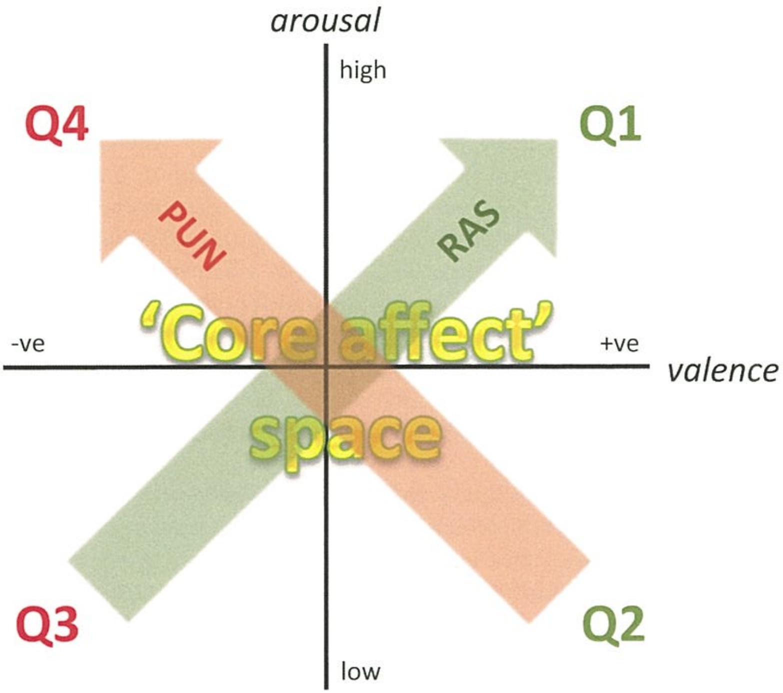


Figure 4. The core affect model of emotion. Valence and arousal are viewed as the key dimensions that both define, and discriminate between, emotional states. Some theorists suggest that activation and deactivation of reward acquisition (RAS) and punishment avoidance (PAS) systems generate respectively Q1 and Q3 states (RAS) and Q4 and Q2 states (PAS). Adapted from Russell (2003), Burgdorf and Panksepp (2006), Mendl et al. (2010b). See text for further details.

Here we should note that the term *affect* is often used in the study of human and animal emotion to denote states that have valence. This includes short-term 'object-focused' emotions that occur in response to a particular stimulus or situation, and longer-term 'free-floating' moods that are not directly linked to any specific event but reflect some cumulative function of previous short-term emotional experiences. Affect is thus an over-arching term for a variety of emotional states. Whilst it is derived from studies of reported conscious emotions, it has fewer connotations of subjectivity than do the words emotion and mood, and so we will use it here when referring to animals, but without necessarily implying conscious experience.

Proponents of both models of human emotion exist, and it is possible to conceptualise their interplay by visualising discrete emotions as being located in core affect space. Thus, 'happiness' and 'joy' would lie in the high arousal / positive valence quadrant (Q1 in Figure 4). The bone of contention is whether happiness is a fundamental discrete emotion that contributes to a 'higher level' abstraction of the organism's overall valence and arousal as reflected in core affect space, or whether core affect processes combine with other information about the organism to generate the experience of an emotion that falls in the 'happiness' category. Such arguments about the primacy of each model – whether one set of processes gives rise to the other, or *vice versa*, or both influence each other – are ongoing (e.g. Barrett, 2006, Izard, 2007, Panksepp, 2007, Adolphs, 2017, Barrett, 2017).

Although a clear resolution is still sought, our view is that the dimensional core affect model has some advantages as a basis for studying animal emotion-like states. It is less reliant than the discrete emotions approach on using human emotion-words to define different types of putative animal emotion. This is important for at least two reasons. First, the fact that emotion words are not universal across human cultures calls into question the validity of generalising them across species. Although it is plausible that, for example, fear-like states may be widespread across the animal kingdom, as species' sensory, perceptual, and cognitive abilities become increasingly different from ours, and their evolved repertoire of behavioural responses also diverge from our own, the chances that they will share similar emotional states are likely to diminish. Second, the use of human emotion words inevitably implies that we are talking about felt subjective states whereas, as we have discussed, we cannot be sure that such states are consciously experienced in other species. Consequently, in a comparative context, the use of discrete emotion words such as 'happiness', 'sadness', and especially terms such as 'guilt' or jealousy', becomes increasingly questionable and subject to the criticism of anthropomorphism as we move along the phylogenetic tree away from humans. This problem has led Joseph LeDoux, a pioneer in the study of animal affect, to argue that we should abandon use of the word 'fear' when studying animals unless we are specifically referring to the conscious experience of fear. Instead, he suggests that we use terms such as 'defensive survival circuits' to label the neural phenomenon that he and other neuroscientists actually study, and which may or may not be accompanied by some 'fear-like' feeling (LeDoux, 2012, 2014, 2017).

The core affect model avoids some of these problems by offering four simple states, identified by its four quadrants (Q1-4 in Figure 4), that can be readily translated to other species and which, if one takes a constructionist perspective, can be viewed as the source of a potentially wide range of affective states. These may be influenced by species' sensory, perceptual, and cognitive capacities and hence species-unique and not always easily represented by human emotion words (Bliss-Moreau, 2017). Furthermore, in contrast to the discrete emotions approach which treats individual emotional states separately and in a piecemeal fashion, the core affect model provides a framework for conceptualising how different types of emotional state may be related to each other (e.g. joy and contentment may primarily differ in arousal). And, as we now describe, it also fits closely with a simple operational definition of emotion that avoids the complicating issue of conscious experience, and provides a behavioural grounding that makes studying animal affect empirically tractable.

Operationally defining animal emotion-like states

Reinforcement-based concepts of emotional states (e.g. Millenson, 1967, Gray and McNaughton, 2000) offer a definition of affect that we believe is particularly suited to the study of non-human animals. A recent version of this definition has been provided by the neuroscientist Edmund Rolls: 'Emotions are states elicited by rewards and punishers' where a reward is anything for which an animal will work, and a punisher is anything that it will work to avoid (Rolls, 2014). By operationalizing the notion of reward and punishment behaviourally, this definition allows us to study emotions or, in animals, affective or emotion-like states, without needing to address the question of consciousness. We can assume that when animals are exposed to things that they will work to access, they will be in a positively valenced state, whereas when exposed to things that they will work to avoid, they will be in a negatively valenced state. If we agree with these assumptions, this provides us with a way of 'ground-truthing' an animal's affective state at any one time and hence allows us to study these states scientifically. Whether the states are accompanied by conscious experience becomes a separate question.

