University of Sussex

A University of Sussex PhD thesis

Available online via Sussex Research Online:

http://sro.sussex.ac.uk/

The Role of the Eyes in Animal-Human Emotional Communication

Dissertation submitted to the

University of Sussex for the degree of

Doctor of Philosophy

Tasmin Humphrey

September, 2019

I hereby declare that this thesis has not been and will not be submitted in whole or in part to another University for the award of any other degree.

Signature…………………………………………………………………

Tasmin Humphrey

Acknowledgements

First, I want to express my deepest gratitude and to my supervisor, Prof. Karen McComb. Thank you for your mentoring, support, and most of all for believing in me throughout the years, particularly during some tough times. I would also like to extend an enormous thank you to my co-supervisor, Dr Leanne Proops, for your invaluable advice and help throughout.

Thank you to the Cats and Dogs of Hanover, and all of the other cat, dog and horse owners that participated in my research - your enthusiasm made this research possible. I am enormously grateful to Kate Grounds and Amy Smith for taking me under their helpful wing, particularly in the early stages of my PhD. Hollie, Faye and Jemma; for your help with running the projects.

To my fellow office mates, Kate, Leanne, Amy, Jordan Raine, Fiona Clements, Karen Hiestand, Jon King, and Andrey Anikin. The valuable conversations, games nights and craft events kept my spirits up on more than one occasion. To the avocados, James Livermore, Meike Sieburg, Mateo Leganes Fonteneau, Michael Sorhaindo, Becks Atkinson, Van Gelis, Heather Iriye, Zofia Bednarczyk, and Abi Wright. Thank you for filling me with some treasured memories during my PhD, whether it be our travels around Europe, amazing parties, hilarious group chats, or simply a kind discussion over lunch.

Thank you to Natalie Davies and Miles Fowler for being inspirational friends and giving me comfort when I have needed it most. To my family; I am incredibly grateful for your continued support throughout the years and throughout my doubts. To Gilly, for forcing me to get some fresh air and teaching me so much in our time together – you

are deeply missed and always loved. And to Callum, my partner, I am grateful to you in so many ways that this small section cannot begin to describe – thank you for always being there.

University of Sussex

Doctor of Philosophy in Psychology

The Role of the Eyes in Human-Animal Emotional Communication

Summary

Emotional communication is crucial in social groups in order for individuals to signal their intentions and motivations. Previous research on interspecific emotional communication has primarily concentrated on documenting animals' abilities to recognise human emotion. However, the ways in which animals signal about their emotions to humans has largely been overlooked. Such insights could have important implications for animal welfare assessments, particularly in relation to how positive emotions are communicated (providing an indicator of good welfare). For domestic animals, interspecific emotional communication could be highly adaptive to facilitate the human-animal relationship. Indeed, research on domestic animals has revealed advanced socio-cognitive abilities in the context of human-animal communicative behaviour (e.g. social cue use, individual recognition, and the attribution of attention to others), suggesting that domestic animals are an appropriate study species in which to explore interspecific emotional communication. This thesis investigates the role of a potential universal signal of positive emotions, narrowing of the eye aperture, in animal-human interactions.

Articles I, II and III systematically examined slow blinking in domestic cats, a behaviour that had previously been anecdotally observed during interactions between humans and cats. Slow blinking involves a series of eye movements (half blinking, eye narrowing and eye closure) that act to narrow the eye aperture. These three articles specifically explore the role of slow blinking in emotional communication, including how both cats and humans perceive slow blinking as well as investigating underlying

cognitive aspects of this behaviour in cats. Article IV then tested whether similar eye narrowing movements were present in other domestic species, namely dogs and horses, during a non-communicative positive human-animal interaction.

Evidence was found that cats actively engage in human-initiated slow blink interactions and perceive these interactions as positive. In addition, shelter cats who produce salient responses to slow blinking are rehomed faster, indicating that humans have a preference for cats who slow blink. Furthermore, cats who present a lateral bias in paw use, which is linked to owners' perceptions of their cats as being more affectionate, friendly, confident, obedient, active and less aggressive, responded more to slow blinking and had greater behavioural synchrony during cat-human slow blink interactions. Finally, eye narrowing movements in non-communicative contexts revealed varied results depending on the species, which may reflect the extent to which these species were aroused by the grooming stimulus used.

These findings contribute to our understanding of positive emotions in domestic animals and the potential universality of emotional expressions, and have implications for assessing animals' wellbeing, as well as stimulating further research in the area of animal emotion.

Author Contributions

The thesis has been prepared as a series of papers written for publication in a style that is appropriate for peer-reviewed journals. The first and final chapters conform to a traditional thesis format and present an introduction to and discussion of the research undertaken in the field. I am the lead author on all manuscripts and take responsibility for the design, implementation, analysis, and write-up of this research. Prof. Karen McComb is listed as senior author on Articles I, II, III, & IV. Dr Leanne Proops is listed as second author on Article I, and third author on Articles II, III, & IV. These authors are my main academic supervisors and authorship reflects contributions of their expertise and advice throughout all stages of the research process. Rebecca Spooner and Jemma Forman are listed as authors on Article I. Faye Stringer is listed as an author on Article II, and Hollie Panther on Article III. These authors contributed to data collection and experimental design as part of their undergraduate projects.

Article I is under review with Scientific Reports (September 2019) as:

Humphrey, T., Proops, L., Forman, J., Spooner, R. & McComb, K. The role of cat eye narrowing movements in cat-human communication.

Article II has been prepared for Animals as:

Humphrey, T., Stringer, F., Proops, L. & McComb, K. Shelter cats that slow blink are adopted more quickly.

Article III has been prepared for Applied Animal Behaviour Science as:

Humphrey, T., Panther, H., Proops, L. & McComb, K. Lateral paw use in cats predicts emotional communication with humans.

.

Table of Contents

List of Figures and Tables

Aims and Research Questions

The current thesis aims to investigate how domestic animals signal positive emotions to humans, primarily through studying a potential means of cat (*Felis catus)*-human (*Homo sapiens*) communication based on eye movements. Positive emotional signalling in animals has previously been neglected in the literature in favour of studies on negative emotions. By exploring these potential indicators of positive emotions, we aim to gain a greater understanding of the use of these signals, and to facilitate developments in animal welfare assessments. Additionally, the aim of this thesis is to build on our current understanding of cats' communicative abilities with humans, cats being a species that has previously received little scientific interest compared to the other most common companion animal, the domestic dog (*Canis lupus familliaris*). All experiments are conducted within the animals' own environments, allowing us to observe animals' responses to interactions with humans in naturalistic contexts, and reduce unnecessary stress in the subjects.

Article I will provide the first systematic study of an anecdotally described cat signalling mechanism, the slow blink, and demonstrate its role in cat-human emotional communication. Article II will investigate this behaviour in the shelter environment, investigating how humans perceive slow blinking when considering cat adoption and how anxious cats utilise slow blinking. Article III will test the relationship between cats' underlying cognitive biases and slow blink behaviour. Finally, Article IV will examine whether the key features of this behaviour represent universal indicators of positive emotion by exploring their presence in other domestic species (dogs and horses (*Equus caballus*)), as well as in other positive emotional contexts. The results will be discussed in the context of the universality of positive emotional expressions, and possible links between signals of positive emotions and submission will be explored. In

addition, the role of lifetime learning and domestication in the development of slow-blinking will be discussed. Lastly, suggestions for future research are made – in particular how the current research could be extended to bear more directly on assessments of animal welfare and enhancement of the human-animal bond.

"An animal's eyes have the power to speak a great language."

- **Martin Buber**

Introduction

1. Social Cognition and Emotion

Living in a social group can be advantageous not merely through allowing an individual to better avoid harm but also to gain important resources. Social living can therefore increase ecological success (e.g. enhanced defence) as well as social success (e.g. more reproductive choice; Parrish & Edelstein-Keshet, 1999). Living in a social group requires exchanges of information in the form of social cues, and these social cues are not limited to group members (e.g. territorial behaviour by members of an out-group). Communication is therefore considered to function to alter another individual's behaviour in ways that increase the signaller's fitness (Wiley, 1983). One of the many ways an individual signals such motivations is through the expression of emotions (Rolls, 2005; Tooby & Cosmides, 1990). Emotions can broadly be defined as states which result in highly adaptive responses to rewarding or punishing stimuli (Damasio, 2004; Paul, Harding, & Mendl, 2005; Rolls, 2005).

Emotions include behavioural, physiological, neuronal and cognitive processes, including (at least in the human experience) subjective feelings (Paul et al., 2005). Debate is ongoing as to whether the latter subjective component is present in non-human animals' experiences of emotion (Dawkins, 2000; Duncan, 2006; Proctor, 2012), which I will introduce later in this thesis. However, a lack of subjective feelings does not preclude other cognitive processes that are important in the experience of emotions. In fact, cognitive skills are fundamental to many social interactions. Social cognition relates to a set of cognitive processes that operate on information derived from, or relevant to, other animals (Rooney & Bradshaw, 2006), such as rewarding or punishing

stimuli. These abilities include, but are not limited to, attention, memory, decision-making, cooperation and emotion. Furthermore, many of these socio-cognitive skills are interdependent. For example, recognising the identity of a social partner and the direction of their attention can provide important clues that aid the interpretation of emotion in others. Thus, social cognition is an important topic to consider when attempting to understand emotion.

Research on emotional expressions had largely been thwarted by an underestimation of the role of cognition. For a large part of the 20th century behaviourism dominated the field of psychology, and cognitive processes, including emotion, were discarded (Duncan, 2006; Nesse, 1990). Rather surprisingly, the previous zeitgeist was that emotions are adaptations, as described by Charles Darwin in '*The Expression of Emotions in Man and Animals*' (Darwin, 1872). Darwin was one of the first to properly address the study of emotions, and he recognised that emotions across taxa differ in degree rather than kind (Darwin, 1872). More recently, a return to the evolutionary approach in considering animal cognition and emotion has led to a surge of studies on the socio-cognitive abilities previously thought to be uniquely human. For instance, there is now growing evidence of the socio-cognitive abilities of animals for understanding attention (Call, Bräuer, Kaminski, & Tomasello, 2003; Soproni, Miklósi, Topál, & Csányi, 2001; Virányi, Topál, Gácsi, Miklósi, & Csányi, 2004), social cue use (Gácsi, Miklód, Varga, Topál, & Csányi, 2004; Hernádi, Kis, Turcsán, & Topál, 2012; Kaminski, Riedel, Call, & Tomasello, 2005; Leavens & Hopkins, 1998; Nawroth, Ebersbach, & von Borell, 2014; Platt, Seyfarth, & Cheney, 2016; Pongrácz & Szapu, 2018a; Proops, Walton, & McComb, 2010), the recognition of social partners (Coulon, Deputte, Heyman, & Baudoin, 2009; Gilfillan, Vitale, McNutt, & McComb, 2016; Proops & Mccomb, 2012) and, increasingly, emotion (dogs: Albuquerque et al., 2016;

Buttelmann & Tomasello, 2013; cats: Galvan & Vonk, 2016; goats (*Capra aegagrus hircus)*: Nawroth, Albuquerque, Savalli, Single, & McElligott, 2018; horses: Smith, Proops, et al., 2018).

2. Emotion

2.1 What are Emotions?

Before discussing the literature on emotion, it is important to give due attention to the definitions scientists have applied in their study of the topic. Researchers use many terms to describe emotion processes. Firstly, emotion is often discussed alongside affect and moods. Some authors have attempted to separate these terms by characterising affect as referring to the quality of events, such as pleasantness and unpleasantness (e.g. valence; Berridge, 2003; Frijda, 1993; Panksepp, 2005). Others have described core affect as non-directed 'free-floating' moods that ebb and flow over time (Russell & Barrett, 1999). Emotion, however, appears to be associated with a deeper level of cognitive processing about an object, event or person (Russell & Barrett, 1999) which involves some level of appraisal, including appraising the affective feeling itself (Frijda, 1993). Thus, an individual may feel frustrated without any conscious reason why (affect), while an individual may experience anger, due to the obstruction of one's goals, by a perceived intentional other (emotion). However, as in this thesis, these terms are commonly used interchangeably in the research on animal emotions (Paul et al., 2005), largely due to the lack of verbal report in non-human animals making it difficult to investigate the subjective appraisals of emotion. This thesis therefore characterises emotion as a reaction to an object, event or person that requires an adaptive response which involves changes in behaviour, physiology, feeling state and cognition (Rottenberg, 2005).

Difficulty in testing the subjective component of animals' emotions has led some researchers to be sceptical of the existence of emotion in animals. However, the subjective aspect of emotion necessitates conscious processing, which is the subject of debate. Clore (1994) argued that emotions involve feelings and therefore must be conscious. However, in the human literature, subliminal presentations of emotional faces during cognitive discrimination tasks cause affective reactions in participants by altering how much they drink of a sweet beverage, while such presentations however do not affect participants' subjective ratings of their emotion (Berridge & Winkielman, 2003). This suggests that individuals' behaviour can be influenced by emotional stimuli even without reported conscious awareness. Dissociation between subjective experiences and emotion processes are also evident in human neuroanatomy, where the subcortical structures of the brain which are responsible for emotional processing (e.g. the amygdala, hypothalamus and nucleus accumbens) have evolved much earlier than the cortex, the area involved in consciousness and verbal functioning (Winkielman & Berridge, 2004). Thus, this evidence suggests that conscious subjective feelings are a sufficient measure rather than a necessary component of an emotional process. Furthermore, the large number of implicit measures available (physiological, behavioural or neuronal) may actually provide more valid insights on emotion processes, given the variability indicated in self-report data (Chan, 2008).

2.2 Theories of Emotion

Firstly, the following overview of the theoretical approaches to emotion is by no means exhaustive. However, this section will describe the approaches to studying emotion used to inform this thesis.

The discrete (or basic) approach to studying emotion describes several distinct, universal emotions that are considered the foundation of all mammals' emotional repertoire (Ekman, 1992b; Mendl, Burman, & Paul, 2010). These primary emotions are sadness, fear, anger, joy, surprise and disgust, and in humans appear to be displayed as well as recognised cross-culturally (Ekman & Friesen, 1971a). Panksepp (2011) states that there are specific brain systems in all mammals which relate to these basic emotions. However, research on the neural structures associated with emotion such as the amygdala, which is considered to be related to experiencing fear, show that these structures are not reliably activated by fear stimuli (Barrett & Wager, 2006). Furthermore, electrical brain stimulation of these areas do not consistently produce discrete emotional feelings in subjects (Barrett et al., 2007; Valenstein, 1974). In addition, the basic emotion approach lacks an underlying framework for studying other possible emotions (Mendl, Burman, et al., 2010), such as gratitude or jealousy. Thus, a broader approach is required to explain the structure of emotion and to encompass the full emotional spectrum.

The dimensional approach provides an alternative account of emotion and is characterised by two fundamental elements: valence and arousal. Theorists propose that these dimensions are the building blocks of emotion (Barrett & Wager, 2006), and they are often represented along axes in 2D space (see Figure 1). Valence refers to the positivity or negativity of the affective experience, and arousal is defined by the level of excitation the affective experience elicits. The dimensional approach can encapsulate a wide variety of emotional experiences, as well as the strength of an emotion. This theory does not rely on labelled emotions, which are highly linked to the subjective experience, making this approach more suitable for studying animal emotion by avoiding anthropomorphic interpretations.
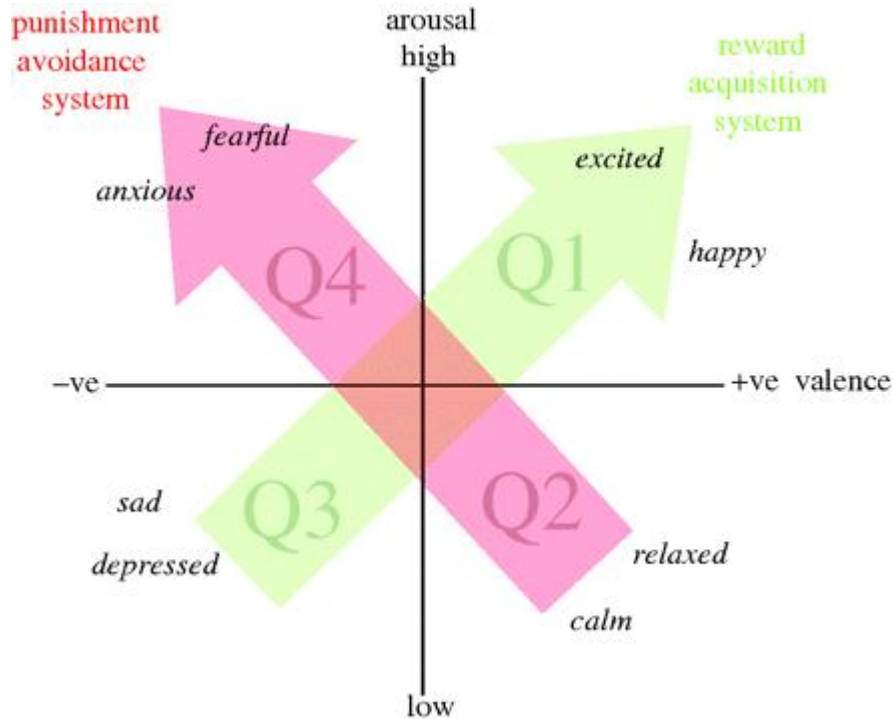
Figure 1. The valence-arousal framework for studying emotion. *Note.* Reproduced from "An integrative and functional framework for the study of animal emotion and mood" by M. Mendl, O. H. Burman, & E. S. Paul, 2010, *Proceedings of the Royal Society of London B: Biological Sciences*, *277*(1696), 2895-2904. Copyright 2010 by The Royal Society.

2.3 Positive Emotions

At the turn of the millennium Martin E. P. Seligman, president of the American Psychological Association, after many years of studying mental illness realised that two fundamental missions of psychology were being largely ignored. The first mission being improving people's lives, and the second the nurturance of genius. Alongside Mihaly Csikszentmihalyi, who also recognised the need to study the positive aspects of human behaviour, the field of positive psychology was born (Seligman & Csikszentmihalyi, 2014). At the same time a rising interest in animal sentience and animal emotion was developing among animal welfare scientists (Boissy et al., 2007).

These combined events led to the now widely accepted understanding that well-being is not just the absence of negative emotions but perhaps most importantly, the presence of positive emotions (Seligman & Csikszentmihalyi, 2014), and the call for further investigations of positive emotions in animals (Boissy et al., 2007). Such studies have important applications in animal welfare by identifying markers of flourishing, rather than focusing on conditions which simply avoid suffering.

The historical focus on negative emotion, and consequent neglect of positive emotions, is primarily due to the salience of negative affect on an individual's thought-action repertoire (Boissy et al., 2007; Fredrickson, 2001) and the urgent contexts in which negative states are elicited. For instance, anger urges an individual to attack, which is evolutionarily adaptive in circumstances that prompt quick defence (Tooby & Cosmides, 1990). Discrete emotion theorists have attempted to link positive emotions with similar specific action tendencies, such as joy with goalless locomotive activation (e.g. jumping around, wagging tail; Frijda, 1986). However, such action tendencies are vague (Levenson & Fredrickson, 1998), and often fail to discriminate between positive emotions. Other researchers argue that positive emotions share the ability to broaden an individual's thought-action repertoires, as well as build lasting physical, psychological and social resources (Fredrickson, 2001). An example of the 'Broaden and Build' theory is play, play behaviour is often exhibited most frequently by juveniles, and functions to facilitate and refine immature animals' development (Pellis, 2010). Play enables individuals to develop responses to unpredictable outcomes and therefore the ability to cope with inevitable experiences of losing control ('Broadening effect'; Spinka, Newberry, & Bekoff, 2004). Play also facilitates the development of the motor and neural systems to enhance the performance of adult-typical behaviours ('Building effect'; Fairbanks, 2000; Pellis, 2010). Adult play similarly shares these benefits, Palagi

(2006) found that social play in apes can be used to gain information on social partners and enhance relationships ('Building effect'). Thus, positive emotions play an important role in an individual's continuous development, particularly in regards to its social environment. This thesis is concerned with how such positive emotions are signalled in domestic species. Such insights aid our understanding of emotional behaviour in non-human animals, as well as facilitate animal welfare assessments by identifying key markers that signify flourishing.

2.4 How Can we Examine Emotion in Non-Human Animals?

Investigating emotional responses in the absence of self-report is not an issue solely for comparative and evolutionary psychologists, developmental psychologists wishing to measure emotions in pre-verbal infants also face this challenge, and effective methodologies have been developed in this field (Read, 1982). These approaches can then be applied to studies of animal emotion, with reasonable adjustments to the relevance for the species. For example, eye tracking has recently been modified for use with chimpanzees (Terburg, Hooiveld, Aarts, Kenemans, & van Honk, 2011) and dogs (Barber, Randi, Muller, & Huber, 2016). Many technological advancements are also making the study of emotional responses possible, allowing systematic investigations of emotion. Some of these approaches include:

Neurobiological. Areas of the brain active during the presentation of emotional stimuli can be explored using fMRI techniques. Such methodology has been used in studies on unrestrained dogs who are listening to conspecific and human emotional vocalisations. These studies found that dogs showed comparable brain sensitivity to both species' auditory cues of emotion (Andics, Gácsi, Faragó, Kis, & Miklósi, 2014). Adapting fMRI techniques to non-human animals is a recent approach with limitations regarding

species appropriateness, however this technology points to the potential of gaining promising insights into the neuroscientific processes of animal emotion, both comparatively and evolutionarily.

Cognitive. Emotional states change the way individuals process information through attention, perception and memory. In human psychological research, anxious or depressed individuals are more likely to attend to or perceive threatening stimuli compared to those in a happier state (Mathews & Macleod, 1994). This approach is the basis of the cognitive bias test where an individual in a more positive emotional state is predicted to judge an ambiguous stimulus more positively than one in a more negative emotional state. This paradigm has been effectively applied in animal emotion studies with a variety of species (honeybees (*Apis mellifera*): Bateson, Desire, Gartside, & Wright, 2011; rhesus macaques (*Macaca mulatta*): Bethell, Holmes, MacLarnon, & Semple, 2012; rats (*Rattus norvegicus*): Brydges, Leach, Nicol, Wright, & Bateson, 2010; pigs (*Sus scrofa domesticus*): Douglas, Bateson, Walsh, Bédué, & Edwards, 2012; sheep (*Ovis aries*) Doyle et al., 2011; dogs: Mendl et al., 2010; chickens (*Gallus gallus domesticus*): Salmeto et al., 2011). Cognitive biases also reflect the reports of subjective emotion in humans (Mendl, Burman, Parker, & Paul, 2009), and therefore the successful applications of cognitive bias tests to animal research offer important understanding on how human and animal experiences of emotions compare. However, cognitive bias tests often involve a pre-test training period or habituation to the study protocol which is time-consuming and limits investigations to domestic and captive animals.

Physiological. The presence of environmental and psychological stressors activates the hypothalamo-pituitary-adrenocortical (HPA) axis, as part of the 'fight or flight' response controlled by the sympathetic nervous system, in humans and other taxa. A

number of different physiological processes are then activated, one of these being the release of the hormone cortisol. Cortisol is considered to be a key indicator of stress and negative emotions in a variety of species, and evidence has linked this hormone to emotional behaviour, less favourable contexts and other physiological responses (Bergamasco et al., 2010; Haubenhofer & Kirchengast, 2006, 2007; Kojima et al., 1995; Reimert, Bolhuis, Kemp, & Rodenburg, 2013). Conversely, oxytocin: a hormone related to stress relief and possible inhibition of the HPA axis (Bello, White-Traut, Schwertz, Pournajafi-Nazarloo, & Carter, 2008; DeVries, Glasper, & Detillion, 2003), has also been applied as a biomarker of emotion. Oxytocin is typically stimulated during social interactions but can be elicited by a range of stimuli, including food, smell and touch (Bello et al., 2008; Hernandez et al., 2002; Mitsui et al., 2011; Verbalis, McCann, McHale, & Stricker, 1986). There is evidence for greater concentrations of this hormone during the presentation of a range of positive emotional stimuli (Mitsui et al., 2011), and a decreased fear response has been shown in those given oxytocin injections (Viviani & Stoop, 2008). In dogs, nasal oxytocin treatments also produce positive cognitive biases toward ambivalent stimuli and emotional faces (Kis, Hernádi, Kanizsár, Gácsi, & Topál, 2015; Somppi et al., 2017), and increase attention towards the eye region (an area important for emotion perception) of conspecific faces in rhesus macaques (Dal Monte, Noble, Costa, & Averbeck, 2014). Furthermore, oxytocin antagonists eradicate empathy-like consolation responses in rodents (Burkett et al., 2016). Measures of cortisol and oxytocin are usually taken via salivary or urinary samples. Thus, this method does not allow for instantaneous recording of hormonal changes in response to emotional stimuli and typically requires controlled settings to gain samples.

Heart rate variability (HRV) is another physiological measure that can be used to assess the internal states of individuals. HRV reflects fluctuations in the sympathovagal

balance that are associated with emotional triggers (von Borell et al., 2007) that might

not otherwise be apparent via measures of heart rate or respiration rates alone (Tiller,

McCraty, & Atkinson, 1996). Research measuring HRV in animals has produced

insightful results, where HRV has been associated with behavioural indicators of

emotion (Coulon et al., 2015a) and other physiological indicators (Bergamasco et al.,

2010), as well as indicating both positive and negative emotions (Katayama et al.,

2016), strength of emotional stimuli within valence (Zupan, Buskas, Altimiras, &

Keeling, 2016), type of emotional appraisal (Désiré, Veissier, Després, & Boissy, 2004)

and emotional reactivity (Frondelius, Järvenranta, Koponen, & Mononen, 2015). HRV

is recorded using electrodes that may be incorporated in to a harness or strap that fits

around the body of the animal and oftentimes the animal's fur/hair needs to be wetted to

enable clear readings. Consequently, this may disrupt the subject and cause slight

distress, therefore this method is potentially problematic in the study of positive and/or

low arousal emotions.

Infrared thermal imaging of the face is a recent non-invasive development for

measuring emotional responses using a thermal camera. Thermal imaging records

cutaneous thermal radiation which is affected by the autonomic nervous system

(Ioannou, Gallese, & Merla, 2014). Several areas of the face have been studied and

shown to change in temperature as a result of emotional stimuli in humans and animals,

including the nasal tip (Ioannou, Chotard, & Davila-Ross, 2015; Kano, Hirata,

Deschner, Behringer, & Call, 2016; Kosonogov et al., 2017; Kuraoka & Nakamura,

2011; Nakayama, Goto, Kuraoka, & Nakamura, 2005; Proctor & Carder, 2015b), the

eye region (Ikkatai & Watanabe, 2015; Ioannou et al., 2014; Jerem, Herborn,

McCafferty, McKeegan, & Nager, 2015; Travain et al., 2016; Valera et al., 2012) and

the upper lip (Hahn, Whitehead, Albrecht, Lefevre, & Perrett, 2012; Ioannou et al.,

2014). Experimental designs using thermal imaging measures require a great deal of control (e.g. minimal movements by the subject to control for distance, angle and attention to confounding factors like direct sunlight influencing temperature) in order to gain accurate readings. However, this truly non-invasive measure offers a promising way to study animal emotion.

Behavioural. The most common and widespread method of studying animal emotions is through behavioural observations. Behavioural methods include examining a range of sensory modalities, for example, the auditory modality in vocalisations. The four main areas that have been linked to emotions are facial expressions, vocalisations, posture and lateralisation patterns. From observations of these behaviours, either in a laboratory or naturalistic setting, interpretations are made about the emotional state of the individual. Such interpretations are susceptible to subjective bias and therefore more rigorous tools have been developed, such as the Facial Action Coding System (FACS, Ekman & Friesen, 1971), an anatomically based manual for coding facial movements, which allows more objective measurements rather than evaluations of the whole face. FACS has now been extended to multiple species (cats: Caeiro, Burrows, & Waller, 2017; orangutans (*Pongo spp.*): Caeiro, Waller, Zimmermann, Burrows, & Davila-Ross, 2013; macaques: Parr, Waller, Burrows, Gothard, & Vick, 2010; chimpanzees (*Pan troglodytes*): Vick, Waller, Parr, Smith-pasqualini, & Bard, 2006; gibbons: Waller, Lembeck, Kuchenbuch, Burrows, & Liebal, 2012; dogs: Waller et al., 2013; horses: Wathan, Burrows, Waller, & McComb, 2015).

Facial expressions are typically considered the 'gold standard' in emotion research. Since Ekman & Friesen's (1971a) seminal work on the universality of facial expressions in signalling discrete human emotions, facial actions have been examined across different taxa. Mammals take centre stage in this research, since non-mammals often

lack the same complex facial musculature (Waller & Micheletta, 2013), and homologies across mammalian species have been identified which provide insights into the evolutionary continuity of emotional expressions. For example, canids, rats, brown bears (*Ursus arctos*) and several species of primate all display a 'play-face' which involves an open mouth expression that is considered to also be a homologue to the human smile (Egbert & Stokes, 1974; Fox, 1970; Panksepp & Burgdorf, 2003; Van Hooff, 1972). Thus, facial expressions are a fruitful measure of emotional signalling and are relatively easy to observe in a multitude of affective contexts.

In the human literature, vocal indicators of emotion have been extensively studied, and variations in several vocal parameters are associated with emotional arousal and valence (Pollermann & Archinard, 2003; Scherer, 2003; Schröder, 2001). The physiological changes in the body as a result of an emotional experience cause, a largely involuntary, increase in vocal fold tension that affects vocalisations (Briefer, 2012). Source-filter theory shows that sound produced by vibrations of the vocal folds ('source') is filtered by the vocal tract ('filter') to produce vocalisations (Taylor & Reby, 2010), and therefore emotionally induced muscle constriction or relaxation of the vocal apparatus affect parameters of the voice (Scherer, 2003). For example, several species produce increases in vocalisation rate, call duration, mean fundamental frequency and range, and energy distribution across frequencies during high arousal emotional contexts (Briefer, 2012). Similarly, there is some evidence that positively valenced contexts are characterised by shorter vocalisations, however the findings on vocal differentiation of emotional valence are much less clear than the research on arousal (Briefer, 2012). Vocalisations are an adaptive mode of expressing emotions as they can be conveyed to the perceiver from a greater distance than most behavioural signals. This also allows greater non-invasive measurement of vocal cues of emotion. However, investigating

natural vocal correlates of emotion is restrictive as researchers are bound by the type of emotions that elicit vocalisations.

Emotional body language, including posture and movement, is a relatively understudied area of emotional behaviour. Researchers exploring posture and motion assume that emotional body language is an extension of facial expressions, providing an alternative way for individuals to physically express emotions (Schindler, Van Gool, & de Gelder, 2008). In animals, emotional body language is often related to functional relevance, such as hierarchical rank relations. For example, Smith, Wilson, McComb, & Proops (2018) found that domestic horses can discriminate and attribute communicatory significance to dominant and submissive human body postures via the horses' preference to approach submissive versus dominant postures. Furthermore, chimpanzees have a wide gestural repertoire that facilitates socio-emotional communication between conspecifics (e.g. the use of a wrist present or rump present during conflict resolution; Bard et al., 2014). Despite broad similarities in regards to body posture (e.g. a small body position can signal submission), the body can move into a large number of positions and the availability of postures is different between species. As a result there is a great deal of variation, which is challenging when investigating indicators of emotion and may explain why this area has typically received less attention in the comparative domain.

Lateralisation with respect to use of different sides of the body on the other hand provides a more general method of examining emotion across species. Lateral biases have been explored through paw preference and gaze bias, as well as tail and ear movements. The behavioural biases which manifest are a result of activity in the contralateral hemispheres of an individual's brain. Such differential hemispheric processing is considered to reflect how a stimulus has been perceived, such as the

association of avoidance behaviour with the right hemisphere, such as in toads (*Bufo bufo*) and dunnarts (*Sminthopsis macroura*; Vallortigara & Rogers, 2005). Evidence has also revealed a link between the presence of a lateralisation (as opposed to non-lateralisation) and higher emotional functioning (dogs: Batt, Batt, Baguley, & McGreevy, 2009; Branson & Rogers, 2006; cats: McDowell, Wells, Hepper, & Dempster, 2016). Although studying lateralisation does not provide in depth information into the specific neurological mechanisms involved in emotions, the research regarding asymmetrical biases is largely consistent across species (Davidson, 1993).

Overall, the aforementioned measures are useful tools for investigating animal emotion, and provide valuable information regarding the emotional experience. It is important to note that this account was not an attempt to create a complete list of how emotional experiences can be assessed in animals. Rather, my aim is to highlight the range of methods available, demonstrating the relevance of studying animal emotions as a line of scientific investigation. Given the limitations of each method, however, these measures would be best utilised in combination. Such comprehensive studies would provide a better picture of how animals express emotions, as well insights into the mechanisms that have been conserved over evolutionary time.

2.5 Universal Signalling

The wide variety of emotional expressions manifesting from the physiological and neural processes of an emotional experience evolved to facilitate survival in particular contexts (Levenson, 2003). Thus, these emotional signals adapted to serve a specific function. For example, the facial expression of fear consists of wide open eyes in order to enhance the visual field of the signaller and facilitate observation in threat detection

(Kohler et al., 2004; Lee, Susskind, & Anderson, 2013). In addition, anger involves a lowered brow which is consistent with mature faces, and angry faces are judged as appearing more mature than other expressions (Marsh, Adams, & Kleck, 2005) and therefore potentially more dominant. Successful signals have then been ritualised and stereotyped over time for effective emotional communication, and as a result such signals have become universally displayed and recognised across cultures as well as species.

One area of the face that appears to be particularly important in signalling emotions is the eyes (Baron-Cohen, Wheelwright, & Jolliffe, 1997). In neuro-typical humans, attention to the eye region is automatic (Driver et al., 1999), and the eyes are preferred over other facial areas, with adult subjects spending more looking time focused on the eye region than other areas of the face (Janik, Wellens, Goldberg, & Dell'Osso, 2011). Such a preference is also seen in very young infants (Batki, Baron-Cohen, Wheelwright, Connellan, & Ahluwalia, 2000; Dupierrix et al., 2014), even when other areas of the face are more salient, such as moving of the lips during talking (Haith, Bergman, & Moore, 1977). This suggests that attention to the eyes may be an innate mechanism in humans. In addition, the eyes play a significant role in correctly assigning complex mental states (Baron-Cohen et al., 1997). Those with a deficit in recognising emotions in others, such as individuals with autism, brain damage, or psychopathy, focus less on the eye region when looking at facial expressions (Adolphs et al., 2005; Baron-Cohen et al., 1997; Dadds et al., 2006; Pelphrey et al., 2002). Furthermore, such emotion recognition impairments can be treated by instructing individuals to look at the eyes of others during social interactions (Adolphs et al., 2005; Dadds et al., 2006) and studies examining the effects of the administration of oxytocin (the neuropeptide associated with positive emotional and social behaviour) on the processing of facial stimuli in

neurotypical humans found that oxytocin increases gaze toward the eye region of the face (Auyeung et al., 2015; Domes, Steiner, Porges, & Heinrichs, 2013; Guastella, Mitchell, & Dadds, 2008).

The informative role of the eyes during the perception of emotion is argued to be different depending on the valence of the emotional expression (Beaudry, Roy-Charland, Perron, Cormier, & Tapp, 2014). Beaudry et al. (2014) found that the mouth was more important than the eyes for recognising happiness in faces, but that the eyes were more useful than the mouth for the recognition of sadness in humans. However, this study showed subjects static pictures of actors performing stereotypical emotions from the Japanese and Caucasian Facial Expressions of Emotion database (Matsumoto & Ekman, 1988). The features of these emotion faces therefore lacked ecological validity and may have been exaggerated, not displaying honest signals of emotion. Conversely, in humans the Duchenne smile, the smile that is linked to positive emotions and pleasant experiences, differs from other forms of smiling in that it involves the activation of the muscle around the eye (Ekman, Davidson, & Friesen, 1990). Thus, the eyes do appear to provide an important indication of true positive emotion in others.

Gazing toward the eye region for gaining information from others is not just a mechanism observed in humans. Primates, including rhesus monkeys and baboons (*Papio hamadryas*), also have greater attention and a higher number of fixations on the eye region when viewing conspecific and interspecific faces (Keating & Keating, 1982; Kyes & Candland, 1987). Dogs also look to the eyes before any other region of the face, and look for longer at the eyes than other expressive areas of the face, like the mouth, across both conspecific and human emotional faces (Somppi et al., 2016). Eye lid movements, such as eye narrowing or widening, are also an important aspect of emotional signalling in a range of species. A common example of this behaviour is the

'whale eyes' or 'eye flash' display in dogs. This occurs when dogs are stressed or feel threatened, and involves the eyes widening revealing the whites of the eye (Handelman, 2012; Siniscalchi, d'Ingeo, Minunno, & Quaranta, 2018b). Alternatively, 'soft eyes', which are described as eyes that are partially closed, indicates that a dog is relaxed and non-threatening (Handelman, 2012; Siniscalchi et al., 2018b). Narrowing of the eyes are also seen in the faces of canids during play and consummatory contexts (Fox, 1970). In cows, a low percentage of visible eye white is observed during positive emotional contexts, such as being stroked by humans or being fed (Proctor & Carder, 2015a). Similarly, a high percentage of visible eye whites is seen in cows that are deprived of food, and is associated with aggressive behaviour (Sandem, Braastad, & Bøe, 2002). In addition, horses and sheep both show narrowing of the eyes during grooming (Hintze, Smith, Patt, Bachmann, & Würbel, 2016; Reefmann, Wechsler, & Gygax, 2009; Tamioso et al., 2018), and eye narrowing in sheep is correlated with increased heart rate variability (Reefmann, Wechsler, et al., 2009). Collectively, these results suggest that relaxed eyes indicate positive emotional valence and wide open eyes indicate negative valence. However, there is some evidence that wide eyes may also occur in contexts that elicit positive, high arousal states as well as negative, high arousal states in cows (Lambert (Proctor) & Carder, 2017). Furthermore, dog owners describe their dog's eyes as partly or fully closed during positive, low arousal states and as wide open and bright eyes in positive, high arousal states, which suggests that arousal may contribute to differences in the size of the eye aperture during emotional experiences as well. Thus, relaxed eye narrowing is key - appearing to be associated with positive, low arousal emotional states across species and with the potential to be a universal indicator of such emotional experiences. It is important to note that this relaxed eye narrowing is distinct from the orbital tightening that has been documented in the Grimace Scales of multiple

species during the experience of pain as orbital tightening involves activation of the muscles around the eye (horses: Dalla Costa et al., 2014; sheep: Häger et al., 2017; mice (*Mus musculus*): Langford et al., 2010; rabbits (*Oryctolagus cuniculus*): Leach, 2012; rats: Sotocinal et al., 2011; and pigs: Viscardi, Hunniford, Lawlis, Leach, & Turner, 2017).

3   Emotional Communication in Human-Animal Interactions

Emotional signalling is important for the effective workings of a social group, and rarely occurs in solitary contexts. Human laughter, for example, is 30 times more common in social settings than solitary ones (Provine, 2004). For domestic species, humans can be key members of the animal's social group (Proops & McComb, 2012). However, much is unknown in the empirical research on how emotions are communicated between domestic animals and humans, specifically in how domestic animals signal positive and negative emotions to humans. Understanding interspecific emotional signalling would have significant benefits for the human-animal relationship by increasing emotional awareness, and consequently reducing the relinquishment of pets due to problematic behavioural issues and the risk of injury to owners through instances of aggression. This section of the thesis will describe the current evidence for domestic animals' abilities to engage in emotional communication with humans, including their ability to perceive and respond to cues of human emotion using a range of modalities, such as facial expressions and vocal cues. Since the literature on positive emotional signalling in human-animal communication is scant, this section will include both positively and negatively valenced emotional signalling.

3.1 Human-given Cues of Emotion

Research on interspecific emotional signalling investigates the ability of domestic animals to read human-given cues of emotion as an important part of the emotional exchange. Since the way humans signal emotions is much better understood than animal emotional signalling, using human-given cues of emotion provides a valid entry point into gaining insights into animals' abilities to perceive and experience emotions. Such studies have primarily focussed on dogs' abilities to read human-given cues of emotion.

Object-choice tasks, in which an object is hidden out of the dog's sight and humans give cues to indicate where the food is located, are often used to investigate animals' abilities to read human-given cues. Buttelmann & Tomasello (2013) presented dogs with three expressions performed live by an experimenter (happy, neutral and disgust) in relation to hidden contents within two different boxes, after which the dog was given a chance to choose one of the boxes. Dogs appropriately chose to approach the box that the experimenter had expressed happiness towards (when choosing between happy and disgust expressions) which suggests that dogs can discriminate between emotional valence. Similarly, Merola, Prato-Previde, Lazzaroni, & Marshall-Pescini (2014) found that dogs could successfully discriminate between happy and fearful expressions in their owners when choosing between the contents of two boxes. In another paradigm using a visible novel object, dogs chose to avoid the object when their owner showed fear directed toward it, whereas dogs were more likely to approach when the owner signalled joy (Merola, Prato-Previde, & Marshall-Pescini, 2012). This experiment has been replicated in cats, who also show emotion-specific responses, such as escape-seeking behaviour in the fearful condition (Merola, Lazzaroni, Marshall-Pescini, & Prato-Previde, 2015). However, it has been argued that such responses represent confusion in

the subjects rather than the ability to use social referencing of human emotion (Yong & Ruffman, 2015).

Further research using presentations of emotional signals supports the above evidence that domestic animals can discriminate between different human emotions. For example, when dogs are presented with an emotional facial expression paired with either a congruent or an incongruent vocalisation, or a control noise, dogs preferentially look at the congruent face-vocalisation pairing for longer (Albuquerque et al., 2016). In addition, cats who are presented with facial and postural cues of emotion by their owner, show a higher number of positive behaviours and spend more time in contact with their owner when they are displaying happiness versus anger (Galvan & Vonk, 2016). Horses also show functionally relevant responses to human emotions, such as a left-gaze bias and an increased HR when viewing angry faces (Smith, Proops, Grounds, Wathan, & McComb, 2016), freeze behaviour upon hearing negative human vocalisations (Smith et al., 2018) and an increased tendency to approach a submissive human posture than a dominant one (Smith et al., 2018). Furthermore, goats prefer to first approach a photograph of a positive human facial expression over a negative expression (Nawroth et al., 2018). It can be argued that domestic animals' abilities to discriminate between human emotions may be due to learning, particularly as dogs can be trained to discriminate between happy and angry faces and this can be generalised to novel human faces (Müller, Schmitt, Barber, & Huber, 2015). However, dogs in this study learnt to discriminate quicker when happy faces were rewarded compared to rewarding angry faces (Müller et al., 2015), suggesting that there is an inherent preference for positively valenced emotions in animals in these contexts.

There is some evidence that animals not only recognise emotion in humans, but can also offer comfort to a person who is upset. Custance & Mayer (2012) examined such

behaviour by presenting dogs with four experimental conditions: the dogs' owner crying, the dog's owner humming, a stranger crying, and a stranger humming. When either the owner or the stranger cried, it was predicted that if dogs recognised the emotion and felt emotional contagion they would seek comfort for themselves through approaching their owner, or approaching both people in order to find someone who would offer them comfort. However, the researchers found that dogs submissively (rather than in an alert, playful or calm manner) approached whoever was crying, and stayed in contact with them despite being ignored. This suggests that the dogs were displaying empathic consolation-related behaviours. Past learning factors cannot be ruled out in this study – although it should be noted that learning plays a key role in human emotional awareness too. Cats display similar reassurance-related behaviours in interactions with their owners, by allo-rubbing (a communicative signal of affiliation; Cameron-Beaumont (1997)) more toward (non-clinically) depressed owners than less depressed owners (Rieger & Turner, 1999). Further investigation however is required to determine whether such behaviours are the result of emotional contagion and learning history rather than indicating prosocial empathy. Collectively, these studies point to animals' abilities to have rich emotional lives, shared across their social group (which in these cases includes humans).