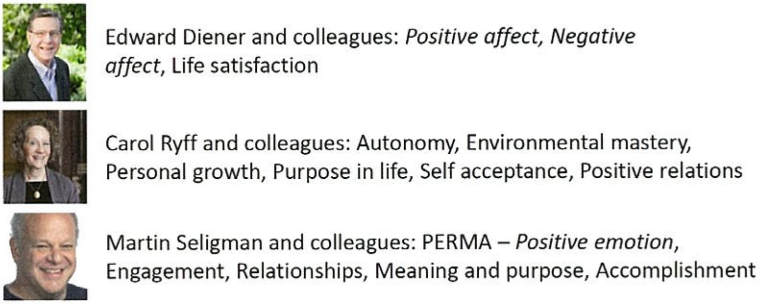
The definition also fits nicely with the dimensional approach to conceptualising emotion. Some dimensional models suggest that the key axes which explain variation between reported human emotions actually lie at 45° to the core affect axes of valence and arousal, and may reflect the activity of two putative neurobehavioural systems evolved to facilitate the two fundamental domains of activity that all animals need to carry out if they are to survive and reproduce – acquiring resources (rewards), and avoiding threat and harm (punishers). These systems have been given labels such as positive / negative activation; behavioural activation / inhibition / fight, flight, freeze; approach / avoidance process systems (Watson et al., 1999, Carver, 2001, Burgdorf and Panksepp, 2006, Mendl et al., 2010b, Corr and McNaughton, 2012). Candidate neural substrates for these systems include the mesolimbic dopaminergic system which is involved in reward prediction and acquisition, and serotonergic circuits that may play a role in punishment avoidance, although evidence for this is weaker (Niv et al., 2007, Dayan and Huys, 2008, Dayan and Huys, 2009, Boureau and Dayan, 2011). Activation and deactivation of these systems may influence location in core affect space. Thus, presence of a reward activates what we may call the 'reward acquisition system' (RAS) to generate a high arousal, positively valenced state (Q1 in Figure 4), whilst absence of reward results in low levels of activation and a low arousal, negatively valenced state (Q3). Similarly, presence of a punisher activates the 'punishment avoidance system' (PAS) and generates a high arousal, negatively valenced state (Q4), whilst absence of punishers is associated with a low arousal, positively valenced state (Q2). In this way, we can see how the operational definition of emotion maps directly to locations in core affect space, thus providing a coherent scientific framework for the study of affective states in animals.

Can animal welfare be measured as location in core affect space?

We have argued that the key determinant of an animal's welfare is its affective state, and that it is possible to study animal affect scientifically using operational definitions and the notion of core affect space. If so, it follows that we can assess an animal's welfare by estimating its location in core affect space. Very simply, when the animal's affective state lies in the negatively valenced quadrants, its welfare will be relatively poorer than when it lies in the positively valenced quadrants. We can also add specificity by suggesting that states in the Q1 location indicate that the animal is successfully acquiring rewarding resources, Q2 states indicate that the animal is experiencing a relatively calm environment in which threats and harm are infrequent or absent, Q3 states indicate that rewards and resources are lacking, and Q4 states tell us that the animal is facing frequent danger or threats. In this way, location in core affect space doesn't just provide us with a measure of animal welfare. For captive animals, it also tells us what we can do to improve it – an animal in a Q3 state should be given greater access to the resources that it desires, and an animal in a Q4 state needs to be offered more protection from harms in its environment. Furthermore, with growing acceptance of the idea that generating good animal welfare is not just about minimising negative states, but also about inducing positive states to create 'a life worth living' (Boissy et al., 2007, Yeates and Main, 2008, Yeates, 2011), the core affect model provides a clear way of conceptualising and evaluating these positive states.

The arguments above make the assumption that animal welfare is indeed equivalent to something like 'net positive affect'. This is similar to early ideas about the basic determinants of human quality of life. For example, Norman Bradburn's (1969) seminal research on psychological well-being viewed the balance between positive and negative affect as the critical influence on how well a person felt; when positive affect predominates, a person's well-being will be good. However, recent theorists have suggested that there are other more cognitively complex factors that independently contribute to human well-being, including 'life satisfaction', 'environmental mastery', 'engagement', 'personal growth', 'accomplishment, 'positive relationships', and 'meaning and purpose' (e.g. Diener et al., 1999, Ryff and Singer, 2008, Seligman, 2011, Franks and Higgins, 2012); see Figure 5. The notion of agency – the ability of an organism to engage actively with its environment, including beyond just satisfying immediate needs, as opposed to being passive and acted upon (Spinka and Wemelsfelder, 2011) – also overlaps with some of these ideas.

Some of these factors may be translatable to non-human animals. For example, it is certainly possible to measure an animal's social interactions and thereby assess the extent to which it is experiencing affiliative or antagonistic relationships with others. Likewise, 'accomplishment' could be



Edward Diener and colleagues: *Positive affect, Negative affect*, Life satisfaction

Carol Ryff and colleagues: Autonomy, Environmental mastery, Personal growth, Purpose in life, Self acceptance, Positive relations

Martin Seligman and colleagues: PERMA – *Positive emotion*, Engagement, Relationships, Meaning and purpose, Accomplishment

Figure 5. Some of the determinants of human wellbeing and quality of life as proposed by different theorists. See text for further details.

estimated by assessing how effective an animal is at achieving the apparent goals of its behaviour (cf. Franks et al., 2012). Agency may be reflected in behaviours such as play, exploration, and contrafreeloading that demonstrate an animal's tendency to act on its environment, even in preference to obtaining 'free' rewards, and also, as argued by Wemelsfelder (1997) through the expressive nature of an individual's behaviour. And 'environmental mastery' might be reflected in measures of how much control the animal is able to exert over its environment, and how predictable that environment is. However, concepts such as 'life satisfaction', 'personal growth' and 'meaning and purpose' are much more difficult and perhaps impossible to translate.