3.2 Animal-given Cues of Emotion

To understand how animals experience emotions, it is not enough to simply show that they respond appropriately to the emotional signals of others. Studies that explore the animal's own expressions given to emotional stimuli should also be conducted. This range of approaches would allow researchers to more fully investigate the similarities and differences in emotional signals across the species barrier, and gain insights into the evolution of emotion. Unfortunately, little scientific research has considered how

domestic animals signal emotions to humans. Studies that measure animals' responses to human emotion cues often rely on anecdotal evidence to evaluate the nature of these responses. Similarly, studies using presentations of conspecific emotional expressions use signals that are captured during an emotionally-charged event, with little validation as to whether this expression is typical of that emotion.

One way to assess interspecific signalling in an experimental context is through humans adopting behaviours that replicate the animal's intraspecific communication, but which are not part of humans' typical behavioural repertoire. For instance, Rooney, Bradshaw, & Robinson (2001) investigated how dogs respond to humans adopting play signals (bowing and lunging), which mirrored how dogs naturally solicit play with conspecifics (Bekoff, 1974; Byosiere, Espinosa, & Smuts, 2016). Bows and lunges performed by the humans increased subsequent bouts of dog-human play (Rooney et al., 2001). This suggests that these signals can be an effective means of communication across, as well as within, species. Eavesdropping on the alarm calls of heterospecifics is another example of how intraspecific communication can be transferred across species. Approximately 70 species of vertebrates have been shown to be able to eavesdrop on heterospecific vocalisations, reflecting the important evolutionary benefits interspecific communication can entail (Magrath, Haff, Fallow, & Radford, 2015).

Through the process of domestication, some species are able to engage human attention by exploiting human preferences for particular signal characteristics. McComb, Taylor, Wilson, & Charlton (2009) investigated solicitation purring in cats (which occurs in contexts where the cat is seeking food) by playing these purrs versus non-solicitation purrs to humans. Solicitation purrs were judged by humans as less pleasant and more urgent. However, when the solicitation purrs were re-synthesised to omit a high-pitched vocal component embedded in the purr, comparable to the frequency that of an infant

cry, these purrs were judged by humans as being less urgent. This suggests that cats have developed modified purrs which exploits the human sensitivity to babies crying in order to gain increased attention and care (McComb et al., 2009). In addition, shelter dogs who display an inner brow raiser facial action (AU 101), an expression that gives the animal a more infant-like appearance, are rehomed faster (Waller et al., 2013). The authors also explain this human preference for the inner brow raiser facial expression in dogs as a result of the display being reminiscent of human sadness (the worry expression). The inner brow raiser is displayed in dogs but not in wolves, suggesting that this facial action is the result of human selection (Kaminski, Waller, Diogo, Hartstone-Rose, & Burrows, 2019). Thus, studies of this sort further demonstrate that animals can display, as well as perceive, interspecific communicative signals, which are adaptive.

Researchers can directly elicit emotions in animals through generating emotional contexts that occur during everyday situations and through the course of typical human-animal interactions, such as eliciting fear or providing a positive stimulus like grooming. Grooming has been shown to be a positive interaction for both animals and humans, and can decrease signs of stress and negative emotion in a range of species (sheep: Coulon et al., 2015b; cats: Gourkow, Hamon, & Phillips, 2014; horses: Hama, Yogo, & Matsuyama, 1996; dogs: Handlin et al., 2011; rats: Kurosawa, Lundeberg, Ågren, Lund, & Uvnäs-Moberg, 1995; cows (*Bos taurus*): Windschnurer, Barth, & Waiblinger, 2009). Thus, researchers can examine the emotional expressions animals make during such contexts (see section 2.5 for discussion of the relevance of signals in the eye region). This method can also be used to explore negative emotional responses of animals. Bennett, Gourkow, & Mills (2017) tested cats placed in a cage, either in a condition on their own or during a human interaction condition. The authors stated that

the two conditions clustered into three groups which reflect relaxed engagement, frustration and fear in the cats, and they found specific facial expressions that correlated with these different emotional states, such as hissing, nose-licking and tongue showing during frustration (Bennett et al., 2017). However, it is impossible to determine whether the animals in these observational studies are truly experiencing the intended emotion. One individual, for example, may find stroking pleasant but another individual may find this stimulus stressful, depending on the subject's temperament and learning history. Thus, further study of these responses is needed to support such observations.

4. Study Species:

4.1 The domestic cat

4.1.1 Cat Social Organisation

Feral domestic cats can either live solitary lives or form non-linear hierarchical colonies, where each animal does not always dominate over those below them, and colony size depends on the dispersion of food resources readily available (Crowell-Davis, Curtis, & Knowles, 2004). This variability in social structure allows cats to thrive in a variety of different environments (Pontier, Rioux, & Heizmann, 2006). Cats in the human home also live either alone, or with one or multiple other cats. However, feral colonies differ from human household environments. Feral colonies are matrilineal and females display co-operative rearing of young, with other queens assisting during parturition (Crowell-Davis et al., 2004). Kittens from these co-operative rearing groups leave the nest around 10 days earlier than kittens from lone-rearing cats (Feldman, 1993), which shows the benefits of communal litters.

Cats within a colony display largely amicable behaviour towards one another, and dominance hierarchies are maintained through ritualised signals or avoided completely

through spatial divides, rather than through overt aggression (Crowell-Davis, Barry, & Wolfe, 1997; Knowles, Curtis, & Crowell-Davis, 2004). In addition, cats are polygamous and mating success appears to depend on social attachments, rather than body size (Crowell-Davis et al., 2004). Cats prefer to associate with kin and highly familiar cats (of both genders), who display affiliative behaviours, such as allogrooming, allorubbing, and play (Crowell-Davis et al., 2004). Thus, cats can live in complex social systems and form close familial bonds. Such diverse social relationships would require an effective communication system in order for individuals to signal intent to others, and shows the flexibility of cats' sociality which may have helped them during domestication.

4.1.2   Cat Domestication History

The process of domestication of the cat is said to have begun over 6,000 years ago (Driscoll et al., 2007), although it is also reported that cats were only fully domesticated in the last 200 years (Serpell, 2013). This is much more recent than the domestication of the dog, the domestication of the latter being thought to occur around 11 to 36,000 years ago (Skoglund, Ersmark, Palkopoulou, & Dalén, 2015). The exact lineage of the cat has been much debated, but researchers now largely agree that the domestic cat descended from *Felis silvestris libyca,* the North African/Near Eastern wildcat (Driscoll et al., 2007; O'Brien et al., 2008). Interestingly, these larger wildcats (in comparison to the domestic cat) have been found in the archaeological remains of the earliest human settlements in Cyprus during the Neolithic period, when humans first practiced agriculture (Davis, 2012), with one of the remains of one cat being buried only 40cm away from a person (Vigne, Guilaine, Debue, Haye, & Gérard, 2004). Cyprus does not have any native felid species, so such findings suggest human introduction of cats as

early as 9,500 years ago (Vigne et al., 2004), with domestication occurring a few thousand years later.

During a period when farming was being introduced into human culture, and food could be stored, cats would have been a useful asset to control rodents (Serpell, 2013). Thus, cats may have domesticated themselves by being attracted to the food available in Neolithic settlements and tolerated by the human settlers for their practicality. However it is thought that the domestication of cats was not entirely utilitarian, as capturing and keeping wild animals is a widespread phenomenon among people from all historical periods (Galton, 2007). Cats may therefore have had a deeper emotional connection with humans, rather than humans simply tolerating cats for their functions in pest control (Serpell, 2014). Over time cats may have been selected to reciprocate this affection, or cats may have benefitted from reciprocating this affection.

4.1.3 Cat Social Behaviour

Domestic cats use a variety of modalities to communicate, including olfactory, visual, auditory and tactile sensory signals. The signals cats use may differ according to whether the receivers are conspecifics or humans, and may include multiple modalities at once. Cats have relatively recently evolved from a solitary ancestor where these signals may not have been present, or modalities may have been used for other functions, therefore such signals may also reflect this recent adaptation (Brown & Bradshaw, 2013).

Olfactory communication is arguably one of the most important ways of signalling in cats. A specialised structure within the olfactory system of felids, known as the vomeronasal or Jacobson's organ, is exclusively used during social signalling (Brown & Bradshaw, 2013). Cats usually sniff interesting or informative scents and then produce a

flehmen response, which involves raising the upper lip and keeping the mouth open slightly. The flehmen response facilitates the transference of information to the vomeronasal organ (Brown & Bradshaw, 2013). Faecal and urinary odours are used to distinguish between familiar and unfamiliar donors, and may be used to regulate relationships with other cats (Nakabayashi, Yamaoka, & Nakashima, 2012; Natoli, 1985). However, it is only sprayed urine, rather than excretory urine, which contains such identifying information (Natoli, 1985). The use of odour is adaptive in this context as it allows cats to signal their presence within a large territory. Cats are also able to distinguish the odours of their own kittens from kittens they are not familiar with (Bánszegi, Jacinto, Urrutia, Szenczi, & Hudson, 2017). However, in the aforementioned study, mothers did not differ in the degree of maternal care they provided kittens despite being able to discriminate between young in this way (Bánszegi et al., 2017). This is likely due to the presence of cooperative rearing practices in cats, as discussed earlier in this chapter.

Similarly, scent is used during greeting behaviours, when cats are often observed rubbing against one another close to where the scent glands are located on the cat's body (Crowell-Davis et al., 2004; Vitale Shreve & Udell, 2017). This marking can also occur against objects within the cat's core home range. Scratching can both lay scent and act as a locus of olfactory information (Mengoli et al., 2013), as well as a visual cue (Brown & Bradshaw, 2013). Cats will avoid a scratching site that has been used by a fearful cat (Pageat & Gaultier, 2003), which suggests that emotional information is carried via olfactory modalities. In addition, specific odours can be used to reduce anxiety in the cat (Vitale Shreve & Udell, 2017). Although humans are not as readily able to detect scent marks produced by cats for social signalling as conspecifics. Humans also use different scents to provide positive enrichment for cats, such as the use

of catnip (Ellis & Wells, 2010), and cats deposit scent through rubbing on their owners (Brown & Bradshaw, 2013).

Cats are also able to use visual cues to communicate with each other. Tail positions are a very salient form of communication employed by cats, and the tail up position in which the cat's tail is held upright, is often exhibited alongside a social rub when interacting with both conspecifics and humans (Cameron-Beaumont, 1997). This posture may signal similar affiliative intentions to rubbing. In addition, cats have an extensive range of muscle movement in the face including to move the whiskers (Caeiro et al., 2017), suggesting that facial expressions may be important for communication. Indeed, cats have been found to make distinct facial expressions during different emotional contexts, such as nose-licking in frustration (Bennett et al., 2017). There is also evidence that cats respond to human facial and postural expressions of emotion, where they spend more time in contact with positive versus negative expressions (Galvan & Vonk, 2016). Human referential visual cues, such as pointing, are also interpreted by cats, who can successfully follow human gestures toward the location of hidden food (Miklósi et al., 2005). Cats can also use social referencing from humans when deciding whether to approach an ambiguous object (Merola et al., 2015).

Cats have a wide vocal repertoire, including 9 different vocalisations as kittens and 16 documented vocalisations in adulthood (Moelk, 1944). Vocalisations by cats range from trills, which occur when the mouth is closed, to growls, which occur when the mouth is held open. Researchers suggest that many of the cat's auditory abilities are honed by selection pressures arising from the need to hunt prey (Brown & Bradshaw, 2013). However cats obviously use this in their sense of hearing in vocal communication too. For example, cats display plasticity in the vocalisations they emit, depending on whether they have been socialised. Yeon et al. (2011) tested feral cats and house cats in

5 situations that were assumed to induce vocalisations. The authors found that feral cats produced higher frequency growls and hisses but lower frequency meows than house cats (Yeon et al., 2011). Cats also appear to alter their purring towards humans in contexts where the cats solicit food from their owner (as discussed in 3.2 of this chapter; McComb et al., 2009). Cats are one of the few species from the Felidae family that produce meows (for other felids that meow, see cheetahs (*Acinonyx jubatus;* Smirnova, Volodin, Demina, & Volodina, 2016; Wielebnowski & Brown, 1998) and African Wild Cats (Nicastro, 2004), and these vocalisations occur mainly in cat-human interactions (Brown & Bradshaw, 2013). This is possibly due to the human's attraction to these call types leading such vocalisations to be reinforced (Nicastro, 2004). Furthermore, there is evidence that cats can recognise the vocal cues of their owners over unfamiliar humans (Saito & Shinozuka, 2013).

For an ancestrally solitary species with an evolved flexible social structure, cats are surprisingly proficient communicators both within and across species. However, due to the cat's reputation for being independent and possibly even "unfeeling" (Vitale Shreve & Udell, 2015), research is still required to better understand this species' social and emotional abilities, specifically in relation to humans.

4.2 The domestic dog

4.2.1   Dog Social Organisation

Despite dogs being a highly social species, urban and rural stray dogs usually live solitary lives (Daniels & Bekoff, 2006; Daniels, 1983). This is possibly due to the advantage single living over pack forming gives stray dogs in accessing food from humans. Nonetheless, stray dogs do share long-term social bonds with conspecifics (Cafazzo, Valsecchi, Bonanni, & Natoli, 2010). Feral domestic dogs, on the other hand,

form packs with male and female conspecifics (Daniels & Bekoff, 2006). It was previously thought that wolf packs had an alpha female who had reproductive dominion, whereas females in dog packs appeared to breed freely, with pregnant bitches temporarily splitting from the pack to give birth (Daniels & Bekoff, 2006). However, dogs appear to show some semblance of a dominance hierarchy, and use dominance postures (including but not exclusive to aggressive behaviour) to maintain rank-order between individuals (Cafazzo et al., 2010; Pal, Ghosh, & Roy, 1998). Some researchers have been disputing the presence of dominance in dogs, preferring to view dog relationship regulation through an associative learning lens instead (Bradshaw, Blackwell, & Casey, 2009). Thus, further research is needed on dog-dog relationship maintenance to determine whether dominance hierarchies or associative learning predicts social structures in dogs.

4.2.2 Dog Domestication History

Genetic and morphological evidence shows that the domestic dog originated from the grey wolf (*Canis lupus*; Dayan, 1994; Fox, 1970; Hemmer, 1990; Serpell, 1995; Wayne, Nash, & O'Brien, 1987; Wayne & O'Brien, 2006; Wayne & Ostrander, 1999). Records dating back as far as 300,000 years ago show the remains of wolves in association with humans (Serpell, 1995). Domestic dogs are said to have been domesticated approximately 11 to 36,000 years ago (Skoglund et al., 2015), potentially being the first animal to have been domesticated, during a time when humans still predominantly relied on hunting and gathering (Serpell, 1995). Dog morphology has diverged dramatically from that of their wolf ancestors, resulting in many different breeds, sizes and facial characteristics.

The long domestication history of dogs has also led to their widespread distribution globally among human populations. Since dogs and humans have shared the same environments for thousands of years, researchers propose that dogs share particular cognitive skills with humans through the process of cognitive convergent evolution (Hare & Tomasello, 2005). It is suggested that dogs also show similar social traits to humans, which may have developed through domestication (Hare et al., 2010; Hare & Tomasello, 2005; Miklósi & Topál, 2013). However, such similarities may also be a result of ontogenetic processes, such as socialisation with humans in a puppy's development (Udell, Dorey, & Wynne, 2010), or a combination of both (Kaminski & Marshall-Pescini, 2014). Nevertheless, dogs appear to have developed key social-emotional systems that provide a precursor to high-level social skills (Hare, 2007) and allow the human-dog relationship to flourish.

4.2.3 Dog Social Behaviour

A large body of work exists on dogs' communicative abilities, particularly in the area of human-dog interactions. This thesis will not cover all of the research in this area, rather it simply gives an overview of dog social behaviour as background information. In the initiation of conspecific play, dogs watch visual cues to determine their partner's attentional state, and produce flexible, responsive signals to gain their partner's attention (Horowitz, 2009). Preliminary evidence shows that calming signals, such as head turning, paw lifting and nose licking, are also employed by dogs and act to de-escalate aggressive displays between two unfamiliar individuals (Mariti et al., 2017). Dogs are also able to perceive and appropriately respond to complex gestures. For example, dogs are very skilled at utilising human pointing in a variety of situations (Hare & Tomasello, 1999; Miklösi, Polgárdi, Topál, & Csányi, 1998; Soproni et al., 2001), and even indirectly by following a chain of human pointing leading to the

location of hidden food (Lakatos, Gácsi, Topál, & Miklósi, 2012). Furthermore, dogs can intentionally use referential cues to signal to humans, adapting such cues to work with their own as well as the human's line of sight (Gaunet & Deputte, 2011). By following a human's line of sight, dogs can also determine where a human is attentive and subsequently produce more facial expressions when a human is attentive to them (Kaminski, Hynds, Morris, & Waller, 2017). Dogs are also able to produce specific facial expressions, such as the inner brow raiser facial action (AU 101), to their advantage in interactions with humans (Waller et al., 2013). This demonstrates that dogs can perceive and produce elaborate signals to communicate with humans. In addition, dogs can discriminate between conspecific and human emotional faces (Racca, Guo, Meints, & Mills, 2012), as well as integrate these facial cues with emotional information from vocal signals to enhance their discrimination of positive and negative emotions in humans and conspecifics (Albuquerque et al., 2016). Nevertheless, gestural signals appear to be more salient than verbal commands, such as 'sit', 'stay', 'lie down', where dogs faced with incongruent visual and verbal signals primarily chose to follow the visual signals (D'Aniello, Scandurra, Alterisio, Valsecchi, & Prato-Previde, 2016).

Nevertheless, vocal cues are an important part of dogs' communicative repertoire, with dogs displaying around 12 different vocalisations (Cohen & Fox, 1976). Dogs are able to discriminate between different contexts and the identity of the caller using individual specific barks (Maros et al., 2008; Molnár, Pongrácz, Faragó, Dóka, & Miklósi, 2009). Furthermore, growls vary according to context, with aggressive growls being of longer duration than playful growls (Taylor, Reby, & McComb, 2009), as well as body size (Faragó et al., 2010; Taylor et al., 2009). Thus, dogs use vocalisations to convey information to one another. Empirical evidence of humans listening to playbacks of dog barks show that dog vocalisations also carry emotional information to humans, which is

independent of the human's familiarity with dogs (Pongrácz, Molnár, & Miklósi, 2006).

This encoding of emotions in vocalisations may also explain the observed social

contagion which occurs during dogs' barking (Adams & Johnson, 1994).

Olfactory communication is also an important signalling modality in dogs. Dogs

primarily carry olfactory signals through urine. Scent marking is a prevalent behaviour

which occurs in both males and females and has been linked to territorial behaviour

(Bradshaw & Rooney, 2016; Cafazzo, Natoli, & Valsecchi, 2012). In domestic feral

dogs, males tend to direct urine more than females, and scent marking is most frequent

in late monsoon when many females are in oestrus, which suggests that urine marking

may play a role in mating (Pal, 2003). Greeting behaviours in dog-dog interactions

involve olfactory examinations of the face, neck, inguinal and perianal regions to gain

information about the other (Siniscalchi, d'Ingeo, Minunno, & Quaranta, 2018a), and

recent research shows that body size might affect olfactory communication with smaller

dogs scent marking more frequently than larger dogs (McGuire & Bemis, 2017).

Nevertheless further research is needed in this area to understand how dogs use

olfactory communication with conspecifics and what information can be conveyed.

4.3 The domestic horse

4.3.1   Horse Social Organisation

Feral horses form bands that are composed of one stallion (occasionally multiple males,

that are usually related) and his harem (females and their offspring), or bachelor bands

which are composed of stallions not associated with a mare (Linklater, 2000; Pacheco &

Herrera, 2006). Home ranges among horse social groups are flexible, with bands living

in either unprotected overlapping spaces (Feist & McCullough, 1976), overlapping

spaces with specific group areas (Rutberg, 1990), or occasionally live in territorial

spaces (Linklater, 2000; Rubenstein, 1981). Both male and female offspring typically leave the family band after 2 – 3 years of age when the young horse becomes sexually mature (Feh, 2005). Apart from these departures, social groups remain relatively stable leading to long-term relationships between group members.

Horses arrange themselves into stable dominance hierarchies which are based on the length of time an individual has been part of the social group (Feh, 2005; Monard & Duncan, 1996). Thus, young mares joining a new harem after leaving their natal group will usually rank lowest. Offspring inherit the rank of their mothers within the group, and stallions are usually dominant over the females in the harem (Feh, 2005). Generally, horses avoid physical conflict to maintain group cohesion, opting instead to signal to others through non-contact threats (Jørgensen, Borsheim, Mejdell, Søndergaard, & Bøe, 2009). In cases where intra-group conflict does occur, reconciliation behaviours are used to manage group stability in horses, where former opponents display post-conflict affiliative interactions with one another (Cozzi, Sighieri, Gazzano, Nicol, & Baragli, 2010). Horses' social lives are therefore complex, and intricate signalling repertoires are present to facilitate these dynamics.

4.3.2   Horse Domestication History

Horses are considered to have been domesticated multiple times in separate regions where agricultural human societies were present (Outram et al., 2009; Vilà et al., 2001). This contrasts with other domestic species, such as dogs and cattle where domestication occurred in a limited geographic area (Vilà et al., 2001). Evidence of archaeological dental records of horses also indicate that in the Ukraine, as early as 6,000 years ago, horse riding began (Anthony, Telegin, & Brown, 2010), which suggests that horses had been tamed by this point. The techniques required to tame wild horses were likely

transferred quickly between communities, given the technological advantage horses gave human civilisations in transport, food, and warfare (Vilà et al., 2001).