It may be possible to expand our concept of animal welfare to include some, though not all, of the factors listed above. If so, one argument would be that in order to fully assess animal welfare, we would need to measure affective state and also obtain independent measures of the other factors, for example how affiliative and supportive the animal's social relationships were, and then somehow amalgamate the different data to make an overall evaluation of welfare. This argument assumes that the different factors contribute to well-being in ways that are independent from each other, and also from affective state, and hence do not necessarily correlate, and must be measured separately. Another view is that, at least in non-human animals, many of the factors directly influence affective state. For example, lack of 'mastery' generates negative affect when goals (acquiring reward and/or avoiding punishment) cannot be achieved as desired, the opportunity to express agency is hypothesised to be rewarding in its own right

(Spinka and Wemelsfelder, 2011), and 'positive relationships' and successful 'accomplishment' are intrinsically rewarding and hence generate positive affect. If this is the case, affective state could be thought of as a 'common currency' (cf. Cabanac, 1992, McNamara and Houston, 1986) which integrates a range of experiences, including those listed above, and does indeed provide the best indication of an individual's well-being. If so, we might expect some degree of correlation between the summed positive and negative impacts of the different factors and core affect.

Whichever view of animal welfare one accepts, it is more than likely that an important determinant of welfare, perhaps the key one as we have argued, is animal affect. Measuring location in core affect space will therefore be necessary if we are to scientifically assess an animal's welfare. We now discuss how this can be done.

Measuring location in core affect space

Studies of animal affect have traditionally followed a discrete emotions model, labelling the behaviour or physiological measurements made as indicators of, for example, 'fear', 'rage' or 'lust' (Panksepp, 2005), and interpreting more complex scenarios as generating states such as 'grief', 'guilt' or 'disappointment' (e.g. Douglas-Hamilton et al., 2006, Hecht et al., 2012, Burman et al., 2008a). As discussed earlier, translating human emotion words to other species is not without hazards and susceptible to the accusation of non-critical anthropomorphism. Establishing a 'ground truth' for when an animal is in each of these emotion states is also challenging because of our inherent reliance on subjective feelings as the key defining characteristic of these states. Nevertheless, this approach has made considerable inroads into our understanding of rodent fear-like states in particular, and their underlying neural control by 'defensive survival circuits' (LeDoux, 2012, 2017, see also Panksepp, 2005). In doing so, a range of behavioural and physiological measures have traditionally been employed to monitor the animal's putative discrete emotion-like state. Are these also useful indicators of core affect?

Behavioural measures include spontaneous actions such as approaching, avoiding, freezing, fleeing, exploring, vocalizing, making facial expressions and adopting distinctive body postures, and responding to open-field, elevated-plus maze, forced swim, startle, light-dark box and many other testing situations. Some of these behaviours may be useful indicators of affective valence or arousal. For example, our operational definition implies that approach behaviour is likely to be accompanied by, or lead to, a positively-valenced state if the approached object is acquired (an exception may be predator-inspection). In contrast, avoidance and fleeing may be accompanied by a negative affective state. These inferences can be strengthened if the animal is prepared to work to access or escape the situation in question, as well as simply approach or avoid. Potentiated and attenuated startle responses to an unexpected noise have also been proposed to reflect negative and positive valence respectively (Lang et al., 2000). However, many of these behaviours are likely to be both situation and species-specific and it is therefore unclear whether they reflect, for example, all negatively-valenced states, or are restricted to the particular elucidating conditions of the situation being studied, and/or the biological characteristics of the study species. There are also far fewer potential indicators of positive affect than negative affect.

Changes in activity of the classic physiological 'stress systems' – the hypothalamic-pituitary-adrenal system and the sympathetic-adrenomedullary system – have also been widely used as indicators of fear- and anxiety-like states in animals. However, both of these systems may also be activated (e.g. as reflected by elevated heart rate, blood pressure, and glucocorticoid levels) in states which appear rewarding – for example in anticipation of a preferred food stuff (Braesicke et al., 2005) or when meeting a sexual partner (Buwalda et al., 2012) – and hence may reflect heightened affective arousal, but not affective valence which is the key measure of interest from an animal welfare perspective.

Measures that have been used in the traditional discrete emotions approach to studying animal affect may thus also be useful indicators of core affect. In particular, arousal levels may be reliably indicated by stress physiology measurements. Clearly, however, there is also a need for new measures that are specifically designed to gauge location in core affect space, especially affective valence. In recent years, a number of such measures have been developed, some of which have their roots in the work of the animal welfare research community.

A group of animal welfare researchers led by Berry Spruijt and colleagues (Spruijt et al., 2001) have developed a method for assessing the relative balance of reward or punishment that an animal is experiencing. Their suggestion, based on interpretation of ideas about the neuroscience

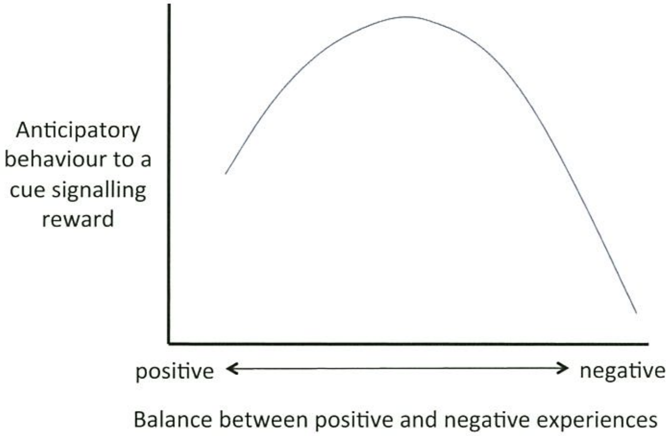


Figure 6. Hypothetical links between the overall balance between positive and negative states and its effects on anticipatory behaviour in response to a cue signalling impending reward. Thus in short-term negative states, there may be increased anticipatory behaviour but in longer-term negative states anhedonic processes may result in decreased anticipation. Adapted from van der Harst & Spruijt (2007). See text for further details.

of reward (Cabib and Puglisi-Allegra, 1996, 2012, Berridge and Robinson, 2003), is that negative states increase an animal's reward sensitivity, perhaps to increase chances of reward acquisition and 're-balancing' of state towards 'neutral' or positive (Spruijt et al., 2001). This can be monitored by measuring 'anticipatory behaviour' during the presentation of a Pavlovian cue that predicts arrival of reward after a short time delay (e.g. 30s). Animals in a short-term negative state are predicted to show enhanced 'anticipatory behaviour'. In rodents this anticipation is quantified as an increase in transitions between behaviour patterns, whilst in cats as a decrease in transitions (van den Bos et al., 2003). However, in longer-term negative states, there is evidence that sensitivity to, and valuation of, reward decreases (cf. anhedonia) and hence anticipatory behaviour in response to a Pavlovian cue actually reduces (e.g. Van der Harst and Spruijt, 2007); see Figure 6. These complications mean that to use the approach as a measure of affective valence requires knowledge of species-specific anticipatory behaviour and also the time course of the subject animal's experiences. Another example of animal-welfare research in this area is Wemelsfelder et al's Qualitative Behavioural Assessment approach (Wemelsfelder et al., 2001). This uses generalised procrustes or principal components analyses to detect an underlying structure to the choice and weighting of terms that observers provide when describing the expressive actions of animals. Very often, the two main dimensions that are detected appear similar to the arousal and valence dimensions of core affect space.

A different approach to assessing affective valence has been developed in human cognitive psychology. The emotional valence lateralization hypothesis derives from studies which suggest that the right hemisphere of most people's brains plays a dominant role in sensory processing of negatively valenced, novel, or threatening events, whilst the left hemisphere is dominant in processing more positive events (Davidson and Irwin, 1999). This idea has been translated to animals (see Rogers, 2010, Leliveld et al., 2013) and, for example, it has been shown that dogs show right-hemisphere bias by favouring use of the right nostril (ipsilaterally connected to the right hemisphere) or the left visual field (contralaterally connected to the right hemisphere) when faced with novel or threatening stimuli (Siniscalchi et al., 2010, 2011). It has also been suggested that animals who are already in a negative state show a stronger right-hemisphere bias (Larose et al., 2006), although this has not always been observed in the few studies that have been done so far (see Kappel et al., 2017).

So, there are methods in existence which may provide us with useful information about affective valence in animals and, in some cases, arousal too. They come from a diverse set of theoretical and empirical backgrounds, none of which are directly tied to the concept of core affect or to a specific operational definition. However our own method, which we now describe, is closely integrated with the operational definition of animal affect presented above, grounded in empirical findings from studies of human affect and in theoretical arguments for links between affective state and decision-making, and directly translatable to the concept of core affect.

'Cognitive biases' in decision-making under ambiguity as a measure of location in core affect space

Empirical and theoretical background

Empirical findings from human psychology show that people experiencing positive or negative affective states exhibit reliable differences in how they process information. For example, people in negative states

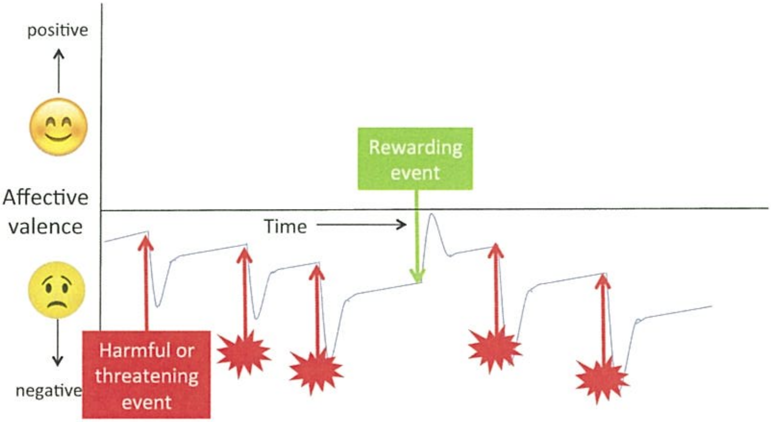


Figure 7. A simple model of the impact of short-term affective responses to discrete events (emotion-like states) on longer-term 'baseline' mood-like states. In an environment categorised by high levels of danger, cumulative experience of threatening or harmful events leads to a more negative mood-like state. See text for further details.

attend more to negatively valenced information, preferentially recall negative memories, and make more negative (pessimistic) judgements about ambiguous situations or the future (see Mathews and MacLeod, 1994, Mineka et al., 1998, Mogg and Bradley, 2005, Paul et al., 2005, Mogg et al., 2006). These so-called 'cognitive biases' may thus provide a new indicator of affective valence in animals, if they exist in other species and can be measured objectively.

Cross-species conservation of affect-induced cognitive biases is likely if such biases have adaptive survival value. In initiating research into the potential use of cognitive bias as an indicator of animal affect, we focused on biases in judgement of ambiguity. We developed a hypothesis for why these might occur across taxa. Following the operational definition of affect, we propose that cumulative experience of reward and punishment across time determines an individual's background affective, or mood-like, state, just as a person's previous experience of stressful life events increases their susceptibility to develop a longer-term state of generalised anxiety or depression (e.g. Beck, 2008). A very simple model of this is shown in Figure 7. Rewarding and punishing events create brief short-term positive or negative states. These then return to a baseline level which is slightly displaced from previously according to the valence and intensity of the event (e.g. a short-term negative state slightly increases the negativity of the baseline mood-like state). Each individual's baseline affective state can thus change across time according to their experiences, and also other factors such as personality characteristics which influence their responsiveness to these experiences, and current physical condition which influences the costs and benefits of outcomes and which is likely to be positively correlated with environmental conditions (Nettle and Bateson, 2012).

For simplicity, Figure 7 represents affective valence on a single-dimension but, as we have discussed, rewards and punishments may influence the activity of separate reward acquisition (RAS) and punishment avoidance (PAS) systems which determine location in core affect space. Thus, an individual who has been experiencing an environment where it frequently succeeds in obtaining rewards would be in a Q1 state (activated RAS; see Figure 4), whereas if it was in an environment where it encountered frequent threats and dangers, it would be in a Q4 state (activated PAS). Likewise, an environment characterised by lack of reward would tend to generate a Q3 state (low active RAS), whereas a safe environment would generate a Q2 state (low active PAS). In this way, an individual's background or 'resting' mood-like state in core affect space provides information about its environment and its recent experience of success or failure in acquiring reward or avoiding punishment.

Given this background, we propose that one function of this mood-like state is to guide future decision-making, particularly under ambiguous situations where there is limited or uncertain information about the likely decision outcome. Thus, a rustle in the undergrowth could predict a reward (prey) or punisher (predator), and whether the animal decides to approach or avoid the sound may have important survival consequences. If the individual is in a dangerous environment, it makes adaptive sense for it to be cautious and avoid this situation, whereas if it is in a resource-abundant environment an approach is likely to be rewarded. We propose that core affect mood-like states act as Bayesian priors providing information about the probability distribution of outcomes and hence influencing decisions accordingly, particularly in ambiguous situations. Thus, a Q1 state would favour approach behaviour compared to a Q3 state which would favour inhibition of reward-seeking behaviour to conserve energy (Nesse, 2000). Likewise, a Q4 state would favour avoidance relative to a Q2 state in which active escape behaviour is likely to waste time and energy (Nesse, 2005).