The appearance of horses during the process of domestication has remained relatively unchanged, although overall size now varies greatly (Christensen, Zharkikh, Ladewig, & Yasinetskaya, 2002), with most horses having been selectively bred for greater performance-related characteristics. However, domestic horses' social behaviour has changed to allow more amenable horse-human interactions and relationships. For example, Przewalski horses, a wild horse species, have been observed to display more aggressive behaviours than domestic horses (Feh, 1988). Thus, domestic horses' socio-cognitive processes may have developed alongside these changes in interspecific social behaviour.

4.3.3   Horse Social Behaviour

Horses, like cats and dogs, use different ways to communicate both inter- and intra-specifically. Horses in a herd seldom lose visual contact with conspecifics (Feh, 2005), and therefore visual cues are important in horse social communication. For example, horses will follow conspecific gaze, ear and head orientation in order to judge the attentional state of others (Wathan & McComb, 2014). Facial expressions are also used to display the emotional state of the signaller, with aggressive displays comprising of pinned back ears, nostril wings drawn back, and facial muscle tension. Positive anticipation however involves relaxation of the lower face, ears faced forward and pricked up, and open eyes (Waring, 1983). Evidence shows that conspecifics respond to these expressions in functionally appropriate ways, such as avoiding facial expressions related to aggression, which indicates that such expressions are important within horse communication (Wathan, Proops, Grounds, & McComb, 2016).

Olfactory communication is also important for horses, who are able to acquire social information through smelling conspecific faeces. Faecal scent can encode information regarding the familiarity of other individuals, relative threat potential if familiar with the other (Rubenstein & Hack, 1992), and the gender of other horses (Stahlbaum & Houpt, 1989). Similar to cats, horses have a vomeronasal organ and produce a flehmen response which involves opening of the mouth with the upper lip retracted and gums bared whilst the neck is extended and the nose is wrinkled (Estes, 1972). Empirical evidence shows that flehmen responses may facilitate reproductive priming (Christensen, Keeling, & Nielsen, 2005; Stahlbaum & Houpt, 1989).

Finally, horses are able to detect sound in the frequency range of 55Hz to 33KHz and an amplitude starting from 7dB (Heffner & Heffner, 1983), which indicates that auditory cues play a significant role in horse communication. Horses use a variety of vocal signals to communicate, including nickers, whinnies, squeals, and snorts (Yeon, 2012). Horses also use auditory cues to recognise other individuals within their herd (Proops, McComb, & Reby, 2009), as well as familiar humans (Lampe & Andre, 2012; Proops & McComb, 2012). In addition, contact can be maintained within a herd through the use of long distance whinnies, and horses are able to extract reliable information regarding a caller's sex, body size, identity, and emotion (Lemasson, Boutin, Boivin, Blois-Heulin, & Hausberger, 2009). Emotional information regarding the affective valence of another horse can be carried within a given vocalisation type. For example, horses are able to discriminate between the whinnies made during positive and negative emotional events (Briefer et al., 2017). Horses are also able to distinguish between positive and negative human non-verbal vocalisations of emotion (Smith et al., 2018).

5. Chapter Summary

This chapter is intended to provide a solid background for the work undertaken in the following articles of this thesis. Domestic animals have shown promising communicative skills with humans, including their ability to perceive emotional cues. These species therefore present appropriate models for the study of emotional signalling in animals during interactions with humans. To date, empirical research has rarely focussed on how animals express their emotions in this context and there is a particular paucity of information on domestic cats. The next chapters include the first systematic set of studies of a specific eye movement behaviour observed in cat-human interactions – the slow blink – as well as a comparative study on cats', dogs', and horses' use of eye movements in apparently positive but non-communicative interactions with humans.

References

Adams, G. J., & Johnson, K. G. (1994). Behavioural responses to barking and other auditory stimuli during night-time sleeping and waking in the domestic dog (*Canis familiaris*). *Applied Animal Behaviour Science*. https://doi.org/10.1016/0168-1591(94)90135-X

Adolphs, R., Gosselin, F., Buchanan, T. W., Tranel, D., Schyns, P., & Damasio, A. R. (2005). A mechanism for impaired fear recognition after amygdala damage. *Nature*. https://doi.org/10.1038/nature03086

Albuquerque, N., Guo, K., Wilkinson, A., Savalli, C., Otta, E., & Mills, D. (2016). Dogs recognize dog and human emotions. *Biology Letters*. https://doi.org/10.1098/rsbl.2015.0883

Andics, A., Gácsi, M., Faragó, T., Kis, A., & Miklósi, Á. (2014). Voice-sensitive regions in the dog and human brain are revealed by comparative fMRI. *Current Biology*. https://doi.org/10.1016/j.cub.2014.01.058

Anthony, D., Telegin, D. Y., & Brown, D. (2010). The origin of horseback riding. *Scientific American*. https://doi.org/10.1038/scientificamerican1291-94

Auyeung, B., Lombardo, M. V., Heinrichs, M., Chakrabarti, B., Sule, A., Deakin, J. B., … Baron-Cohen, S. (2015). Oxytocin increases eye contact during a real-time, naturalistic social interaction in males with and without autism. *Translational Psychiatry*. https://doi.org/10.1038/tp.2014.146

Bánszegi, O., Jacinto, E., Urrutia, A., Szenczi, P., & Hudson, R. (2017). Can but don't: olfactory discrimination between own and alien offspring in the domestic cat. *Animal Cognition*. https://doi.org/10.1007/s10071-017-1100-z

Barber, A. L. A., Randi, D., Muller, C. A., & Huber, L. (2016). The processing of

    human emotional faces by pet and lab dogs: Evidence for lateralization and

    experience effects. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0152393

Bard, K. A., Dunbar, S., Maguire-Herring, V., Veira, Y., Hayes, K. G., & Mcdonald, K.

    (2014). Gestures and social-emotional communicative development in chimpanzee

    infants. *American Journal of Primatology*. https://doi.org/10.1002/ajp.22189

Baron-Cohen, S., Wheelwright, S., & Jolliffe, T. (1997). Is there a "language of the

    eyes"? Evidence from normal adults, and adults with autism or Asperger

    Syndrome. *Visual Cognition*. https://doi.org/10.1080/713756761

Barrett, L. F., Lindquist, K. A., Bliss-Moreau, E., Duncan, S., Gendron, M., Mize, J., &

    Brennan, L. (2007). Of mice and men: natural kinds of emotions in the mammalian

    brain? A response to Panksepp and Izard. *Perspectives on Psychological Science*.

    https://doi.org/10.1111/j.1745-6916.2007.00046.x

Barrett, L. F., & Wager, T. D. (2006). The structure of emotion evidence from

    neuroimaging studies. *Current Directions in Psychological Science*.

    https://doi.org/10.1111/j.0963-7214.2006.00411.x

Bateson, M., Desire, S., Gartside, S. E., & Wright, G. A. (2011). Agitated honeybees

    exhibit pessimistic cognitive biases. *Current Biology*.

    https://doi.org/10.1016/j.cub.2011.05.017

Batki, A., Baron-Cohen, S., Wheelwright, S., Connellan, J., & Ahluwalia, J. (2000). Is

    there an innate gaze module? Evidence from human neonates. *Infant Behavior and

    Development*. https://doi.org/10.1016/S0163-6383(01)00037-6

Batt, L. S., Batt, M. S., Baguley, J. A., & McGreevy, P. D. (2009). The relationships

between motor lateralization, salivary cortisol concentrations and behavior in dogs. *Journal of Veterinary Behavior: Clinical Applications and Research*. https://doi.org/10.1016/j.jveb.2009.02.001

Beaudry, O., Roy-Charland, A., Perron, M., Cormier, I., & Tapp, R. (2014). Featural processing in recognition of emotional facial expressions. *Cognition and Emotion*. https://doi.org/10.1080/02699931.2013.833500

Bekoff, M. (1974). Social play and play-soliciting by infant canids. *Integrative and Comparative Biology*. https://doi.org/10.1093/icb/14.1.323

Bello, D., White-Traut, R., Schwertz, D., Pournajafi-Nazarloo, H., & Carter, C. S. (2008). An exploratory study of neurohormonal responses of healthy men to massage. *The Journal of Alternative and Complementary Medicine*. https://doi.org/10.1089/acm.2007.0660

Bennett, V., Gourkow, N., & Mills, D. S. (2017). Facial correlates of emotional behaviour in the domestic cat (*Felis catus*). *Behavioural Processes*. https://doi.org/10.1016/j.beproc.2017.03.011

Bergamasco, L., Osella, M. C., Savarino, P., Larosa, G., Ozella, L., Manassero, M., … Re, G. (2010). Heart rate variability and saliva cortisol assessment in shelter dog: Human-animal interaction effects. *Applied Animal Behaviour Science*. https://doi.org/10.1016/j.applanim.2010.03.002

Berridge, K. C. (2003). Pleasures of the brain. *Brain and Cognition*. https://doi.org/10.1016/S0278-2626(03)00014-9

Berridge, K. C., & Winkielman, P. (2003). What is an unconscious emotion? (The case for unconscious "liking"). *Cognition and Emotion*.

https://doi.org/10.1080/02699930302289

Bethell, E. J., Holmes, A., MacLarnon, A., & Semple, S. (2012). Cognitive bias in a

non-human primate: Husbandry procedures influence cognitive indicators of

psychological well-being in captive rhesus macaques. *Animal Welfare*.

https://doi.org/10.7120/09627286.21.2.185

Boissy, A., Manteuffel, G., Jensen, M. B., Moe, R. O., Spruijt, B., Keeling, L. J., …

Aubert, A. (2007). Assessment of positive emotions in animals to improve their

welfare. *Physiology and Behavior*. https://doi.org/10.1016/j.physbeh.2007.02.003

Bradshaw, John, W., & Rooney, N. J. (2016). Dog social behavior and communication.

The Domestic Dog (pp. 133–159). Cambridge, UK: Cambridge University Press.

Bradshaw, J. W. S., Blackwell, E. J., & Casey, R. A. (2009). Dominance in domestic

dogs-useful construct or bad habit? *Journal of Veterinary Behavior: Clinical

Applications and Research*. https://doi.org/10.1016/j.jveb.2008.08.004

Branson, N. J., & Rogers, L. J. (2006). Relationship between paw preference strength

and noise phobia in *Canis familiaris*. *Journal of Comparative Psychology*.

https://doi.org/10.1037/0735-7036.120.3.176

Briefer, E. F. (2012). Vocal expression of emotions in mammals: Mechanisms of

production and evidence. *Journal of Zoology*. https://doi.org/10.1111/j.1469-

7998.2012.00920.x

Briefer, Elodie F., Mandel, R., Maigrot, A. L., Briefer Freymond, S., Bachmann, I., &

Hillmann, E. (2017). Perception of emotional valence in horse whinnies. *Frontiers

in Zoology*. https://doi.org/10.1186/s12983-017-0193-1

Brown, S. L., & Bradshaw, J. W. S. (2013). Communication in the domestic cat:

Within- and between-species. *The Domestic Cat: The Biology of its Behaviour*.
https://doi.org/10.1017/CBO9781139177177.006

Brydges, N. M., Leach, M., Nicol, K., Wright, R., & Bateson, M. (2010).
Environmental enrichment induces optimistic cognitive bias in rats. *Animal Behaviour*. https://doi.org/10.1016/j.anbehav.2010.09.030

Burkett, J. P., Andari, E., Johnson, Z. V., Curry, D. C., De Waal, F. B. M., & Young, L. J. (2016). Oxytocin-dependent consolation behavior in rodents. *Science*.
https://doi.org/10.1126/science.aac4785

Buttelmann, D., & Tomasello, M. (2013). Can domestic dogs (*Canis familiaris*) use referential emotional expressions to locate hidden food? *Animal Cognition*.
https://doi.org/10.1007/s10071-012-0560-4

Byosiere, S. E., Espinosa, J., & Smuts, B. (2016). Investigating the function of play bows in adult pet dogs (*Canis lupus familiaris*). *Behavioural Processes*.
https://doi.org/10.1016/j.beproc.2016.02.007

Caeiro, C. C., Burrows, A. M., & Waller, B. M. (2017). Development and application of CatFACS: Are human cat adopters influenced by cat facial expressions? *Applied Animal Behaviour Science*. https://doi.org/10.1016/j.applanim.2017.01.005

Caeiro, Cátia C., Waller, B. M., Zimmermann, E., Burrows, A. M., & Davila-Ross, M. (2013). OrangFACS: A muscle-based facial movement coding system for orangutans (*Pongo spp.*). *International Journal of Primatology*.
https://doi.org/10.1007/s10764-012-9652-x

Cafazzo, S., Natoli, E., & Valsecchi, P. (2012). Scent-marking behaviour in a pack of free-ranging domestic dogs. *Ethology*. https://doi.org/10.1111/j.1439-

0310.2012.02088.x

Cafazzo, S., Valsecchi, P., Bonanni, R., & Natoli, E. (2010). Dominance in relation to age, sex, and competitive contexts in a group of free-ranging domestic dogs. *Behavioral Ecology*. https://doi.org/10.1093/beheco/arq001

Call, J., Bräuer, J., Kaminski, J., & Tomasello, M. (2003). Domestic dogs (*Canis familiaris*) are sensitive to the attentional state of humans. *Journal of Comparative Psychology*. https://doi.org/10.1037/0735-7036.117.3.257

Cameron-Beaumont, C. (1997). Visual and tactile communication in the domestic cat *(Felis silvestris catus)* and undomesticated small-felids (doctoral dissertation). University of Southampton.

Chan, D. (2008). So why ask me? Are self-report data really that bad? *Statistical and Methodological Myths and Urban Legends: Doctrine, Verity and Fable in the Organizational and Social Sciences*. https://doi.org/10.4324/9780203867266

Christensen, J. W., Keeling, L. J., & Nielsen, B. L. (2005). Responses of horses to novel visual, olfactory and auditory stimuli. *Applied Animal Behaviour Science*. https://doi.org/10.1016/j.applanim.2005.06.017

Christensen, J. W., Zharkikh, T., Ladewig, J., & Yasinetskaya, N. (2002). Social behaviour in stallion groups (*Equus przewalskii* and *Equus caballus*) kept under natural and domestic conditions. *Applied Animal Behaviour Science*. https://doi.org/10.1016/S0168-1591(01)00208-8

Clore, G. L. (1994). Why emotions are never nonconscious. *The nature of emotion: Fundamental questions*, 285-290.

Cohen, J. A., & Fox, M. W. (1976). Vocalizations in wild canids and possible effects of

domestication. *Behavioural Processes*. https://doi.org/10.1016/0376-6357(76)90008-5

Coulon, M., Deputte, B. L., Heyman, Y., & Baudoin, C. (2009). Individual recognition in domestic cattle (*Bos taurus*): Evidence from 2D-images of heads from different breeds. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0004441

Coulon, M., Nowak, R., Peyrat, J., Chandèze, H., Boissy, A., & Boivin, X. (2015a). Do lambs perceive regular human stroking as pleasant? behavior and heart rate variability analyses. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0118617

Coulon, M., Nowak, R., Peyrat, J., Chandèze, H., Boissy, A., & Boivin, X. (2015b). Do lambs perceive regular human stroking as pleasant? Behavior and heart rate variability analyses. *PLOS ONE*. https://doi.org/10.1371/journal.pone.0118617

Cozzi, A., Sighieri, C., Gazzano, A., Nicol, C. J., & Baragli, P. (2010). Post-conflict friendly reunion in a permanent group of horses (*Equus caballus*). *Behavioural Processes*. https://doi.org/10.1016/j.beproc.2010.07.007

Crowell-Davis, S. L., Barry, K., & Wolfe, R. (1997). Social behavior and aggressive problems of cats. *The Veterinary Clinics of North America. Small Animal Practice*. https://doi.org/10.1016/S0195-5616(97)50054-4

Crowell-Davis, Sharon L., Curtis, T. M., & Knowles, R. J. (2004). Social organization in the cat: A modern understanding. *Journal of Feline Medicine and Surgery*. https://doi.org/10.1016/j.jfms.2003.09.013

Custance, D., & Mayer, J. (2012). Empathic-like responding by domestic dogs (*Canis familiaris*) to distress in humans: An exploratory study. *Animal Cognition*. https://doi.org/10.1007/s10071-012-0510-1

D'Aniello, B., Scandurra, A., Alterisio, A., Valsecchi, P., & Prato-Previde, E. (2016). The importance of gestural communication: a study of human–dog communication using incongruent information. *Animal Cognition*. https://doi.org/10.1007/s10071-016-1010-5

Dadds, M. R., Perry, Y., Hawes, D. J., Merz, S., Riddell, A. C., Haines, D. J., … Abeygunawardane, A. I. (2006). Attention to the eyes and fear-recognition deficits in child psychopathy. *British Journal of Psychiatry*. https://doi.org/10.1192/bjp.bp.105.018150

Dal Monte, O., Noble, P. L., Costa, V. D., & Averbeck, B. B. (2014). Oxytocin enhances attention to the eye region in rhesus monkeys. *Frontiers in Neuroscience*. https://doi.org/10.3389/fnins.2014.00041

Dalla Costa, E., Minero, M., Lebelt, D., Stucke, D., Canali, E., & Leach, M. C. (2014). Development of the Horse Grimace Scale (HGS) as a pain assessment tool in horses undergoing routine castration. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0092281

Damasio, A. R. (2004). Emotions and Feelings: A Neurobiological Perspective. In *Feelings and emotions: The Amsterdam symposium.*

Daniels, T. J., & Bekoff, M. (2006). Population and social biology of free-ranging dogs, *Canis familiaris*. *Journal of Mammalogy*. https://doi.org/10.2307/1381709

Daniels, Thomas J. (1983). The social organization of free-ranging urban dogs. I. Non-estrous social behavior. *Applied Animal Ethology*. https://doi.org/10.1016/0304-3762(83)90184-0

Darwin, C. (1872). The expression of emotion in man and animals. *Animals*.

Davidson, R. J. (1993). Cerebral asymmetry and emotion: Conceptual and

methodological conundrums. *Cognition and Emotion*.

https://doi.org/10.1080/02699939308409180

Davis, S. J. M. (2012). The archaeology of animals. *The Archaeology of Animals*.

https://doi.org/10.4324/9780203060131

Dawkins, M. S. (2000). Animal minds and animal emotions. *American Zoologist*.

https://doi.org/10.1093/icb/40.6.883

Dayan, T. (1994). Early domesticated dogs of the near east. *Journal of Archaeological

Science*. https://doi.org/10.1006/jasc.1994.1062

Désiré, L., Veissier, I., Després, G., & Boissy, A. (2004). On the way to assess emotions

in animals: Do lambs (*Ovis aries*) evaluate an event through its suddenness,

novelty, or unpredictability? *Journal of Comparative Psychology*.

https://doi.org/10.1037/0735-7036.118.4.363

DeVries, A. C., Glasper, E. R., & Detillion, C. E. (2003). Social modulation of stress

responses. *Physiology and Behavior*. https://doi.org/10.1016/S0031-

9384(03)00152-5

Domes, G., Steiner, A., Porges, S. W., & Heinrichs, M. (2013). Oxytocin differentially

modulates eye gaze to naturalistic social signals of happiness and anger.

Psychoneuroendocrinology. https://doi.org/10.1016/j.psyneuen.2012.10.002

Douglas, C., Bateson, M., Walsh, C., Bédué, A., & Edwards, S. A. (2012).

Environmental enrichment induces optimistic cognitive biases in pigs. *Applied

Animal Behaviour Science*. https://doi.org/10.1016/j.applanim.2012.02.018

Doyle, R. E., Lee, C., Deiss, V., Fisher, A. D., Hinch, G. N., & Boissy, A. (2011).

Measuring judgement bias and emotional reactivity in sheep following long-term exposure to unpredictable and aversive events. *Physiology and Behavior*. https://doi.org/10.1016/j.physbeh.2011.01.001

Driscoll, C. A., Menotti-Raymond, M., Roca, A. L., Hupe, K., Johnson, W. E., Geffen, E., … Macdonald, D. W. (2007). The near eastern origin of cat domestication. *Science*. https://doi.org/10.1126/science.1139518

Driver, J., Davis, G., Ricciardelli, P., Kidd, P., Maxwell, E., & Baron-Cohen, S. (1999). Gaze perception triggers reflexive visuospatial orienting. *Visual Cognition*. https://doi.org/10.1080/135062899394920

Duncan, I. J. H. (2006). The changing concept of animal sentience. *Applied Animal Behaviour Science*. https://doi.org/10.1016/j.applanim.2006.04.011

Dupierrix, E., de Boisferon, A. H., Méary, D., Lee, K., Quinn, P. C., Di Giorgio, E., … Pascalis, O. (2014). Preference for human eyes in human infants. *Journal of Experimental Child Psychology*. https://doi.org/10.1016/j.jecp.2013.12.010

Egbert, A. L., & Stokes, A. W. (1974). The social behaviour of brown bears on an Alaskan salmon stream. *International Conference on Bear Research and Management*, *3*, 41–56.

Ekman, P. (1992). Are there basic emotions? *Psychological Review*. https://doi.org/10.1037/0033-295X.99.3.550

Ekman, P., Davidson, R. J., & Friesen, W. V. (1990). The Duchenne smile: Emotional expression and brain physiology II. *Journal of Personality and Social Psychology*. https://doi.org/10.1037/0022-3514.58.2.342

Ekman, P., & Friesen, W. V. (1971a). Constants across cultures in the face and emotion.

Journal of Personality and Social Psychology. https://doi.org/10.1037/h0030377

Ekman, P., & Friesen, W. V. (1971b). Facial action coding system: A technique for the measurement of facial movement. *Journal of Personality and Social Psychology*. https://doi.org/10.1037/h0030377

Ellis, S. L. H., & Wells, D. L. (2010). The influence of olfactory stimulation on the behaviour of cats housed in a rescue shelter. *Applied Animal Behaviour Science*. https://doi.org/10.1016/j.applanim.2009.12.011

Estes, R. D. (1972). Mammalia: The role of the vomeronasal organ in mammalian reproduction. *Mammalia*. https://doi.org/10.1515/mamm.1972.36.3.315

Fairbanks, L. A. (2000). The developmental timing of primate play: A neural selection model. In *Biology, brains, and behavior: The evolution of human development*.

Faragó, T., Pongrácz, P., Miklósi, À., Huber, L., Virányi, Z., & Range, F. (2010). Dogs' expectation about signalers' body size by virtue of their growls. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0015175

Feh, C. (1988). Social behaviour and relationships of Prezewalski horses in Dutch semi-reserves. *Applied Animal Behaviour Science*. https://doi.org/10.1016/0168-1591(88)90101-3

Feh, C. (2005). Relationships and communication in socially natural horse herds. *The Domestic Horse: The Origins, Development and Management of Its Behaviour*.

Feist, J. D., & McCullough, D. R. (1976). Behavior patterns and communication in feral horses. *Zeitschrift Für Tierpsychologie*. https://doi.org/10.1111/j.1439-0310.1976.tb00947.x

Feldman, H. N. (1993). Maternal care and differences in the use of nests in the domestic

cat. *Animal Behaviour*. https://doi.org/10.1006/anbe.1993.1002

Fox, M. W. (1970). A comparative study of the development of facial expressions in

canids; wolf, coyote and foxes. *Behaviour*.

https://doi.org/10.1163/156853970X00042

Fredrickson, B. L. (2001). The role of positive emotions in positive psychology: The

broaden-and-build theory of positive emotions. *American Psychologist*.

https://doi.org/10.1037/0003-066X.56.3.218

Frijda, N. H. (1986). *The emotions*. Cambridge University Press.

Frijda, N. H. (1993). The place of appraisal in emotion. *Cognition and Emotion*.

https://doi.org/10.1080/02699939308409193

Frondelius, L., Järvenranta, K., Koponen, T., & Mononen, J. (2015). The effects of

body posture and temperament on heart rate variability in dairy cows. *Physiology

and Behavior*. https://doi.org/10.1016/j.physbeh.2014.12.002

Gácsi, M., Miklód, Á., Varga, O., Topál, J., & Csányi, V. (2004). Are readers of our

face readers of our minds? Dogs (*Canis familiaris*) show situation-dependent

recognition of human's attention. *Animal Cognition*.

https://doi.org/10.1007/s10071-003-0205-8

Galton, F. (2007). Inquiries into human faculty and its development, 1883. *Readings in

the history of psychology*. https://doi.org/10.1037/11304-032

Galvan, M., & Vonk, J. (2016). Man's other best friend: domestic cats (*F. silvestris

catus*) and their discrimination of human emotion cues. *Animal Cognition*.

https://doi.org/10.1007/s10071-015-0927-4

Gaunet, F., & Deputte, B. L. (2011). Functionally referential and intentional

communication in the domestic dog: Effects of spatial and social contexts. *Animal Cognition*. https://doi.org/10.1007/s10071-011-0418-1

Gilfillan, G., Vitale, J., McNutt, J. W., & McComb, K. (2016). Cross-modal individual recognition in wild African lions. *Biology Letters*. https://doi.org/10.1098/rsbl.2016.0323

Gourkow, N., Hamon, S. C., & Phillips, C. J. C. (2014). Effect of gentle stroking and vocalization on behaviour, mucosal immunity and upper respiratory disease in anxious shelter cats. *Preventive Veterinary Medicine*. https://doi.org/10.1016/j.prevetmed.2014.06.005

Guastella, A. J., Mitchell, P. B., & Dadds, M. R. (2008). Oxytocin increases gaze to the eye region of human faces. *Biological Psychiatry*. https://doi.org/10.1016/j.biopsych.2007.06.026

Häger, C., Biernot, S., Buettner, M., Glage, S., Keubler, L. M., Held, N., … Bleich, A. (2017). The sheep grimace scale as an indicator of post-operative distress and pain in laboratory sheep. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0175839

Hahn, A. C., Whitehead, R. D., Albrecht, M., Lefevre, C. E., & Perrett, D. I. (2012). Hot or not? Thermal reactions to social contact. *Biology Letters*. https://doi.org/10.1098/rsbl.2012.0338

Haith, M. M., Bergman, T., & Moore, M. J. (1977). Eye contact and face scanning in early infancy. *Science*. https://doi.org/10.1126/science.918670

Hama, H., Yogo, M., & Matsuyama, Y. (1996). Effects of stroking horses on both humans' and horses' heart rate responses. *Japanese Psychological Research*. https://doi.org/10.1111/j.1468-5884.1996.tb00009.x

Handelman, B. (2012). *Canine Behavior: A Photo Illustrated Handbook*. Wenatchee, WA, USA: Dogwise Publishing.

Handlin, L., Hydbring-Sandberg, E., Nilsson, A., Ejdebäck, M., Jansson, A., & Uvnäs-Moberg, K. (2011). Short-term interaction between dogs and their owners: Effects on oxytocin, cortisol, insulin and heart rate-an exploratory study. *Anthrozoos*. https://doi.org/10.2752/175303711X13045914865385

Hare, B. (2007). From nonhuman to human mind: what changed and why? *Current Directions in Psychological Science*, *16*(2), 60–64.

Hare, B. A., & Tomasello, M. (1999). Domestic dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food. *Journal of Comparative Psychology*. https://doi.org/10.1037//0735-7036.113.2.173

Hare, B., Rosati, A., Kaminski, J., Bräuer, J., Call, J., & Tomasello, M. (2010). The domestication hypothesis for dogs' skills with human communication: a response to Udell et al. (2008) and Wynne et al. (2008). *Animal Behaviour*. https://doi.org/10.1016/j.anbehav.2009.06.031

Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences*. https://doi.org/10.1016/j.tics.2005.07.003

Haubenhofer, D. K., & Kirchengast, S. (2006). Physiological arousal for companion dogs working with their owners in animal-assisted activities and animal-assisted therapy. *Journal of Applied Animal Welfare Science*. https://doi.org/10.1207/s15327604jaws0902_5

Haubenhofer, D. K., & Kirchengast, S. (2007). Dog handlers' and dogs' emotional and cortisol secretion responses associated with animal-aassisted therapy sessions.

Society and Animals. https://doi.org/10.1163/156853007X187090

Heffner, R. S., & Heffner, H. E. (1983). Hearing in large mammals: Horses (*Equus caballus*) and cattle (*Bos taurus*). *Behavioral Neuroscience*. https://doi.org/10.1037/0735-7044.97.2.299

Hemmer, H. (1990). *Domestication: The Decline of Environmental Appreciation*. Cambridge: Cambridge University Press.

Hernádi, A., Kis, A., Turcsán, B., & Topál, J. (2012). Man's underground best friend: Domestic ferrets, unlike the wild forms, show evidence of dog-like social-cognitive skills. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0043267

Hernandez, H., Serafin, N., Terrazas, A. M., Marnet, P. G., Kann, G., Delgadillo, J. A., & Poindron, P. (2002). Maternal olfaction differentially modulates oxytocin and prolactin release during suckling in goats. *Hormones and Behavior*. https://doi.org/10.1006/hbeh.2002.1812

Hintze, S., Smith, S., Patt, A., Bachmann, I., & Würbel, H. (2016). Are eyes a mirror of the soul? What eye wrinkles reveal about a horse's emotional state. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0164017

Horowitz, A. (2009). Attention to attention in domestic dog (*Canis familiaris*) dyadic play. *Animal Cognition*. https://doi.org/10.1007/s10071-008-0175-y

Ikkatai, Y., & Watanabe, S. (2015). Eye surface temperature detects stress response in budgerigars (*Melopsittacus undulatus*). *NeuroReport*. https://doi.org/10.1097/WNR.0000000000000403

Ioannou, S., Chotard, H., & Davila-Ross, M. (2015). No strings attached: physiological monitoring of rhesus monkeys (*Macaca mulatta*) with thermal imaging. *Frontiers*

in Behavioral Neuroscience. https://doi.org/10.3389/fnbeh.2015.00160

Ioannou, S., Gallese, V., & Merla, A. (2014). Thermal infrared imaging in psychophysiology: Potentialities and limits. *Psychophysiology*. https://doi.org/10.1111/psyp.12243

Janik, S. W., Wellens, A. R., Goldberg, M. L., & Dell'Osso, L. F. (2011). Eyes as the center of focus in the visual examination of human faces. *Perceptual and Motor Skills*. https://doi.org/10.2466/pms.1978.47.3.857

Jerem, P., Herborn, K., McCafferty, D., McKeegan, D., & Nager, R. (2015). Thermal imaging to study stress non-invasively in unrestrained birds. *Journal of Visualized Experiments*. https://doi.org/10.3791/53184 <http://dx.doi.org/10.3791/53184>) (PMID:26575985)

Jørgensen, G. H. M., Borsheim, L., Mejdell, C. M., Søndergaard, E., & Bøe, K. E. (2009). Grouping horses according to gender-effects on aggression, spacing and injuries. *Applied Animal Behaviour Science*. https://doi.org/10.1016/j.applanim.2009.05.005

Kaminski, J., Hynds, J., Morris, P., & Waller, B. M. (2017). Human attention affects facial expressions in domestic dogs. *Scientific Reports*. https://doi.org/10.1038/s41598-017-12781-x

Kaminski, J., & Marshall-Pescini, S. (2014). *The social dog: behavior and cognition*. Elsevier.

Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2005). Domestic goats, *Capra hircus*, follow gaze direction and use social cues in an object choice task. *Animal Behaviour*. https://doi.org/10.1016/j.anbehav.2004.05.008

Kaminski, J., Waller, B. M., Diogo, R., Hartstone-Rose, A., & Burrows, A. M. (2019). Evolution of facial muscle anatomy in dogs. *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.1820653116

Kano, F., Hirata, S., Deschner, T., Behringer, V., & Call, J. (2016). Nasal temperature drop in response to a playback of conspecific fights in chimpanzees: A thermo-imaging study. *Physiology and Behavior*. https://doi.org/10.1016/j.physbeh.2015.11.029

Katayama, M., Kubo, T., Mogi, K., Ikeda, K., Nagasawa, M., & Kikusui, T. (2016). Heart rate variability predicts the emotional state in dogs. *Behavioural Processes*. https://doi.org/10.1016/j.beproc.2016.04.015

Keating, C. F., & Keating, E. G. (1982). Visual scan patterns of rhesus monkeys viewing faces. *Perception*. https://doi.org/10.1068/p110211

Kis, A., Hernádi, A., Kanizsár, O., Gácsi, M., & Topál, J. (2015). Oxytocin induces positive expectations about ambivalent stimuli (cognitive bias) in dogs. *Hormones and Behavior*. https://doi.org/10.1016/j.yhbeh.2014.12.004

Knowles, R. J., Curtis, T. M., & Crowell-Davis, S. L. (2004). Correlation of dominance as determined by agonistic interactions with feeding order in cats. *American Journal of Veterinary Research*. https://doi.org/10.2460/ajvr.2004.65.1548

Kohler, C. G., Turner, T., Stolar, N. M., Bilker, W. B., Brensinger, C. M., Gur, R. E., & Gur, R. C. (2004). Differences in facial expressions of four universal emotions. *Psychiatry Research*. https://doi.org/10.1016/j.psychres.2004.07.003

Kojima, K., Maki, S., Hirata, K., Higuchi, S., Akazawa, K., & Tashiro, N. (1995).

Relation of emotional behaviors to urine catecholamines and cortisol. *Physiology and Behavior*. https://doi.org/10.1016/0031-9384(94)00233-U

Kosonogov, V., De Zorzi, L., Honoré, J., Martínez-Velázquez, E. S., Nandrino, J. L., Martinez-Selva, J. M., & Sequeira, H. (2017). Facial thermal variations: A new marker of emotional arousal. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0183592

Kuraoka, K., & Nakamura, K. (2011). The use of nasal skin temperature measurements in studying emotion in macaque monkeys. *Physiology and Behavior*. https://doi.org/10.1016/j.physbeh.2010.11.029

Kurosawa, M., Lundeberg, T., Ågren, G., Lund, I., & Uvnäs-Moberg, K. (1995). Massage-like stroking of the abdomen lowers blood pressure in anesthetized rats: influence of oxytocin. *Journal of the Autonomic Nervous System*. https://doi.org/10.1016/0165-1838(95)00056-7

Kyes, R. C., & Candland, D. K. (1987). Baboon (*Papio hamadryas*) visual preferences for regions of the face. *Journal of Comparative Psychology (Washington, D.C. : 1983)*. https://doi.org/10.1037/0735-7036.101.4.345

Lakatos, G., Gácsi, M., Topál, J., & Miklósi, Á. (2012). Comprehension and utilisation of pointing gestures and gazing in dog-human communication in relatively complex situations. *Animal Cognition*. https://doi.org/10.1007/s10071-011-0446-x

Lambert (Proctor), H. S., & Carder, G. (2017). Looking into the eyes of a cow: Can eye whites be used as a measure of emotional state? *Applied Animal Behaviour Science*. https://doi.org/10.1016/j.applanim.2016.11.005

Lampe, J. F., & Andre, J. (2012). Cross-modal recognition of human individuals in

domestic horses (*Equus caballus*). *Animal Cognition*.
https://doi.org/10.1007/s10071-012-0490-1

Langford, D. J., Bailey, A. L., Chanda, M. L., Clarke, S. E., Drummond, T. E., Echols,
S., … Mogil, J. S. (2010). Coding of facial expressions of pain in the laboratory
mouse. *Nature Methods*. https://doi.org/10.1038/nmeth.1455

Leach, M. (2012). Rabbit grimace scale (RbtGS) manual. *PloS One*.
https://doi.org/10.1371/journal.pone. 0044437

Leavens, D. A., & Hopkins, W. D. (1998). Intentional communication by chimpanzees:
a cross-sectional study of the use of referential gestures. *Developmental
Psychology*. https://doi.org/10.1037/0012-1649.34.5.813

Lee, D. H., Susskind, J. M., & Anderson, A. K. (2013). Social transmission of the
sensory benefits of eye widening in fear expressions. *Psychological Science*.
https://doi.org/10.1177/0956797612464500

Lemasson, A., Boutin, A., Boivin, S., Blois-Heulin, C., & Hausberger, M. (2009). Horse
(*Equus caballus*) whinnies: a source of social information. *Animal Cognition*.
https://doi.org/10.1007/s10071-009-0229-9

Levenson, R. W. (2003). Blood, sweat, and fears: The autonomic architecture of
emotion. *Annals of the New York Academy of Sciences*.
https://doi.org/10.1196/annals.1280.016

Levenson, R. W., & L. Fredrickson, B. (1998). Positive emotions speed recovery from
the cardiovascular sequelae of negative emotions. *Cognition & Emotion*.

Linklater, W. L. (2000). Adaptive explanation in socio-ecology: Lessons from the
equidae. *Biological Reviews*. https://doi.org/10.1111/j.1469-185X.1999.tb00039.x

Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2015). Eavesdropping on

heterospecific alarm calls: From mechanisms to consequences. *Biological Reviews*.

https://doi.org/10.1111/brv.12122

Mariti, C., Falaschi, C., Zilocchi, M., Fatjó, J., Sighieri, C., Ogi, A., & Gazzano, A.

(2017). Analysis of the intraspecific visual communication in the domestic dog

(*Canis familiaris*): A pilot study on the case of calming signals. *Journal of*

Veterinary Behavior. https://doi.org/10.1016/j.jveb.2016.12.009

Maros, K., Pongrácz, P., Bárdos, G., Molnár, C., Faragó, T., & Miklósi, Á. (2008).

Dogs can discriminate barks from different situations. *Applied Animal Behaviour*

Science. https://doi.org/10.1016/j.applanim.2008.01.022

Marsh, A. A., Adams, R. B., & Kleck, R. E. (2005). Why do fear and anger look the

way they do? Form and social function in facial expressions. *Personality and*

Social Psychology Bulletin. https://doi.org/10.1177/0146167204271306

Mathews, A., & Macleod, C. (1994). Cognitive approaches to emotion and emotional

disorders. *Annual Review of Psychology*, *45*(1), 25–50.

Matsumoto, D., & Ekman, P. (1988). Japanese and Caucasian facial expressions of

emotion (JACFEE). *San Francisco, CA: Intercultural and Emotion Research ...*

McComb, K., Taylor, A. M., Wilson, C., & Charlton, B. D. (2009). The cry embedded

within the purr. *Current Biology*. https://doi.org/10.1016/j.cub.2009.05.033

McDowell, L. J., Wells, D. L., Hepper, P. G., & Dempster, M. (2016). Lateral bias and

temperament in the domestic cat (*Felis silvestris*). *Journal of Comparative*

Psychology. https://doi.org/10.1037/com0000030

McGuire, B., & Bemis, K. E. (2017). Scent marking in shelter dogs: Effects of body

size. *Applied Animal Behaviour Science*.
https://doi.org/10.1016/j.applanim.2016.11.001

Mendl, M., Brooks, J., Basse, C., Burman, O., Paul, E., Blackwell, E., & Casey, R. (2010). Dogs showing separation-related behaviour exhibit a 'pessimistic' cognitive bias. *Current Biology*. https://doi.org/10.1016/j.cub.2010.08.030

Mendl, M., Burman, O. H. P., Parker, R. M. A., & Paul, E. S. (2009). Cognitive bias as an indicator of animal emotion and welfare: Emerging evidence and underlying mechanisms. *Applied Animal Behaviour Science*.
https://doi.org/10.1016/j.applanim.2009.02.023

Mendl, M., Burman, O. H. P., & Paul, E. S. (2010). An integrative and functional framework for the study of animal emotion and mood. *Proceedings of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rspb.2010.0303

Mengoli, M., Mariti, C., Cozzi, A., Cestarollo, E., Lafont-Lecuelle, C., Pageat, P., & Gazzano, A. (2013). Scratching behaviour and its features: A questionnaire-based study in an Italian sample of domestic cats. *Journal of Feline Medicine and Surgery*. https://doi.org/10.1177/1098612X13481468

Merola, I., Lazzaroni, M., Marshall-Pescini, S., & Prato-Previde, E. (2015). Social referencing and cat–human communication. *Animal Cognition*.
https://doi.org/10.1007/s10071-014-0832-2

Merola, I., Prato-Previde, E., Lazzaroni, M., & Marshall-Pescini, S. (2014). Dogs' comprehension of referential emotional expressions: Familiar people and familiar emotions are easier. *Animal Cognition*. https://doi.org/10.1007/s10071-013-0668-1

Merola, I., Prato-Previde, E., & Marshall-Pescini, S. (2012). Social referencing in dog-

owner dyads? *Animal Cognition*. https://doi.org/10.1007/s10071-011-0443-0

Miklösi, Á., Polgárdi, R., Topál, J., & Csányi, V. (1998). Use of experimenter-given cues in dogs. *Animal Cognition*. https://doi.org/10.1007/s100710050016

Miklósi, Ádam, Pongrácz, P., Lakatos, G., Topál, J., & Csányi, V. (2005). A comparative study of the use of visual communicative signals in interactions between dogs (*Canis familiaris*) and humans and cats (*Felis catus*) and humans. *Journal of Comparative Psychology*. https://doi.org/10.1037/0735-7036.119.2.179

Miklósi, Ádám, & Topál, J. (2013). What does it take to become "best friends"? Evolutionary changes in canine social competence. *Trends in Cognitive Sciences*. https://doi.org/10.1016/j.tics.2013.04.005

Mitsui, S., Yamamoto, M., Nagasawa, M., Mogi, K., Kikusui, T., Ohtani, N., & Ohta, M. (2011). Urinary oxytocin as a noninvasive biomarker of positive emotion in dogs. *Hormones and Behavior*. https://doi.org/10.1016/j.yhbeh.2011.05.012

Moelk, M. (2006). Vocalizing in the house-cat; A phonetic and functional study. *The American Journal of Psychology*. https://doi.org/10.2307/1416947

Molnár, C., Pongrácz, P., Faragó, T., Dóka, A., & Miklósi, Á. (2009). Dogs discriminate between barks: The effect of context and identity of the caller. *Behavioural Processes*. https://doi.org/10.1016/j.beproc.2009.06.011

Monard, A. M., & Duncan, P. (1996). Consequences of natal dispersal in female horses. *Animal Behaviour*. https://doi.org/10.1006/anbe.1996.0198

Müller, C. A., Schmitt, K., Barber, A. L. A., & Huber, L. (2015). Dogs can discriminate emotional expressions of human faces. *Current Biology*. https://doi.org/10.1016/j.cub.2014.12.055

Nakabayashi, M., Yamaoka, R., & Nakashima, Y. (2012). Do faecal odours enable
domestic cats (*Felis catus*) to distinguish familiarity of the donors? *Journal of
Ethology*. https://doi.org/10.1007/s10164-011-0321-x

Nakayama, K., Goto, S., Kuraoka, K., & Nakamura, K. (2005). Decrease in nasal
temperature of rhesus monkeys (*Macaca mulatta*) in negative emotional state.
Physiology and Behavior. https://doi.org/10.1016/j.physbeh.2005.03.009

Natoli, E. (1985). Behavioural responses of urban feral cats to different types of urine
marks. *Behaviour*. https://doi.org/10.1163/156853985X00208

Nawroth, C., Albuquerque, N., Savalli, C., Single, M. S., & McElligott, A. G. (2018).
Goats prefer positive human emotional facial expressions. *Royal Society Open
Science*. https://doi.org/10.1098/rsos.180491

Nawroth, C., Ebersbach, M., & von Borell, E. (2014). Juvenile domestic pigs (*Sus
scrofa domestica*) use human-given cues in an object choice task. *Animal
Cognition*. https://doi.org/10.1007/s10071-013-0702-3

Nesse, R. M. (1990). Evolutionary explanations of emotions. *Human Nature*.
https://doi.org/10.1007/BF02733986

Nicastro, N. (2004). Perceptual and acoustic evidence for species-level differences in
meow vocalizations by domestic cats (*Felis catus*) and African wild cats (*Felis
silvestris lybica*). *Journal of Comparative Psychology*.
https://doi.org/10.1037/0735-7036.118.3.287

O'Brien, S. J., Johnson, W., Driscoll, C., Pontius, J., Pecon-Slattery, J., & Menotti-
Raymond, M. (2008). State of cat genomics. *Trends in Genetics*.
https://doi.org/10.1016/j.tig.2008.03.004

Outram, A. K., Stear, N. A., Bendrey, R., Olsen, S., Kasparov, A., Zaibert, V., … Evershed, R. P. (2009). The earliest horse harnessing and milking. *Science*. https://doi.org/10.1126/science.1168594

Pacheco, M. A., & Herrera, E. A. (2006). Social structure of feral horses in the Llanos of Venezuela. *Journal of Mammalogy*. https://doi.org/10.2307/1382634

Pageat, P., & Gaultier, E. (2003). Current research in canine and feline pheromones. *Veterinary Clinics of North America - Small Animal Practice*. https://doi.org/10.1016/S0195-5616(02)00128-6

Pal, S. K. (2003). Urine marking by free-ranging dogs (*Canis familiaris*) in relation to sex, season, place and posture. *Applied Animal Behaviour Science*. https://doi.org/10.1016/S0168-1591(02)00178-8

Pal, S. K., Ghosh, B., & Roy, S. (1998). Agonistic behaviour of free-ranging dogs (*Canis familiaris*) in relation to season, sex and age. *Applied Animal Behaviour Science*. https://doi.org/10.1016/S0168-1591(98)00108-7

Palagi, E. (2006). Social play in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*): Implications for natural social systems and interindividual relationships. *American Journal of Physical Anthropology*. https://doi.org/10.1002/ajpa.20289

Panksepp, J. (2005). On the embodied neural nature of core emotional affects. *Consciousness and Cognition*. https://doi.org/10.1016/j.concog.2004.10.004

Panksepp, J. (2011). The basic emotional circuits of mammalian brains: Do animals have affective lives? *Neuroscience and Biobehavioral Reviews*. https://doi.org/10.1016/j.neubiorev.2011.08.003

Panksepp, J., & Burgdorf, J. (2003). "Laughing" rats and the evolutionary antecedents of human joy? *Physiology and Behavior*. https://doi.org/10.1016/S0031-9384(03)00159-8

Parr, L. A., Waller, B. M., Burrows, A. M., Gothard, K. M., & Vick, S. J. (2010). Brief communication: MaqFACS: A muscle-based facial movement coding system for the rhesus macaque. *American Journal of Physical Anthropology*. https://doi.org/10.1002/ajpa.21401

Parrish, J. K., & Edelstein-Keshet, L. (1999). Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science*. https://doi.org/10.1126/science.284.5411.99

Paul, E. S., Harding, E. J., & Mendl, M. (2005). Measuring emotional processes in animals: The utility of a cognitive approach. *Neuroscience and Biobehavioral Reviews*. https://doi.org/10.1016/j.neubiorev.2005.01.002

Pellis, S. et al. (2010). The function of play in the development of the social brain. *American Journal of Play*.