Through this reasoning, we suggest that location in core affect space drives 'optimistic' (Q1,Q2) or 'pessimistic' (Q3,Q4) decisions under ambiguity (so-called 'judgement biases') and hence that these decisions can themselves be used as an indication of core affect. At the simplest level, optimistic decisions under ambiguity indicate positive affect, whilst pessimistic decisions indicate negative affect. A layer of complexity is added when considering reward and punishment separately such that, theoretically, optimism about reward reflects a Q1 state whilst pessimism about reward reflects a Q3 state, and optimism about punishment reflects a Q2 state whilst pessimism about punishment reflects a Q4 state. Further complexity in the links between environmental conditions, core affect state, and decision-making is illustrated in Table 1.

Table 1. Hypothetical relationships between reward and punishment prevalence in the environment, resulting core affect states (Q1-Q4), biases in expectation of positive (+ve) or negative (-ve) outcomes, and associated 'optimistic' or 'pessimistic' decisions. Adapted from Mendl et al. (2010b). See text for further details.

	Low reward opportunity environment (leads to Q3 state)	'Intermediate' reward opportunity environment	High reward opportunity environment (leads to Q1 state)
Low threat environment (leads to Q2 state)	Q2 / Q3 ↓ expect. of −ve ↓ expect. of +ve	Q2 ↓ expect. of −ve *'optimism about −ve'*	Q1 / Q2 ↑ expect. of +ve ↓ expect. of −ve *'full optimism'*
'Intermediate' threat environment	Q3 ↓ expect. of +ve *'pessimism about +ve'*	'neutral state' no bias	Q1 ↑ expect. of +ve *'optimism about +ve'*
High threat environment (leads to Q4 state)	Q3 / Q4 ↓ expect. of +ve ↑ expect. of −ve *'full pessimism'*	Q4 ↑ expect. of −ve *'pessimism about −ve'*	Q1 / Q4 ↑ expect. of +ve ↑ expect. of −ve

Measuring judgement biases under ambiguity in animals

Given the empirical and theoretical reasoning for why judgement biases under ambiguity might reflect core affect state, hence providing us with a new measure of animal affect and welfare, we have developed a novel

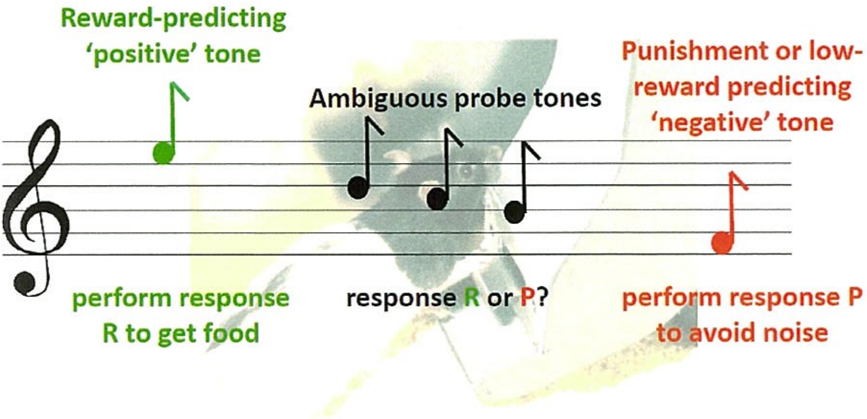


Figure 8. Schematic of the first judgement bias task developed by Harding et al. (2004) for studies of rats. Animals are trained to perform response R when they hear a positive tone to get a reward (food pellet) and response P when they hear a negative tone to avoid a punisher (brief white noise). Once trained they are presented with occasional ambiguous intermediate tones to see whether they make response R indicating anticipation of reward and hypothesised to reflect a positively valenced affective state, or response P indicating anticipation of punishment and hypothesised to reflect a negative state. The effects of affect-induction treatments on these responses can be tested. Cue types, response actions, and reinforcers can all be changed in this generic task design. See text for further details.

generic method for assessing such biases (Figure 8). Subjects are trained that one cue (e.g. a tone of a particular frequency) predicts a reward (e.g. food) and that in order to acquire this reward they need to make response R (e.g. press a lever; press left lever; approach). They are also trained that a different cue (e.g. a tone of a different frequency) predicts a less rewarding event or a punisher (e.g. no food; burst of white noise) and that they need to make response P (e.g. don't press the lever; press right lever; avoid) to acquire that reward or avoid the punisher. Once this discrimination is learnt, the animal is occasionally presented ambiguous cues (e.g. tones of intermediate frequency) and their responses are recorded. The hypothesis is that animals in a positively valenced state will make an 'optimistic-like' response R indicating anticipation of reward, whereas those in a negative state will make a 'pessimistic-like' response P indicating anticipation of the lower value reward or punishment. In this way, the test aims to assess the subject's 'judgement bias' under ambiguity as an indicator of its core affect state and hence of its welfare.

Our initial study of rats found encouraging results in line with our hypothesis – rats housed in unpredictable environments likely to induce mild negative affective states showed evidence of a negative judgement bias (Harding et al., 2004). Since that study, there have been around 100 further published studies by animal welfare scientists, behavioural biologists, neuroscientists, and psychopharmacologists, using the generic judgement bias method across a range of species including mammals (e.g. rats, mice, hamsters, sheep, dogs, pigs, cows, horses, goats, rhesus monkeys, capuchin monkeys, marmosets, peccaries, bears, and humans), birds (e.g. starlings, chickens, canaries), and even insects (e.g. honeybees, bumblebees, ants). Studies have used variants on the initial test design (e.g. using spatial, visual, olfactory or textural cues as well as acoustic ones), and a range of different manipulations designed to induce positive or negative affective states (e.g. unpredictable housing, environmental enrichment, light intensity, isolation, restraint, prior reward, various drug treatments), and many have found results in line with the basic hypothesis.