Pelphrey, K. A., Sasson, N. J., Reznick, J. S., Paul, G., Goldman, B. D., & Piven, J. (2002). Visual scanning of faces in autism. *Journal of Autism and Developmental Disorders*.

Platt, M. L., Seyfarth, R. M., & Cheney, D. L. (2016). Adaptations for social cognition in the primate brain. *Philosophical Transactions of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rstb.2015.0096

Pollermann, B. Z., & Archinard, M. (2003). Acoustic patterns of emotions. *Improvements in Speech Synthesis*. https://doi.org/10.1002/0470845945.ch23

Pongrácz, P., Molnár, C., & Miklósi, Á. (2006). Acoustic parameters of dog barks carry emotional information for humans. *Applied Animal Behaviour Science*. https://doi.org/10.1016/j.applanim.2005.12.004

Pongrácz, P., & Szapu, J. S. (2018). Cats (*Felis silvestris catus*) read human gaze for referential information. *Intelligence*, (January), 0–1. https://doi.org/10.1016/J.INTELL.2018.11.001

Pontier, D., Rioux, N., & Heizmann, A. (2006). Evidence of selection on the orange allele in the domestic cat *Felis catus*: The role of social structure. *Oikos*. https://doi.org/10.2307/3545954

Proctor, H. (2012). Animal sentience: Where are we and where are we heading? *Animals*. https://doi.org/10.3390/ani2040628

Proctor, H. S., & Carder, G. (2015a). Measuring positive emotions in cows: Do visible eye whites tell us anything? *Physiology and Behavior*. https://doi.org/10.1016/j.physbeh.2015.04.011

Proctor, H. S., & Carder, G. (2015b). Nasal temperatures in dairy cows are influenced by positive emotional state. *Physiology and Behavior*. https://doi.org/10.1016/j.physbeh.2014.11.011

Proops, L., & Mccomb, K. (2012). Cross-modal individual recognition in domestic horses (*Equus caballus*) extends to familiar humans. *Proceedings of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rspb.2012.0626

Proops, L., McComb, K., & Reby, D. (2009). Cross-modal individual recognition in domestic horses (*Equus caballus*). *Proceedings of the National Academy of Sciences of the United States of America*. https://doi.org/10.1073/pnas.0809127105

Proops, L., Walton, M., & McComb, K. (2010). The use of human-given cues by domestic horses, *Equus caballus*, during an object choice task. *Animal Behaviour*. https://doi.org/10.1016/j.anbehav.2010.02.015

Provine, R. R. (2004). Laughing, tickling, and the evolution of speech and self. *Current Directions in Psychological Science*. https://doi.org/10.1111/j.0963-7214.2004.00311.x

Racca, A., Guo, K., Meints, K., & Mills, D. S. (2012). Reading faces: Differential lateral gaze bias in processing canine and human facial expressions in dogs and 4-year-old children. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0036076

Read, P. B. (1982). *Measuring emotions in infants and children* (Volume 2). Cambridge University Press.

Reefmann, N., Wechsler, B., & Gygax, L. (2009). Behavioural and physiological assessment of positive and negative emotion in sheep. *Animal Behaviour*. https://doi.org/10.1016/j.anbehav.2009.06.015

Reimert, I., Bolhuis, J. E., Kemp, B., & Rodenburg, T. B. (2013). Indicators of positive and negative emotions and emotional contagion in pigs. *Physiology and Behavior*. https://doi.org/10.1016/j.physbeh.2012.11.002

Rieger, G., & Turner, D. C. (1999). How depressive moods affect the behavior of singly living persons toward their cats. *Anthrozoos*. https://doi.org/10.2752/089279399787000066

Rolls, E. T. (2005). *Emotion Explained. Emotion Explained*. https://doi.org/10.1093/acprof:oso/9780198570035.001.0001

Rooney, N. J., & Bradshaw, J. W. S. (2006). Social cognition in the domestic dog:

behaviour of spectators towards participants in interspecific games. *Animal Behaviour*. https://doi.org/10.1016/j.anbehav.2005.10.014

Rooney, N. J., Bradshaw, J. W. S., & Robinson, I. H. (2001). Do dogs respond to play signals given by humans? *Animal Behaviour*. https://doi.org/10.1006/anbe.2000.1661

Rottenberg, J. (2005). Mood and emotion in major depression. *Current Directions in Psychological Science*. https://doi.org/10.1111/j.0963-7214.2005.00354.x

Rubenstein, D. I., & Hack, M. A. (1992). Horse signals: The sounds and scents of fury. *Evolutionary Ecology*. https://doi.org/10.1007/BF02214165

Rubenstein, R. T. (1981). Inter-group transfer in Assateague pony mares. *Animal Behaviour*, *40*(945–952).

Russell, J. A., & Barrett, L. F. (1999). Core affect, prototypical emotional episodes, and other things called emotion: Dissecting the elephant. *Journal of Personality and Social Psychology*. https://doi.org/10.1037/0022-3514.76.5.805

Rutberg, A. T. (1990). Inter-group transfer in Assateague pony mares. *Animal Behaviour*. https://doi.org/10.1016/S0003-3472(05)80996-0

Saito, A., & Shinozuka, K. (2013). Vocal recognition of owners by domestic cats (*Felis catus*). *Animal Cognition*. https://doi.org/10.1007/s10071-013-0620-4

Salmeto, A. L., Hymel, K. A., Carpenter, E. C., Brilot, B. O., Bateson, M., & Sufka, K. J. (2011). Cognitive bias in the chick anxiety-depression model. *Brain Research*. https://doi.org/10.1016/j.brainres.2010.12.007

Sandem, A. I., Braastad, B. O., & Bøe, K. E. (2002). Eye white may indicate emotional state on a frustration-contentedness axis in dairy cows. *Applied Animal Behaviour*

Science. https://doi.org/10.1016/S0168-1591(02)00029-1

Scherer, K. R. (2003). Vocal communication of emotion: A review of research

paradigms. *Speech Communication*. https://doi.org/10.1016/S0167-

6393(02)00084-5

Schindler, K., Van Gool, L., & de Gelder, B. (2008). Recognizing emotions expressed

by body pose: A biologically inspired neural model. *Neural Networks*.

https://doi.org/10.1016/j.neunet.2008.05.003

Schröder, M. (2001). Emotional speech synthesis: A review. *Eurospeech*.

Seligman, M. E. P., & Csikszentmihalyi, M. (2014). Positive psychology: An

introduction. *Flow and the Foundations of Positive Psychology: The Collected*

Works of Mihaly Csikszentmihalyi. https://doi.org/10.1007/978-94-017-9088-8_18

Serpell, J. (2014). Pet keeping and animal domestication: A reappraisal. *The Walking*

Larder: Patterns of Domestication, Pastoralism, and Predation.

Serpell, J. A. (2013). Domestication and history of the cat. *The Domestic Cat: The*

Biology of its Behaviour. https://doi.org/10.1017/CBO9781139177177.011

Serpell, J. a. (1995). The domestic dog: Its evolution, behaviour and interactions with

people. *Canidae: Carnivora, Mammalia, Vertebrata, Chordata, Animalia*.

https://doi.org/citeulike-article-id:2190584

Siniscalchi, M., d'Ingeo, S., Minunno, M., & Quaranta, A. (2018a). Communication in

dogs. *Animals*. https://doi.org/10.3390/ani8080131

Siniscalchi, M., d'Ingeo, S., Minunno, M., & Quaranta, A. (2018b). Communication in

dogs. *Animals*. https://doi.org/10.3390/ani8080131

Skoglund, P., Ersmark, E., Palkopoulou, E., & Dalén, L. (2015). Ancient wolf genome reveals an early divergence of domestic dog ancestors and admixture into high-latitude breeds. *Current Biology*. https://doi.org/10.1016/j.cub.2015.04.019

Smirnova, D. S., Volodin, I. A., Demina, T. S., & Volodina, E. V. (2016). Acoustic structure and contextual use of calls by captive male and female cheetahs (*Acinonyx jubatus*). *PLoS ONE*. https://doi.org/10.1371/journal.pone.0158546

Smith, A. V., Proops, L., Grounds, K., Wathan, J., & McComb, K. (2016). Functionally relevant responses to human facial expressions of emotion in the domestic horse (*Equus caballus*). *Biology Letters*. https://doi.org/10.1098/rsbl.2015.0907

Smith, A. V., Proops, L., Grounds, K., Wathan, J., Scott, S. K., & McComb, K. (2018). Domestic horses (*Equus caballus*) discriminate between negative and positive human nonverbal vocalisations. *Scientific Reports*. https://doi.org/10.1038/s41598-018-30777-z

Smith, A. V., Wilson, C., McComb, K., & Proops, L. (2018). Domestic horses (*Equus caballus*) prefer to approach humans displaying a submissive body posture rather than a dominant body posture. *Animal Cognition*. https://doi.org/10.1007/s10071-017-1140-4

Somppi, S., Törnqvist, H., Kujala, M. V., Hänninen, L., Krause, C. M., & Vainio, O. (2016). Dogs evaluate threatening facial expressions by their biological validity - Evidence from gazing patterns. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0143047

Somppi, S., Törnqvist, H., Topál, J., Koskela, A., Hänninen, L., Krause, C. M., & Vainio, O. (2017). Nasal oxytocin treatment biases dogs' visual attention and emotional response toward positive human facial expressions. *Frontiers in*

Psychology. https://doi.org/10.3389/fpsyg.2017.01854

Soproni, K., Miklósi, Á., Topál, J., & Csányi, V. (2001). Comprehension of human

communicative signs in pet dogs (*Canis familiaris*). *Journal of Comparative*

Psychology. https://doi.org/10.1037/0735-7036.115.2.122

Sotocinal, S. G., Sorge, R. E., Zaloum, A., Tuttle, A. H., Martin, L. J., Wieskopf, J. S.,

… Mogil, J. S. (2011). The rat grimace scale: A partially automated method for

quantifying pain in the laboratory rat via facial expressions. *Molecular Pain*.

https://doi.org/10.1186/1744-8069-7-55

Spinka, M., Newberry, R. C., & Bekoff, M. (2004). Mammalian play: Training for the

unexpected. *The Quarterly Review of Biology*. https://doi.org/10.1086/393866

Stahlbaum, C. C., & Houpt, K. A. (1989). The role of the Flehmen response in the

behavioral repertoire of the stallion. *Physiology and Behavior*.

https://doi.org/10.1016/0031-9384(89)90111-X

Tamioso, P. R., Maiolino Molento, C. F., Boivin, X., Chandèze, H., Andanson, S.,

Delval, É., … Boissy, A. (2018). Inducing positive emotions: Behavioural and

cardiac responses to human and brushing in ewes selected for high vs low social

reactivity. *Applied Animal Behaviour Science*.

https://doi.org/10.1016/j.applanim.2018.08.001

Taylor, A. M., & Reby, D. (2010). The contribution of source-filter theory to mammal

vocal communication research. *Journal of Zoology*. https://doi.org/10.1111/j.1469-

7998.2009.00661.x

Taylor, Anna M., Reby, D., & McComb, K. (2009). Context-related variation in the

vocal growling behaviour of the domestic dog (*Canis familiaris*). *Ethology*.

https://doi.org/10.1111/j.1439-0310.2009.01681.x

Terburg, D., Hooiveld, N., Aarts, H., Kenemans, J. L., & van Honk, J. (2011). Eye

tracking unconscious face-to-face confrontations: Dominance motives prolong

gaze to masked angry faces. *Psychological Science*.

https://doi.org/10.1177/0956797611398492

Tiller, W. A., McCraty, R., & Atkinson, M. (1996). Cardiac coherence: A new,

noninvasive measure of autonomic nervous system order. *Alternative Therapies in

Health and Medicine*.

Tooby, J., & Cosmides, L. (1990). The past explains the present. Emotional adaptations

and the structure of ancestral environments. *Ethology and Sociobiology*.

https://doi.org/10.1016/0162-3095(90)90017-Z

Travain, T., Colombo, E. S., Grandi, L. C., Heinzl, E., Pelosi, A., Prato Previde, E., &

Valsecchi, P. (2016). How good is this food? A study on dogs' emotional

responses to a potentially pleasant event using infrared thermography. *Physiology

and Behavior*. https://doi.org/10.1016/j.physbeh.2016.03.019

Udell, M. A. R., Dorey, N. R., & Wynne, C. D. L. (2010). What did domestication do to

dogs? A new account of dogs' sensitivity to human actions. *Biological Reviews*.

https://doi.org/10.1111/j.1469-185X.2009.00104.x

Valenstein, E. S. (1974). *Brain control: A critical examination of brain stimulation and

psychosurgery*. John Wiley and Sons.

Valera, M., Bartolomé, E., Sánchez, M. J., Molina, A., Cook, N., & Schaefer, A. (2012).

Changes in eye temperature and stress assessment in horses during show jumping

competitions. *Journal of Equine Veterinary Science*.

https://doi.org/10.1016/j.jevs.2012.03.005

Vallortigara, G., & Rogers, L. J. (2005). Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences*. https://doi.org/10.1017/S0140525X05000105

Van Hooff, J. A. R. A. M. (1972). A comparative approach to the phylogeny of laughter and smiling. *Non-verbal communication*. https://doi.org/10.1016/j.apergo.2015.06.002

Verbalis, J. G., McCann, M. J., McHale, C. M., & Stricker, E. M. (1986). Oxytocin secretion in response to cholecystokinin and food: Differentiation of nausea from satiety. *Science*. https://doi.org/10.1126/science.3715453

Vick, S., Waller, B. M., Parr, L. A., Smith-pasqualini, M., & Bard, K. (2006). ChimpFACS - The chimpanzee facial action coding system. *Interchange*.

Vigne, J. D., Guilaine, J., Debue, K., Haye, L., & Gérard, P. (2004). Early taming of the cat in Cyprus. *Science*. https://doi.org/10.1126/science.1095335

Vilà, C., Leonard, J. A., Götherström, A., Marklund, S., Sandberg, K., Lidén, K., … Ellegren, H. (2001). Widespread origins of domestic horse lineages. *Science*. https://doi.org/10.1126/science.291.5503.474

Virányi, Z., Topál, J. Ó., Gácsi, M. Á., Miklósi, Á., & Csányi, V. (2004). Dogs respond appropriately to cues of humans' attentional focus. *Behavioural Processes*. https://doi.org/10.1016/j.beproc.2004.01.012

Viscardi, A. V., Hunniford, M., Lawlis, P., Leach, M., & Turner, P. V. (2017). Development of a piglet grimace scale to evaluate piglet pain using facial expressions following castration and tail docking: A pilot study. *Frontiers in*

Veterinary Science. https://doi.org/10.3389/fvets.2017.00051

Vitale Shreve, K. R., & Udell, M. A. R. (2015). What's inside your cat's head? A review of cat (*Felis silvestris catus*) cognition research past, present and future. *Animal Cognition*. https://doi.org/10.1007/s10071-015-0897-6

Vitale Shreve, K. R., & Udell, M. A. R. (2017). Stress, security, and scent: The influence of chemical signals on the social lives of domestic cats and implications for applied settings. *Applied Animal Behaviour Science*. https://doi.org/10.1016/j.applanim.2016.11.011

Viviani, D., & Stoop, R. (2008). Opposite effects of oxytocin and vasopressin on the emotional expression of the fear response. *Progress in Brain Research*. https://doi.org/10.1016/S0079-6123(08)00418-4

von Borell, E., Langbein, J., Després, G., Hansen, S., Leterrier, C., Marchant-Forde, J., … Veissier, I. (2007). Heart rate variability as a measure of autonomic regulation of cardiac activity for assessing stress and welfare in farm animals - A review. *Physiology and Behavior*. https://doi.org/10.1016/j.physbeh.2007.01.007

Waller, B. M., Lembeck, M., Kuchenbuch, P., Burrows, A. M., & Liebal, K. (2012). GibbonFACS: A muscle-based facial movement coding system for hylobatids. *International Journal of Primatology*. https://doi.org/10.1007/s10764-012-9611-6

Waller, B. M., & Micheletta, J. (2013). Facial expression in nonhuman animals. *Emotion Review*. https://doi.org/10.1177/1754073912451503

Waller, B. M., Peirce, K., Caeiro, C. C., Scheider, L., Burrows, A. M., McCune, S., & Kaminski, J. (2013). Paedomorphic facial expressions give dogs a selective advantage. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0082686

Waring, G. H. (1983). *Horse behavior. The behavioral traits and adaptations of domestic and wild horses, including ponies.* Mill Road: Noyes Publications.

Wathan, J., Proops, L., Grounds, K., & McComb, K. (2016). Horses discriminate between facial expressions of conspecifics. *Scientific Reports.* https://doi.org/10.1038/srep38322

Wathan, Jen, Burrows, A. M., Waller, B. M., & McComb, K. (2015). EquiFACS: The equine facial action coding system. *PLoS ONE.* https://doi.org/10.1371/journal.pone.0131738

Wathan, Jennifer, & McComb, K. (2014). The eyes and ears are visual indicators of attention in domestic horses. *Current Biology.* https://doi.org/10.1016/j.cub.2014.06.023

Wayne, R. K., Nash, W. G., & O'Brien, S. J. (1987). Chromosomal evolution of the canidae: I. Species with high diploid numbers. *Cytogenetic and Genome Research.* https://doi.org/10.1159/000132356

Wayne, Robert K., & O'Brien, S. J. (2006). Allozyme divergence within the canidae. *Systematic Zoology.* https://doi.org/10.2307/2413399

Wayne, Robert K., & Ostrander, E. A. (1999). Origin, genetic diversity, and genome structure of the domestic dog. In *BioEssays.* https://doi.org/10.1002/(SICI)1521-1878(199903)21:3<247::AID-BIES9>3.0.CO;2-Z

Wielebnowski, N., & Brown, J. L. (1998). Behavioral correlates of physiological Estrus in cheetahs. *Zoo Biology.* https://doi.org/10.1002/(SICI)1098-2361(1998)17:3<193::AID-ZOO4<3.0.CO;2-4

Wiley, R. H. (1983). The evolution of communication: information and manipulation.

Volume 2:Communication.

Windschnurer, I., Barth, K., & Waiblinger, S. (2009). Can stroking during milking decrease avoidance distances of cows towards humans? *Animal Welfare*.