For example, rats housed in enriched conditions showed a positive judgement bias (Burman et al., 2008b, Brydges et al., 2011, Richter et al., 2012), as did those who experienced a change from single-level cage housing to more spacious multi-level caging (Wheeler et al., 2015), those who responded positively to 'tickling' by making ultrasonic vocalizations that appear to be associated with positive affective states (Rygula et al., 2012), and those who were exposed to playback of these positive vocalizations as opposed to negatively valenced ones (Saito et al., 2016). On the other hand, rats exposed to psychosocial stressors (Papciak et al., 2013), drugs designed to mimic a physiological stress response (Enkel et al., 2010) or induce an anxiety-like state (Hales et al., 2016), unpredictable environments (Chaby et al., 2013), an unexpected increase in light intensity (Burman et al., 2009), restraint stress and social isolation (Hales et al., 2016), and singly housed in metabolic cages (Barker et al., 2017) exhibited a negative judgement bias. Dogs with separation anxiety were more likely to show a negative judgement bias (Mendl et al., 2010a), and there was evidence that this could be reversed by a behaviour modification plan coupled with antidepressant (fluoxetine) treatment (Karagiannis et al., 2015), whilst dogs given a nasal spray of oxytocin which is associated with positive affect and optimism in humans exhibited a positive judgement bias (Kis et al., 2015). Sheep exposed to long-term unpredictable events (Doyle et al., 2011b, Destrez et al., 2013, 2017), or prenatal stress (Coulon et al., 2015), or a serotonin inhibitor predicted to decrease brain serotonin and hence generate depression-like negative affect (Doyle et al., 2011a) displayed a negative judgement bias, whilst those exposed to positive events, such as grooming and positive interactions with people, alongside unpredictable stressors showed a positive judgement bias relative to those who only experienced the unpredictable treatment (Destrez et al., 2014), as did lambs treated with diazepam to induce a calm positive state (Destrez et al., 2012). Starlings that had been housed in enriched conditions demonstrated a positive judgement bias (Matheson et al., 2008), whilst those that had experienced removal of enrichment showed a negative bias (Bateson and Matheson, 2007).

Calves that had been recently dehorned (Neave et al., 2013), or separated from their dams (Daros et al., 2014), rhesus macaques exposed to veterinary inspection (Bethell et al., 2012), honeybees that had been shaken simulating an attack on the hive (Bateson et al., 2011, Schluns et al., 2017), horses that were housed in conditions likely to generate relatively poor welfare (Henry et al. 2017), pigs exposed to serotonin depletion (Stracke et al. 2017), and peccaries experiencing simulated trapping (Nogueira et al., 2015) all showed negative judgement biases, whilst pigs (Douglas et al., 2012) and hamsters (Bethell and Koyama, 2015) living in enriched conditions, gently handled pigs (Brajon et al., 2015), socially housed as opposed to singly housed canaries (Lalot et al. 2017), chickens exposed to preferred warmer temperatures (Deakin et al., 2016), and bumblebees provided with a pre-test reward (Perry et al., 2016) demonstrated a positive bias. A number of studies using different versions of the generic task in humans ('reverse translation') have also observed judgement biases in line with reported affective state or the predicted effects of manipulations (e.g. Paul et al., 2011, Schick et al., 2013, Iigaya et al., 2016).

Alongside these and other findings that are in line with predictions, there are also null results where the affect manipulation has had no effect. For example, gentle grooming of goats (Baciadonna et al., 2016), enriched housing of mice (Brajon et al., 2015), chickens (Wichman et al., 2012), and quail (Horvath et al., 2016), 2h exposure to enrichment items in bears (Keen et al., 2014), and enriched housing of pigs (Carreras et al., 2016) did not induce the anticipated positive judgement bias even though, in the latter case, enriched pigs appeared to have fewer aggression-related lesions, lower serum cortisol and were scored more positively using QBA. Similarly, pigs housed at high stocking densities (Scollo et al., 2014), dogs separated for a short time from their pen-mate (Walker et al., 2014) or owner (Muller et al., 2012), and honeybees exposed to a formic acid treatment of parasitic mites that also appears aversive to the bees themselves (Schluns et al., 2017) did not show the anticipated negative judgement bias. In a few cases, findings go in the opposite direction to predictions. For example, sheep that were restrained (Doyle et al., 2010) or sheared (Sanger et al., 2011) before testing, and rats housed in unpredictable conditions (Parker et al., 2014) showed positive rather than negative judgement biases, whilst dogs that were rewarded prior to testing (Burman et al., 2011), and horses that were trained using positive as opposed to negative reinforcement techniques (Freymond et al., 2014), demonstrated negative as opposed to positive judgement biases.

Although the majority of published studies support the predicted link between an individual's putative affective state and its decision-making under ambiguity, we have seen that there are also exceptions. An important next step is to quantify the available evidence, and one powerful approach is to carry out a systematic review and meta-analysis of the literature. We are currently doing this, even though such an analysis presents significant challenges because of the wide range of species, techniques, and affect manipulations studied (Zidar et al. in prep.).

Current issues in the study of judgement bias, and future research questions

There are a number of possible reasons for contradictory or null findings in the judgement bias literature and we briefly consider some of these here, together with more general theoretical points. A more in-depth treatment of some of these issues can be found in a series of reviews that have been published on the topic (Mendl et al., 2009, Gygax, 2014, Hales et al., 2014, Baciadonna and McElligott, 2015, Bethell, 2015, Roelofs et al., 2016). These reviews have also discussed a range of technical and methodological considerations that may explain some unpredicted findings, and we will not consider these here.

What affective state is the animal actually in: establishing a ground truth

An issue of fundamental importance in this research area, and in all studies aimed at developing better measures of animal affect, is to clearly identify the affective state that the subject animal is in. Uncertainty about this undermines any attempt to identify reliable markers of affect and it may be that some contradictory or null results occur because the animal is in a different affective state to that hypothesised by the researcher. As we have seen, establishing the 'ground-truth' of an animal's affective state is far from easy. We suggest that use of the operational definition advocated earlier offers a promising and pragmatic way forward. The rationale is that stimuli or treatments which the subject clearly prefers or works to access are assumed to induce Q1 states when present and Q3 states when absent or omitted, and those that it works to avoid induce Q4 states when present and Q2 states when absent. Exceptions to this general rule might occur if an animal works to view a dangerous predator, or in other rare circumstances in which working for, or 'wanting', a stimulus becomes disocciated from actually 'liking' it (Berridge and Robinson, 2003). Ideally, the attractive or aversive properties of affect manipulations would be established experimentally or by reference to the existing literature, and for many published judgement bias studies the required evidence is already available. However, in the absence of such evidence, identifying the ground truth affective state of the subject animal is potentially open to error and circular reasoning.