Winkielman, P., & Berridge, K. C. (2004). Unconscious emotion. *Current Directions in Psychological Science*. https://doi.org/10.1111/j.0963-7214.2004.00288.x

Yeon, S. C. (2012). Acoustic communication in the domestic horse (*Equus caballus*). *Journal of Veterinary Behavior: Clinical Applications and Research*. https://doi.org/10.1016/j.jveb.2011.08.004

Yeon, S. C., Kim, Y. K., Park, S. J., Lee, S. S., Lee, S. Y., Suh, E. H., … Lee, H. J. (2011). Differences between vocalization evoked by social stimuli in feral cats and house cats. *Behavioural Processes*. https://doi.org/10.1016/j.beproc.2011.03.003

Yong, M. H., & Ruffman, T. (2015). Is that fear? Domestic dogs' use of social referencing signals from an unfamiliar person. *Behavioural Processes*. https://doi.org/10.1016/j.beproc.2014.09.018

Zupan, M., Buskas, J., Altimiras, J., & Keeling, L. J. (2016). Assessing positive emotional states in dogs using heart rate and heart rate variability. *Physiology and Behavior*. https://doi.org/10.1016/j.physbeh.2015.11.027

Article I: The role of cat eye narrowing movements in cat-human communication

Tasmin Humphrey, Leanne Proops, Jemma Forman, Rebecca Spooner, Karen McComb

Abstract

Domestic animals are sensitive to human cues that facilitate inter-specific communication, including cues to emotional state. The eyes are important in signalling emotions, with the act of narrowing the eyes appearing to be associated with positive emotional communication in a range of species. This study examines the communicatory significance of a widely reported cat behaviour that involves eye narrowing, referred to as the slow blink sequence. Slow blink sequences typically involve a series of half-blinks followed by either a prolonged eye narrow or an eye closure. Our first experiment revealed that cat half-blinks and eye narrowing occurred more frequently in response to owners' slow blink stimuli towards their cats (compared to no owner-cat interaction). In a second experiment, this time where an experimenter provided the slow blink stimulus, cats had a higher propensity to approach the experimenter after a slow blink interaction than when they had adopted a neutral expression. Collectively, our results suggest that slow blink sequences may function as a form of positive emotional communication between cats and humans.

Introduction

For companion animals, humans act as key social partners, with these species often spending more time with humans than conspecifics (Proops & Mccomb, 2012). The ability to engage in interspecific communication, not only by reading human-given cues but also by producing signals directed at humans, would have obvious adaptive advantages for domestic species, allowing the exchange of important social information. A number of domestic animals have been shown to use human-given cues to derive contextual information and perform tasks. Pet dogs are highly skilled in reading human gestural cues to locate hidden food (Call et al., 2003; Gácsi et al., 2004), and can differentiate between the attentive states of handlers when making choices (Kaminski, Bräuer, Call, & Tomasello, 2009; Soproni et al., 2001; Virányi et al., 2004). More recent studies have revealed that dogs can also gain information through the use of human cues to emotion (Albuquerque et al., 2016; Buttelmann & Tomasello, 2013; Merola et al., 2014; Müller et al., 2015). Horses, pigs and goats also all perform successfully in following certain human-given cues in object choice tasks (Kaminski et al., 2005; Nawroth et al., 2014; Proops et al., 2010), and horses and goats can discriminate between different human emotions (Nawroth et al., 2018; Smith et al., 2016; Smith et al., 2018), adjusting their behaviour in functionally relevant ways (in horses: Proops, Grounds, Smith, & McComb, 2018). Interspecific communication is not one sided either - some domestic animals can also direct communicative behaviour towards humans. Human-directed gazing behaviour has been suggested to be a form of referential and intentional communication (Savalli, Ades, & Gaunet, 2014; Savalli, Resende, & Gaunet, 2016) and is seen in dogs as young as 2 months old (Passalacqua et al., 2011), as well as in other domestic species, such as horses (Malavasi & Huber, 2016) and goats (Nawroth, Brett, & McElligott, 2016).

It is notable that the socio-communicative abilities of another key species in the human household, the domestic cat (*Felis Catus*), have been relatively understudied – perhaps because of the cat's solitary ancestry (Pongrácz & Szapu, 2018a). However, research assessing human-directed gazing by cats in a social referencing paradigm found that most cats do look to their owners when faced with an ambiguous situation (Merola et al., 2015). In addition, domestic cats have been shown to perform equally as well as dogs in object choice tasks using human pointing (Miklósi et al., 2005), and only slightly worse than dogs in tasks that require human-directed attention-getting to obtain food (Pongrácz & Szapu, 2018a). Cats have also been shown to attract and manipulate human attention effectively in the auditory modality, through solicitation purring (McComb et al., 2009), as well as discriminate their name from other words, even when unfamiliar humans are calling (Saito, Shinozuka, Ito, & Hasegawa, 2019). There is evidence that they also display specific facial actions during negative emotional contexts with humans compared to the same emotional contexts without human interaction (Bennett et al., 2017; Ellis, 2018). Furthermore, there is circumstantial evidence that cats may be sensitive to human emotional cues, displaying more allo-rubbing (a communicative signal of affiliation in cats; Cameron-Beaumont, 1997) toward owners in a depressive mood (Rieger & Turner, 1999). Cats also alter their behaviour in different ways, such as tension in their body posture, ear and tail positions, depending on the valence of the emotional cues presented by a familiar human (Galvan & Vonk, 2016). These findings collectively suggest that the cat may be an interesting model for further investigation of inter-specific communication, particularly in the context of emotional communication with humans. This line of study has particular relevance for enhancing the cat-human bond and feline welfare.

One common anecdotally acknowledged yet subtle behavioural display that cats appear to direct at humans is the slow blink sequence (see also; Cats Protection, 2017). Slow blink sequences involve a series of half-blinks (where the eyelids move towards each other without ever fully closing the eye (Caeiro et al., 2017) followed by either prolonged narrowing of the eye aperture or a full eye closure (see Fig. 1). Anecdotal evidence and personal observations suggest that the slow blink sequence can be used as a method of cat-owner communication, and is said to occur in calm, positive contexts (Care & Lincoln, n.d.; Tabor, 1997). Interestingly, narrowing of the eyes, the main characteristic of the slow blink sequence, also features in the positive emotional displays of some other species, including the play and consummatory faces of canids (Fox, 1970), in horses and cows during stroking (Hintze et al., 2016; Proctor & Carder, 2015a; Sandem et al., 2002) and the human Duchenne smile (Duchenne, 1862), and might therefore be a positive emotional indicator in cats.

We performed two experiments with the aim of exploring the communicative significance of slow blink behaviour in human-cat interactions. We first examined whether cats respond to human-initiated slow blink stimuli with slow blink sequences of their own (Experiment 1). We then investigated whether cats were more likely to approach an unknown experimenter after a slow blink interaction (Experiment 2). Across the experiments, the slow blink sequence was compared with two controls: no human interaction, and a neutral face.

Figure 1. The cat slow blink sequence, starting from a neutral face moving to a half blink, then towards eye closure and then eye narrowing expression.

Materials and Methods

Experiment 1

Subjects

A total of 21 cats from 14 different households were included. Fourteen different owners participated in this experiment. Ten of the cats were male and 11 of the cats were female, cat ages ranged from an estimated 0.45 – 16 years (M = 7.05, S.D. = 4.59). All cats were housed indoors with outdoor access and had been living with their owners for a minimum of 3 months. Due to the nature of the study, partially blind/visually impaired cats or cats with medical issues involving the eyes were not included. All subjects were filmed during the slow blink stimulus, and this was counter-balanced with the no human interaction condition. Three dyads were outliers and excluded from subsequent analyses (> 2 standard deviations from the mean rate of eye movements), thus the final analyses included 18 cat-human dyads.

Procedure

Cats were individually tested in a familiar room within their home. The home environment is more comfortable for the cats than laboratory based contexts, increasing the ecologically validity of the testing conditions. The experimenters (RS and TH)

demonstrated the slow blink action, an eye closure (lasting more than 0.5 seconds), and gave advice verbally on how to perform the facial actions associated with slow blinking. Additional exerts from the FACS manual were provided if owners required more detailed descriptions of related movements (see Appendix 1). The experimenter also gave verbal instructions on the intensity of these actions and then asked the owner to produce the slow blink movements to check that the cue was appropriate, giving corrections if necessary. The cat was present at all times throughout the experiment. Once the cat had settled down in one place, the experimenter asked the owner to either sit approximately 1m in front of their cat or not to interact with their cat for the duration of the trial, depending on the condition. A Sony DSC-HX9V video camera was positioned 1.0-1.5m in front of the owner to record their facial expressions, and a second Canon G9 video camera was placed the same distance in front of the cat. The experimenter was situated behind the video camera that recorded the cat's facial expressions.

Paired slow blink stimulus and no human interaction conditions were counterbalanced across cats, with each cat being presented with each condition once. Before delivering each slow blink stimulus, owners were asked to ensure the cats were attentive and if they were not, to gain their cat's attention. Once the cat gave direct eye contact, owners performed the slow blink action. Owners were asked to repeat this procedure until the experimenter indicated the end of the trial. Trials varied slightly in length due to apparent variability in cats' motivations to participate in the interaction but were 2 minutes maximum or when the cat walked away. On average trials lasted 62.75 seconds long and the average owner's stimulus delivery was at a rate of 14.58 slow blink stimulus eye movements per minute. During the no human interaction condition, the owner remained in the room with the cat, but did not sit in front of or interact with the

cat – owners were free to speak to the experimenter and were not filmed during this time. Mean trial length for the no human interaction control condition was 59.86 seconds.

Behavioural coding

Cat's eye movements were coded using actions defined in CatFACS, an anatomically based system designed to objectively measure facial actions based on their underlying muscle movements (Caeiro et al., 2017). One additional code (not specifically accounted for in CatFACS), 'eye narrowing', was included in the current study to take into account situations where the eye aperture was held partially closed for at least 2 frames (0.08 seconds) rather than returning to the neutral eyelid position in a continuous movement, as in the half blink (see Table 1). The eye narrowing and eye closure movements of the owner were also coded. Eye movements of both cats and humans were coded by one researcher (TH) who was blind to the conditions for the cats' eye movements; human facial expressions could not be coded blind, as the condition was obvious from the owner's facial expression. A second independent coder analysed a random 25% of the videos. The independent coder was familiar with the research aims and was blind to the experimental conditions. Both researchers were certified CatFACS coders and the inter-observer reliability on coding the presence of all cats' and owners' eye movements yielded a Cronbach's alpha of 0.9, which is deemed a good level of inter-observer reliability. Figure 1 shows the cat slow blink sequence taken from video frames of one of the subjects; video available as Supplementary Video.

Table 1. Cat and Human Eye Movements and corresponding FACS action units. See
(Caeiro et al., 2017) *and* (Ekman & Friesen, 1971b) *for descriptions and photographs of*
the actions described.

Code Name	Facial Action Unit	Description of Code
Cat Half Blink	AU 147	One or both of the eyelids (upper or lower) moves towards the other without ever closing the eye. It may occur in only one eye. It may occur in a succession of movements or one movement only.
Cat Eye Closure	AU 143	The upper and lower eyelids move towards each other and cover the eye completely. The eye has to remain closed for more than half a second. It may occur in only one eye.
Cat Eye Narrowing		The upper and lower eyelids are held half closed. **This is a prolonged version of AU147.**
Cat Blink	AU 145	The upper and lower eyelids move towards each other and cover the eye completely. The eye has to open within half a second. It can occur in only one eye.

Cat Eye Closures due to Movement		When a cat closes its eyes due to rubbing against a surface, scratching, yawning or any other movement that would naturally cause the eyes to narrow or close.
Human Eye Closure	AU 43	The upper and lower eyelids move towards each other and cover the eye completely. The eye has to remain closed for more than half a second.
Human Eye Narrowing		The upper and lower eyelids are held half closed. The eye aperture is held partially closed for at least 2 frames (0.08 seconds), as in Cat Eye Narrowing.

Statistical Analysis

Due to trials varying in length, the rate of each cat's individual eye movements (half-blink, blink, eye closure, and eye narrowing) was calculated by dividing the total number of a particular eye movement by the total length of the trial in seconds. The resulting rates of the individual cat eye movements were then compared across the slow blink and the no human interaction conditions using Wilcoxon tests. We also tested for the effects of multiple cat occupancy by comparing the differences between single-cat and multi-cat households using a Kruskall-Wallis H test. Instructions for human eye movements across conditions can be found in Appendix 1.

Experiment 2

Pilot Trials

Pilot trials (N = 18 naïve cats) were conducted which included a control condition, involving a neutral facial expression with direct eye contact toward the cat. These trials indicated that cats, like many other species (Emery, 2000), perceive direct eye contact from humans as threatening. Thus, we modified the control condition in Experiment 2 to a neutral face without direct eye contact being made.

Subjects

In total 24 cats were recruited from local online advertisements. Twelve cats were male and 12 cats were female, cat age ranging from an estimated 1 – 17 years old (M = 6.00, S.D. = 4.78). All cats were housed indoors with outdoor access. As in Experiment 1, partially blind/visually impaired cats or cats with medical issues involving the eyes were not included in this study. All subjects were recorded under both slow blink stimulus and neutral face conditions, and the order of conditions was counterbalanced between subjects. Six cats were excluded from the subsequent analyses due to outliers in the data (> 2 standard deviations from the mean number of eye movements), and therefore the final analyses included 18 cats.

Procedure

The experimenter (JF) avoided contact with the cat before trials began, interacting only with the owners, to ensure that a neutral relationship was established with the cat. Before testing, owners were encouraged to uphold the normal atmosphere of the household, and were allowed to talk and move around as they pleased at this stage. During trials they were stationary and did not interfere with the cat but did sometimes

talk. As in Experiment 1, cameras were set up once the subject had settled down, allowing cats to habituate to the presence of the camera equipment. Video footage was obtained using a wide-angle lens Panasonic HC-X920 camera placed 1.0-1.5m away from where the cat had settled and an additional Sony DCR-SR37 camera 1.0-1.5m in front of the experimenter. A 2-minute baseline was captured to record the cat's typical behaviour. The trials began with the experimenter approaching the cat offering a flat hand with palm faced upwards whilst the experimenter was either sat or crouched directly opposite the cat. If the cat was not attentive, the experimenter called the cat's name. This action was carried out to observe the cat's baseline level of approach tendency. After a few seconds, the experimenter retracted her hand and either adopted a neutral expression without eye contact or began performing the slow blinking stimulus. To standardise the experimenter's head position between the neutral stimulus and the slow blink stimulus, the experimenter simply looked away slightly to the side of the cat during the neutral face without eye contact condition.

Delivery of the slow blink stimulus was identical to that in experiment 1. Trials lasted a minute, after which the experimenter again offered her hand for a few seconds, as an approach invitation stimulus. The experimenter's hand was offered for an average of 3.71 seconds, and there were no significant differences in the length of time the experimenter offered her hand in each condition ($Z = -1.02$, $p = 0.31$). Cats' responses to the approach invitation were measured and the retraction of the experimenter's hand signalled the end of the trial. In between trials, there was an interval of approximately 2 minutes in order to give cats a break from social interaction and to avoid any carry-over effects across trial types which may affect the approach response.

Behaviour Coding

Behavioural coding was the same as for experiment 1 (see Table 1), with the exception that the normal reflexive blinking action was omitted from the coding scheme, as normal maintenance blinking had not contributed to the differences found in experiment 1 and did not appear to be part of the cat slow blink sequences. Codes for approach behaviour were also included which consisted of Approach, Neutral and Avoid. Approach was defined as any head or body movement towards the proffered hand, Avoid as any head or body movement away, and Neutral as no change in movement. Experiment 2 also incorporated a factor that accounted for eye responses that could have occurred as a result of the experimenter calling the cat's attention during the trials, these were controlled for by excluding any cat eye movements made within half a second of an experimenter's call, in the absence of an experimenter eye closure.

Statistical Analysis

All trials in experiment 2 lasted the same length of time (1 min), therefore number of the cat's eye movements were used directly in the analyses, rather than being converted into rates as in experiment 1. Non-parametric Wilcoxon tests were used to assess differences in the cat's specific eye narrowing movements (half blink, eye narrowing, and eye closure) between the two conditions. Spearman's rho correlations were used to test the relationship between cat's age and number of cats' specific eye narrowing movements. Sign tests were used to examine differences in tendency to approach across the slow blink stimulus and neutral condition (coded as 1 = avoid, 2 = neutral, and 3 = approach). All analyses in this study used two-tailed tests.

Ethical statement

This research follows Association for the Study of Animal Behaviour Guidelines for the Use of Animals (Animal Behaviour, 2006, 71, 245–253) and all experimental protocols were approved by the University of Sussex Ethical Review Committee (ERC), reference number: Non-ASPA – Nov2013. The experiments were carried out in accordance with the relevant guidelines and regulations. Informed consent for participation and publication of information and images in an online open-access publication was gained from all cat owners and no participants were under the age of 18 years.

Results

Experiment 1

Rate of Cat's Eye Movements

The first analysis examined whether cats responded to the slow blink stimuli of their owners with slow blink sequences of their own (as anecdotally reported). The cats' rates of half-blinking and eye narrowing (per second) during the slow blink stimulus condition were significantly higher than the no human interaction condition (*Slow blink condition* Half blinks: M = 0.21 ± 0.15 (SD), Eye narrowing: M = 0.06 ± 0.07 (SD); *No human interaction condition* Half blink: M = 0.15 ± 0.06 (SD), Eye narrowing: M = 0.03 ± 0.03 (SD); Half blink: Z = -2.64, p = 0.008, Eye narrowing: Z = -2.50, p= 0.012; see Fig. 2). Only 4 cats showed complete eye closures in the slow blink condition and 3 in the no human interaction condition – so analyses could not be performed on this variable (see Fig. 2). It is notable that there were no significant differences between cats' rates of standard blinking in the slow blink condition versus the no human

interaction condition (*Slow blink condition* M = 0.01 ± 0.03 (SD); *No human interaction condition* M = 0.01 ± 0.02 (SD); Z = -1.17, p = 0.866), suggesting that normal (reflexive) blinks were not affected by the experimental condition.
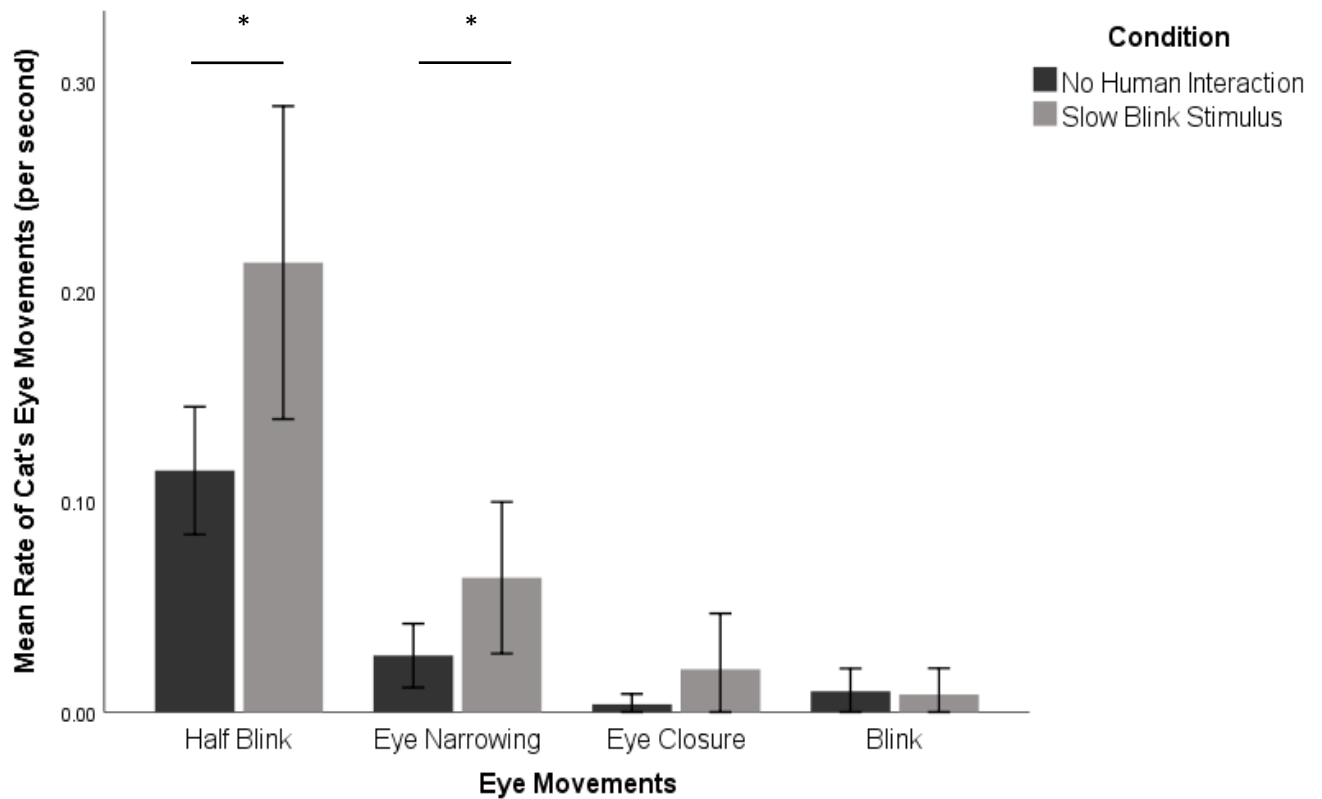
Figure 2. Mean Rate of Cats' Eye Movements during Slow blink stimulus and No human interaction condition in Experiment 1. Cats' Eye Closures could not be analysed due to the small number of cases cats blinked in each condition. Error bars represent 95% Confidence Intervals. *p < 0.05

Rate of Cat's Eye Movements in Single-Cat and Multi-Cat Households

The cats' rates of half blinks, blinks and eye narrowing were not significantly different between households with a single cat occupant (Half-blinks, M = 0.25 ± 0.14 (SD);

Blinks, M = 0.02 ± 0.05 (SD); Eye narrowing, M = 0.04 ± 0.06 (SD)) and households

with multiple cat occupants (Half blinks, M = 0.20 ± 0.16 (SD); Blinks, M = 0.01 ± 0.01

(SD); Eye narrowing, M = 0.07 ± 0.08 (SD)) within the slow blink stimulus condition;

half blinks, $\chi^2(1) = 0.88$, p = 0.35; blinks, $\chi^2(1) = 0.22$, p = 0.64; eye narrowing, $\chi^2(1) =$

0.56, p = 0.46.