Short- vs long-term affective states

Our theoretical predictions for how affect alters decision-making under ambiguity emphasise the role of long-term 'mood-like' affective states. However, many judgement bias studies use short-term affect manipulations and often (but not always – see next point) generate the predicted bias. Why should that be, theoretically? We argued that long-term mood-like states reflect cumulative experience of short-term affect generated by rewarding and punishing events. It is highly likely that the intensity and recency of these states determines their impact such that, for example, more recent affect-inducing events exert a greater influence than those in the past due to temporal discounting of an event's significance as it recedes into history. If so, then short-term affect manipulations, as well as long-term background affective state, may be expected to influence judgement bias. This also makes adaptive sense in that the most recent events, and associated affective states, are likely to be the best predictors of what may happen next to the animal. This predictive value falls off with time (e.g.

as the short-term affective state wanes), but its residual contribution is to alter longer-term mood.

Temporal dynamics of affect

Although we can understand why short-term affect close in time to, or during, a judgement bias test should influence decision-making under ambiguity, the temporal dynamics of how rewarding or punishing events actually alter affective state remains to be properly understood. For example, unexpected changes in reward and punishment may be potent inducers of affective states. Recent studies suggest that such changes result in 'reward prediction errors' (Schultz et al., 1997) that make a significant contribution to a person's ongoing affective experience. Specifically, positive affect may occur when things change to be better than expected (Rutledge et al., 2014, Eldar et al., 2016). It is thus possible that ending a short-term affect manipulation prior to judgement bias testing generates change which results in a counter-intuitive state. Thus, termination of shearing, restraint, and isolation, which are designed to induce a negative state during testing, could conceivably generate 'relief-like' positive affective states, thus explaining some counter-intuitive findings (Doyle et al., 2010, Sanger et al., 2011, see also Burman et al., 2011 for an oppositely-valenced example). The temporal dynamics of affective states thus need to be understood more clearly.

Domain-generality of core affect

The idea that core affect is domain-general – it reflects overall reward and punishment experience across different functional domains (e.g. foraging, competition with conspecifics, predator avoidance) – is inherent in our predictions, and in the notion of a common currency of affective valuation in decision-making (Cabanac, 1992, Eldar et al., 2016). However, it is possible that there may be sub-systems which are domain-specific, particularly in species where the main domains in which rewarding and punishing events occur are unlikely to exhibit correlated valenced experiences across time (Nettle and Bateson, 2012). If this is the case, induction of affective state in one domain (e.g. social stress) and measurement of it in another (e.g. food related decision-making task) may fail to yield the predicted judgement bias. This may underlie some null findings in the literature, and explicit investigation of it requires development of judgement bias tasks that do not just use food as the reward, coupled with systematic cross-domain manipulations of affect and judgement bias testing.

How does affective state influence responses to ambiguous and trained cues in judgement bias tests?

Our central hypothesis is that core affect state influences estimation of the probability of rewarding or punishing outcomes under ambiguity. If so, affect manipulations should alter responses to ambiguous cues but not to the trained cues. Such a pattern of results strongly supports our hypothesis. However, in some cases there are also changes in response to the trained cues. One explanation for this is that, in some studies, initial discrimination training is not adequately achieved (e.g. a weak learning criterion is used) and the subject thus perceives the trained cues themselves as being ambiguous to a degree, and hence displays affect-related biases to these too. However, this is unlikely where discrimination training is thorough. In these cases, affect-manipulations that alter responses to trained cues (as well as ambiguous cues) may do so for at least two reasons.

First, affective states may influence valuation as well as probability estimates of outcomes, as in the case of anhedonia where chronic negative affect may generate a reduction in reward value. If so, the animal may show decreased responding to the trained cue predicting reward during judgement bias testing. This is an affective influence, albeit a different one to that which the judgement bias test is principally designed to detect. Disentangling these effects on outcome probability and value estimation can be achieved by using separate tests to establish how the affect manipulation in question influences reward valuation – we are currently attempting this in our lab (Neville et al. in prep). Alternatively, in the case of manipulations designed to induce long-term negative states, any anhedonic-like influence should become detectable during training as a decreased responsiveness to, or speed of learning about, the cue predicting reward. A further approach is to use computational modelling of judgement bias data to dissect apart changes in the subject's estimates of reward probability and weighting of reward value (Iigaya et al., 2016). However, this requires a large amount of test data which, whilst possible to collect in human studies, may be more challenging to amass in animal studies.

An alternative explanation for changes in response to trained cues is that the experimental treatment has an influence on general levels of activity or arousal that promote or inhibit active responses in the judgement bias test. This is plausible in tasks which require animals to do something active for a reward (e.g. approach / press lever) and relatively passive to avoid punishment (e.g. avoid / don't press lever) – so-called 'Go/NoGo' tasks. Here, an increase in arousal or activity may lead to relatively higher levels of active 'Go-for-reward' responses, including to the trained cue that predicts reward, that are not directly related to the subject's affective valence. Ways to control for this include carrying out independent tests of activity (e.g. Harding et al., 2004), and using counter-balanced 'Go-for-reward' and 'Go-to-avoid-punishment' tasks (Jones et al., 2017).

Are judgement biases actually biases?

Our theoretical framework emphasises that what we are calling 'biases' are actually adaptive decisions as predicted by our view of location in core affect space as a Bayesian prior on decisions under ambiguity. In this sense, the decisions are not 'biased' away from what we would expect of an adapted organism. However, descriptively, they can be thought of as being biased from a simple random 50:50 response to ambiguity, or 'relatively biased' when one group of animals shows a different response to ambiguity than does another group. The distinction between these two uses of the term 'bias' should be noted. It is also important to be clear that, even descriptively, an 'absolute' level of bias cannot easily be determined from judgement bias tests. Thus, if an animal, or group of animals treated in a particular way, make positive responses to an ambiguous cue in 70% of trials, it is not correct to say that they are inherently 'optimistic' because they are showing more than 50% positive responses under ambiguity. This is because responses to ambiguity will be influenced by the relative valuation of the positive and negative outcomes used in the judgement bias task. For example, if the reward for responding to the positive cue is a highly-valued food whilst the negative outcome is simply no food, then one might expect subjects to err on the side of 'optimism' when presented with ambiguous cues. However, the same subjects may well show 'pessimistic' responses in a different task where the reward is a dull food and the negative outcome is electric shock (see Mendl et al., 2009). Furthermore, it is not always clear whether a 'central' ambiguous cue is indeed perceived by the animal as being exactly intermediate between the two trained cues. If it is not, then a 50:50 random response pattern would not be expected. Thus, judgement bias tasks can tell us something about the relative, but not the absolute, levels of 'optimism' or 'pessimism' of different animals or treatment groups.

A final point is that there may be situations in which responses to ambiguity do not reflect adaptive predictions. Instead, the assumed adaptive Bayesian processes may be derailed by features of the situation that the animal is not evolved to deal with and/or by changes in proximate brain mechanisms that guide decisions. The resulting decisions may then be regarded as true biases away from optimal responding. The possibility that corruption of decision-making processes underpins many mental health disorders in humans is the focus of the new discipline of computational psychiatry (Montague et al., 2012, Huys et al., 2016).

Differentiating Q1-Q4 states

The vast majority of judgement bias studies have focused on differentiating positive from negative affective valance. Distinguishing between Q1-Q4 states has not been explicitly attempted although researchers sometimes conclude that if a difference between treatment groups is detected at ambiguous cues that are close to the trained negative cue, this indicates a difference in prediction of punishment and hence in location on the Q2-Q4 axis. Likewise, a difference in response to ambiguity near the trained positive cue is sometimes interpreted as a difference in prediction of reward and hence in location on the Q3-Q1 axis. However, as mentioned in the previous point, such conclusions depend on how the animal actually perceives the relative value and perceptual location of the ambiguous cues and hence should be made cautiously. Tasks that focus purely on either the Q3-Q1 axis (e.g. those using reward vs no reward, or high reward vs low reward, as reinforcers in the task) or Q2-Q4 axis (as for Q3-Q1 tasks but using negative outcomes) will be able to provide more definitive information about how affective treatments influence location in the quadrants of core affect space.

What do judgement biases tell us about conscious affect?

As we have seen, insects can show apparent affect-induced judgement biases. Because most people less readily attribute consciousness to taxa such as insects and other invertebrates that are phylogenetically distant from ourselves (see Klein and Barron, 2016 and associated commentaries), this raises the question of what judgement biases may tell us about conscious affective states (Mendl et al., 2011, Mendl and Paul, 2016). We hope that we have shown that a strength of our approach is to be able to measure affective valence and core affect following operational definitions that allow us to study these phenomena without tying them directly to conscious experience. The question of whether conscious experience accompanies the valenced states that we measure is a separate one and may be addressed by reference to the presence or absence of neural and behavioural functions that are thought to be related to the capacity for conscious experience in humans and other species. There is vigorous debate about what these may or may not be which we cannot cover here, but many excellent papers are available that tackle this challenging question and suggest measurements that can be made to address it (e.g. Clark and Squire, 1998, Panksepp, 2005, Dawkins, 2006, Edelman and Seth, 2009, Boly et al., 2013, Key, 2016, Klein & Barron 2016, LeDoux and Brown, 2017).

Summary

The study of animal affect is an essential part of animal welfare science because, we argue, an animal's affective state is the key determinant of its welfare. However, studying this phenomenon is complex and open to many pitfalls, not least the question of whether animals experience conscious emotion-like states at all and, if so, how can we measure them. We suggest that the concept of core affect developed in research on human emotion, coupled with an operational definition of animal affect grounded in measurable behaviour, provide a way forward. We argue that studying decision-making under ambiguity – so-called judgement biases – provides us with a valuable new method for assessing an animal's core affect state. Whilst many questions remain to be answered, the strengths of this approach include: a grounding in both empirical findings and theory; the ability to specifically measure affective valence which is the key variable of concern from an animal welfare viewpoint; measurement of positive valence in line with the increased interest in enhancing welfare by going beyond simple minimisation of negative states; the potential to identify Q1-Q4 core affect states; generalisability and translatability across species; and an approach that allows progress in this challenging area whilst leaving the question of whether the valenced states are consciously experienced to be addressed via a separate evidence stream.

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Stichting ANIMALES

Algemeen Nut Beogende Instelling
ANBI

De Stichting Animales werd op dertien november 1997 opgericht met als oorspronkelijke doelstelling “het verlenen van hulp aan bedreigde dieren in de ruimste zin des woords”.

Het werkterrein van de stichting was vooral gericht op Latijns Amerika, met name Venezuela, omdat twee van de toenmalige bestuursleden daar enige tijd beroepsmatig werkzaam waren.

In verband met de verslechterde politieke situatie aldaar, werd in 2014 besloten de stichting om te vormen tot een vermogensfonds met ANBI-status en de doelstelling te wijzigen in “het bevorderen van dierenwelzijn bij voorkeur in Nederland, alles in de ruimste zins des woords”.

De stichting tracht haar doel te bereiken door:

a. Het stimuleren van op dieren gericht wetenschappelijk onderzoek op het gebied van welzijn, zoals bijvoorbeeld voeding, medisch handelen en cognitie en emotie.

b. De overdracht van kennis over dierenwelzijn aan dierhouders en beheerders te stimuleren.

c. Het bij voorkeur jaarlijks organiseren van een “Animales-Voordracht” om het belang van dierenwelzijn onder de aandacht te brengen.

d. Het financieel ondersteunen van onderzoek op het gebied van dierenwelzijn.

Op de website www.animales.nl vindt u verdere gegevens over de stichting, zoals de samenstelling van het huidige bestuur en kunt u zich aanmelden voor het bijwonen van de Animales-Voordrachten.

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Michael (Mike) Mendl promoveerde in 1986 aan de Universiteit van Cambrige op een onderzoek naar de invloed van de moeder-kind relatie op de ontwikkeling van het gedrag. Na zijn promotie zette hij zijn onderzoek voort aan de Universiteit van Groningen en via een Postdoc positie aan de Universiteit van Cambridge verkreeg hij een vaste aanstelling aan het Scottish Agricultural College in Edinburg. In 1997 werd hij benoemd tot lector aan de Universiteit van Bristol, waar hij in 2005 de functie van hoogleraar 'Animal Behaviour and Welfare' verkreeg. Zijn werk naar cognitie, welzijn en gedrag bij dieren heeft in zeer belangrijke mate bijgedragen aan het bevorderen van dierenwelzijn.

Elizabeth Paul studeerde psychologie aan de Universiteit van Bristol, waar haar belangstelling werd gewekt voor het verband tussen de menselijke psychologie en het gedrag van dieren. Zij promoveerde aan de Universiteit van Cambridge op een onderzoek naar de psychologie van het bezit van huisdieren bij kinderen. Sinds 2001 is Elizabeth Paul verbonden aan de Universiteit van Bristol waar zij onderzoek doet naar dierlijke en menselijke emotie, dierenwelzijn en de psychologie van de houding van mensen tegenover dieren.

In 2013 verkregen beide auteurs de prestigieuze 'International Society for Applied Ethology Creativity Award'.

Prof. **MICHAEL MENDL** and Dr. **ELIZABETH PAUL**

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