Experiment 2

Cat Eye Movements

The frequencies of cat half blinks and eye narrowing were significantly higher in the

slow blinking condition (half blinks, M = 5.33 ± 6.10 (SD); eye narrowing, M = 2.78 ±

3.73(SD)) compared to the neutral face condition (half blinks, M = 1.94 ± 1.77 (SD);

eye narrowing, M = 0.33 ± 0.97 (SD)); half blinks, Z = -2.61, $p = 0.009$; eye narrowing,

Z = -2.68, $p = 0.007$. No significant difference in eye closure movements was found

between the slow blinking condition (M = 0.78 ± 1.44 (SD)) and the neutral face

condition (M = 0.61 ± 0.78 (SD)), Z = -0.63, $p = 0.53$. However, the low production of

eye closures made this difference difficult to assess statistically. In addition, cat's age

did not significantly correlate with cat half blinks, eye narrowing, eye closures or total

eye movements in the slow blinking condition (half blinks, r = -0.07, p = 0.77; eye

narrowing, r = -0.06, p = 0.81; eye closures, r = 0.21, p = 0.40; total eye movements, r =

-0.05, p = 0.84).

Cat Approach Behaviour

Cats had higher approach scores to the hand of an experimenter after the slow blink

stimulus presentation (M = 2.78 ± 0.43 (SD)) than after the neutral face (M = 2.39 ±

0.70 (SD)), $p = 0.03$ (see Fig. 3).
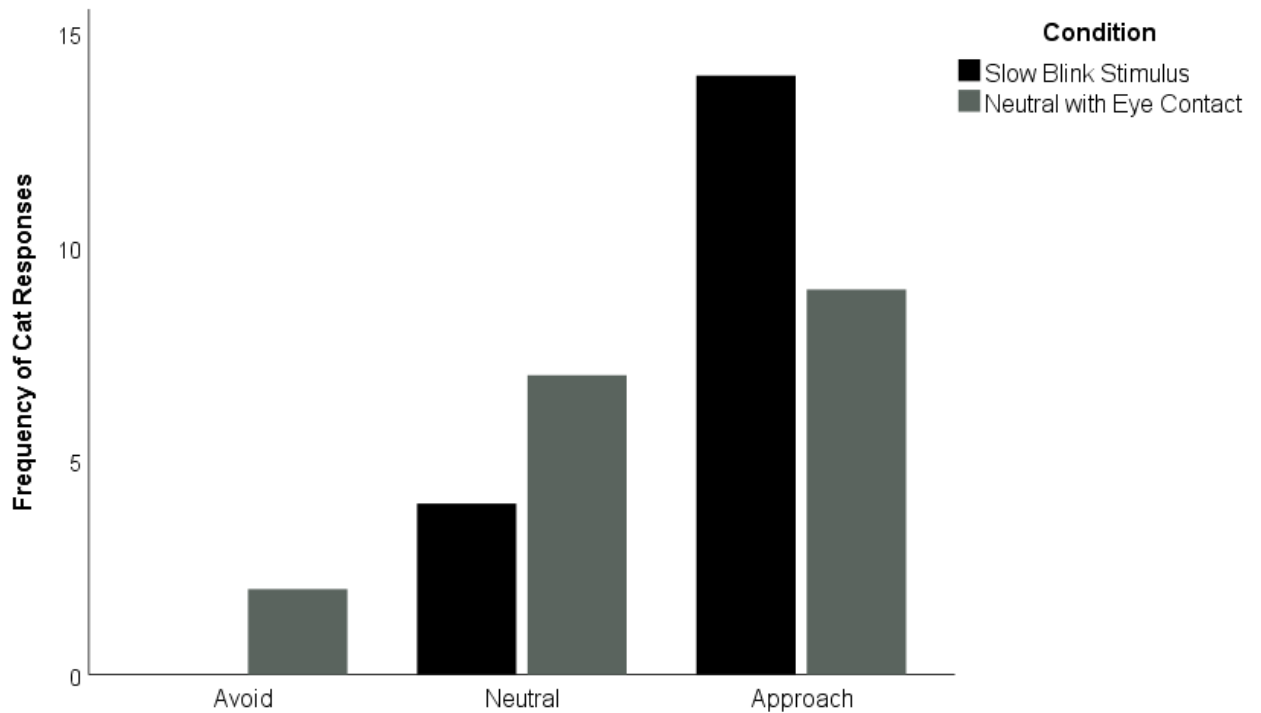
Figure 3. Frequency of Cats Responses (Avoid, Neutral, or Approach) in relation to condition (Slow Blink Stimulus or Neutral). Cats had a significantly higher approach score following the slow blink condition compared to the neutral condition (p = 0.03).

Discussion

This study is the first to experimentally investigate the role of slow blinking in cat-human communication. Our results not only describe the specific movements involved in cat slow blink sequences but also produce several strands of evidence which collectively suggest that cats respond to a human giving a slow blink stimulus by producing eye narrowing movements of their own. Firstly, cats deliver more eye narrowing movements when their owners slow blink at them than when the owner is present in the room but not delivering this stimulus. Secondly, when an unfamiliar experimenter gives the slow blink stimulus compared to adopting a neutral face, cats respond with a higher frequency of eye narrowing movements themselves. In addition,

the study produces evidence that cats perceive human slow blinking in a positive way, as subjects prefer to approach an experimenter after a slow blink interaction has occurred, compared to when the experimenter adopts a neutral facial expression without direct eye contact with the cat. This is in accordance with previous anecdotal reports of this behaviour as signalling relaxation in cats (International Cat Care & University of Lincoln, n.d.; Cats Protection, 2017).

Approach-avoidance has long been used to measure the primary motivation systems that are key to animals' emotional responses (Lang, Bradley, & Cuthbert, 1997), where an individual's approach is taken to indicate that stimuli are perceived as pleasant (Désiré, Boissy, & Veissier, 2002). The propensity of cats to approach humans following a slow blink stimulus could be because the slow blink sequence behaviour itself elicited an inherently positive emotional state in the cats or because they simply perceived the unfamiliar experimenter as pleasant after a slow blink stimulus, having learnt this from prior exposure. It is notable that, anecdotally, cats are often seen to initiate slow blink interactions themselves (Cats Protection, 2017), suggesting that the signalling interaction itself is something they are motivated to engage in. It is also relevant to note that the slow blink stimulus shares certain features with the Duchenne smile (the genuine smile in humans (Duchenne, 1862)) – specifically the narrowing of the eyes is an integral part of both. Thus our results could suggest that cats share some of the same features of positive signalling which have been found universally in humans (Ekman et al., 1987). It would be useful in future studies to explore the potential presence and function of this behaviour in conspecific communication as well as in cat-human signalling – and also consider its occurrence in enculturated captive felids.

Our study used both owners and an unknown experimenter to deliver the slow blink stimulus. In doing this we found that both owners and an unfamiliar other could elicit a

slow blink sequence in the cats. These findings somewhat contrast with Galvan and Vonk's (2016) study which found sensitivity of cats to cues of emotion from owners but not an unknown experimenter. Differences in methodology possibly led to these differing results. In particular, the use of CatFACS (Caeiro et al., 2017) for analysing cats' facial behaviours in our study may have allowed more detailed responses to be observed. One limitation of Experiment 1 was the presence of individual variation between owners in performing the slow blink stimulus, despite instructions having been provided. This added noise to the data, making it potentially difficult to determine which signals the cats were responding to. In Experiment 2, we sought to overcome this by having an experimenter perform the facial stimuli across cats in order to standardize the presentations. The use of an unfamiliar experimenter in Experiment 2 also allowed us to investigate cats' appraisal of a person performing slow blinking. Our experiments were naturalistic, conducted in the cat's home environment, so it was not possible to control exactly where the cat was resting or the precise distance from the cat to the owner's eyes without disrupting the subject. Variation in this is true to real-life interactions between owners and their cats and would be expected to add noise to the experiment – but also robustness – and would not systematically bias the results. However, it would be interesting and worthwhile to replicate the experiments in a lab setting.

It could be argued that cats have developed slow blink behaviours because humans appear to perceive slow blinking as positive (Humphrey, Stringer, Proops, & McComb, n.d.) and cats may have previously been reinforced by their owners for responding to slow blink sequences. Including an unfamiliar human therefore reduced such reinforcement effects, although the cats may still generalize across humans. This initial study showed no relationship between cat's age and slow blinking, as would be

expected with prior reinforcement, but slow blinking in cats may have been learnt. Further research on slow blinking behaviour in cats could consider whether this behaviour is primarily an evolved trait and/or learnt over time. It is also possible that slow-blinking in cats originated as a mechanism to interrupt an unbroken stare, which is potentially threatening in social interactions (Emery, 2000); this could then have been elaborated by a combination of selection and learning in the domestic environment. Understanding specific ways in which cats and humans may interact positively, such as through eye narrowing movements, can enhance public understanding of cats and feline welfare, particularly considering the close bond some cats and humans share (Edwards, Heiblum, Tejeda, & Galindo, 2007; Pongrácz & Szapu, 2018b). From the current study, the slow blink sequence appears to be an indicator of positive emotion in cats. Identifying observable indicators of positive emotions has practical benefits for the welfare of animals by providing assessment markers of an individual's current welfare and pointing to behaviours that can be promoted to produce a better quality of life (Boissy et al., 2007).

In summary, our study provides the first systematic investigation of the role of slow blink behaviour in cat-human communication. We show that slow blink interactions appear to be a positive experience for cats, and may be an indicator of positive emotions. Such findings could potentially be used to assess the welfare of cats in a variety of settings, including veterinary practices and shelter environments as well as enhancing cat-human communication in the human home. Socio-cognitive abilities of cats are an under-studied area, and future research on cat behaviours, such as slow blinking, could enhance our understanding of interspecific communication and the ways in which domestication has shaped the social behaviour of an ancestrally solitary species.

References

Albuquerque, N., Guo, K., Wilkinson, A., Savalli, C., Otta, E., & Mills, D. (2016).
Dogs recognize dog and human emotions. *Biology Letters*.
https://doi.org/10.1098/rsbl.2015.0883

Bennett, V., Gourkow, N., & Mills, D. S. (2017). Facial correlates of emotional
behaviour in the domestic cat (*Felis catus*). *Behavioural Processes*.
https://doi.org/10.1016/j.beproc.2017.03.011

Boissy, A., Manteuffel, G., Jensen, M. B., Moe, R. O., Spruijt, B., Keeling, L. J., …
Aubert, A. (2007). Assessment of positive emotions in animals to improve their
welfare. *Physiology and Behavior*. https://doi.org/10.1016/j.physbeh.2007.02.003

Buttelmann, D., & Tomasello, M. (2013). Can domestic dogs (*Canis familiaris*) use
referential emotional expressions to locate hidden food? *Animal Cognition*.
https://doi.org/10.1007/s10071-012-0560-4

Caeiro, C. C., Burrows, A. M., & Waller, B. M. (2017). Development and application of
CatFACS: Are human cat adopters influenced by cat facial expressions? *Applied
Animal Behaviour Science*. https://doi.org/10.1016/j.applanim.2017.01.005

Call, J., Bräuer, J., Kaminski, J., & Tomasello, M. (2003). Domestic dogs (*Canis
familiaris*) are sensitive to the attentional state of humans. *Journal of Comparative
Psychology*. https://doi.org/10.1037/0735-7036.117.3.257

Cameron-Beaumont, C. (1997). *Visual and tactile communication in the domestic cat
(Felis silvestris catus) and undomesticated small-felids* (doctoral dissertation).
University of Southampton.

Care, I. C., & Lincoln, U. of. (n.d.). Slow Blink. Retrieved from

https://icatcare.org/behaviour-described/maintenance/sedentary/slow-blink

Cats Protection. (2017). *The Behaviour Guide*. Retrieved from

https://www.cats.org.uk/uploads/documents/CP_Behaviour_Guide-web.pdf

Désiré, L., Boissy, A., & Veissier, I. (2002). Emotions in farm animals:: A new

approach to animal welfare in applied ethology. *Behavioural Processes*.

https://doi.org/10.1016/S0376-6357(02)00081-5

Duchenne, B. de. (1862). The mechanism of human facial expression. *RA Cuthbertson,*

Trans.

Edwards, C., Heiblum, M., Tejeda, A., & Galindo, F. (2007). Experimental evaluation

of attachment behaviors in owned cats. *Journal of Veterinary Behavior: Clinical*

Applications and Research. https://doi.org/10.1016/j.jveb.2007.06.004

Ekman, P., & Friesen, W. V. (1971). Facial action coding system: A technique for the

measurement of facial movement. *Journal of Personality and Social Psychology*.

https://doi.org/10.1037/h0030377

Ekman, P., Friesen, W. V., O'Sullivan, M., Chan, A., Diacoyanni-Tarlatzis, I., Heider,

K., … Tzavaras, A. (1987). Universals and cultural differences in the judgments of

facial expressions of emotion. *Journal of Personality and Social Psychology*.

https://doi.org/10.1037/0022-3514.53.4.712

Ellis, S. L. H. (2018). Recognising and assessing feline emotions during the

consultation: History, body language and behaviour. *Journal of Feline Medicine*

and Surgery. https://doi.org/10.1177/1098612X18771206

Emery, N. J. (2000). The eyes have it: The neuroethology, function and evolution of

social gaze. *Neuroscience and Biobehavioral Reviews*.

https://doi.org/10.1016/S0149-7634(00)00025-7

Fox, M. W. (1970). A comparative study of the development of facial expressions in

canids; Wolf, coyote and foxes. *Behaviour*.

https://doi.org/10.1163/156853970X00042

Gácsi, M., Miklód, Á., Varga, O., Topál, J., & Csányi, V. (2004). Are readers of our

face readers of our minds? Dogs (*Canis familiaris*) show situation-dependent

recognition of human's attention. *Animal Cognition*.

https://doi.org/10.1007/s10071-003-0205-8

Galvan, M., & Vonk, J. (2016). Man's other best friend: domestic cats (*F. silvestris

catus*) and their discrimination of human emotion cues. *Animal Cognition*.

https://doi.org/10.1007/s10071-015-0927-4

Hintze, S., Smith, S., Patt, A., Bachmann, I., & Würbel, H. (2016). Are eyes a mirror of

the soul? What eye wrinkles reveal about a horse's emotional state. *PLoS ONE*.

https://doi.org/10.1371/journal.pone.0164017

Humphrey, T., Stringer, F., Proops, L., & McComb, K. (n.d.). *Shelter cats that slow

blink are adopted more quickly* (unpublished maniscript).

Kaminski, J., Bräuer, J., Call, J., & Tomasello, M. (2009). Domestic dogs are sensitive

to a human's perspective. *Behaviour*. https://doi.org/10.1163/156853908X395530

Kaminski, J., Riedel, J., Call, J., & Tomasello, M. (2005). Domestic goats, *Capra

hircus*, follow gaze direction and use social cues in an object choice task. *Animal

Behaviour*. https://doi.org/10.1016/j.anbehav.2004.05.008

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1997). Motivated attention: Affect,

activation, and action. *Attention and orienting: Sensory and motivational*

processes. https://doi.org/10.1080/02699930341000239

Malavasi, R., & Huber, L. (2016). Evidence of heterospecific referential communication from domestic horses (*Equus caballus*) to humans. *Animal Cognition*. https://doi.org/10.1007/s10071-016-0987-0

McComb, K., Taylor, A. M., Wilson, C., & Charlton, B. D. (2009). The cry embedded within the purr. *Current Biology*. https://doi.org/10.1016/j.cub.2009.05.033

Merola, I., Lazzaroni, M., Marshall-Pescini, S., & Prato-Previde, E. (2015). Social referencing and cat–human communication. *Animal Cognition*. https://doi.org/10.1007/s10071-014-0832-2

Merola, I., Prato-Previde, E., Lazzaroni, M., & Marshall-Pescini, S. (2014). Dogs' comprehension of referential emotional expressions: Familiar people and familiar emotions are easier. *Animal Cognition*. https://doi.org/10.1007/s10071-013-0668-1

Miklósi, Á., Pongrácz, P., Lakatos, G., Topál, J., & Csányi, V. (2005). A comparative study of the use of visual communicative signals in interactions between dogs (*Canis familiaris*) and humans and cats (*Felis catus*) and humans. *Journal of Comparative Psychology*. https://doi.org/10.1037/0735-7036.119.2.179

Müller, C. A., Schmitt, K., Barber, A. L. A., & Huber, L. (2015). Dogs can discriminate emotional expressions of human faces. *Current Biology*. https://doi.org/10.1016/j.cub.2014.12.055

Nawroth, C., Albuquerque, N., Savalli, C., Single, M. S., & McElligott, A. G. (2018). Goats prefer positive human emotional facial expressions. *Royal Society Open Science*. https://doi.org/10.1098/rsos.180491

Nawroth, C., Brett, J. M., & McElligott, A. G. (2016). Goats display audience-

dependent human-directed gazing behaviour in a problem-solving task. *Biology Letters*. https://doi.org/10.1098/rsbl.2016.0283

Nawroth, C., Ebersbach, M., & von Borell, E. (2014). Juvenile domestic pigs (*Sus scrofa domestica*) use human-given cues in an object choice task. *Animal Cognition*. https://doi.org/10.1007/s10071-013-0702-3

Passalacqua, C., Marshall-Pescini, S., Barnard, S., Lakatos, G., Valsecchi, P., & Prato Previde, E. (2011). Human-directed gazing behaviour in puppies and adult dogs, *Canis lupus familiaris. Animal Behaviour*. https://doi.org/10.1016/j.anbehav.2011.07.039

Pongrácz, P., & Szapu, J. S. (2018a). Cats (*Felis silvestris catus*) read human gaze for referential information. *Intelligence*, (January), 0–1. https://doi.org/10.1016/J.INTELL.2018.11.001

Pongrácz, P., & Szapu, J. S. (2018b). The socio-cognitive relationship between cats and humans – Companion cats (*Felis catus*) as their owners see them. *Applied Animal Behaviour Science*. https://doi.org/10.1016/j.applanim.2018.07.004

Proctor, H. S., & Carder, G. (2015). Measuring positive emotions in cows: Do visible eye whites tell us anything? *Physiology and Behavior*. https://doi.org/10.1016/j.physbeh.2015.04.011

Proops, L., Grounds, K., Smith, A. V., & McComb, K. (2018). Animals remember previous facial expressions that specific humans have exhibited. *Current Biology*. https://doi.org/10.1016/j.cub.2018.03.035

Proops, L., & Mccomb, K. (2012). Cross-modal individual recognition in domestic horses (*Equus caballus*) extends to familiar humans. *Proceedings of the Royal*

Society B: Biological Sciences. https://doi.org/10.1098/rspb.2012.0626

Proops, L., Walton, M., & McComb, K. (2010). The use of human-given cues by

domestic horses, *Equus caballus*, during an object choice task. *Animal Behaviour*.

https://doi.org/10.1016/j.anbehav.2010.02.015

Rieger, G., & Turner, D. C. (1999). How depressive moods affect the behavior of singly

living persons toward their cats. *Anthrozoos*.

https://doi.org/10.2752/089279399787000066

Saito, A., Shinozuka, K., Ito, Y., & Hasegawa, T. (2019). Domestic cats (*Felis catus*)

discriminate their names from other words. *Scientific Reports*.

https://doi.org/10.1038/s41598-019-40616-4

Sandem, A. I., Braastad, B. O., & Bøe, K. E. (2002). Eye white may indicate emotional

state on a frustration-contentedness axis in dairy cows. *Applied Animal Behaviour*

Science. https://doi.org/10.1016/S0168-1591(02)00029-1

Savalli, C., Ades, C., & Gaunet, F. (2014). Are dogs able to communicate with their

owners about a desirable food in a referential and intentional way? *PLoS ONE*.

https://doi.org/10.1371/journal.pone.0108003

Savalli, C., Resende, B., & Gaunet, F. (2016). Eye contact is crucial for referential

communication in pet dogs. *PLoS ONE*.

https://doi.org/10.1371/journal.pone.0162161

Smith, A. V., Proops, L., Grounds, K., Wathan, J., & McComb, K. (2016). Functionally

relevant responses to human facial expressions of emotion in the domestic horse

(*Equus caballus*). *Biology Letters*. https://doi.org/10.1098/rsbl.2015.0907

Smith, A. V., Proops, L., Grounds, K., Wathan, J., Scott, S. K., & McComb, K. (2018).

Domestic horses (*Equus caballus*) discriminate between negative and positive human nonverbal vocalisations. *Scientific Reports*. https://doi.org/10.1038/s41598-018-30777-z

Soproni, K., Miklósi, Á., Topál, J., & Csányi, V. (2001). Comprehension of human communicative signs in pet dogs (*Canis familiaris*). *Journal of Comparative Psychology*. https://doi.org/10.1037/0735-7036.115.2.122

Tabor, J. (1997). *Understanding Cat Behavior: The Complete Feline Problem Solver*. David & Charles.

Virányi, Z., Topál, J. Ó., Gácsi, M. Á., Miklósi, Á., & Csányi, V. (2004). Dogs respond appropriately to cues of humans' attentional focus. *Behavioural Processes*. https://doi.org/10.1016/j.beproc.2004.01.012

Article II: Shelter cats that slow blink are adopted more quickly

Tasmin Humphrey, Faye Stringer , Leanne Proops and Karen McComb

Simple Summary:

Slow blinking is a type of interaction between humans and cats that involves a sequence of prolonged eye narrowing movements being given by both parties. This interspecific social behaviour has recently been studied empirically and appears to be a form of positive emotional communication for cats, who are more likely to approach a previously unfamiliar human after such interactions. We investigated whether slow blinking can also affect human preferences for cats in a shelter environment. We measured whether cats' readiness to respond to a human-initiated slow blink interaction was associated with rates of rehoming in the shelter. We also examined cats' propensity to slow blink when they were anxious around humans or not. Cats which slow blinked more readily were rehomed faster. Cats that were initially identified as more nervous of humans showed a trend toward being more responsive to slow blinking. Our results suggest that in parallel to the human smile, the cat slow-blink sequence may have a dual function, signalling both positive emotion and submissiveness.

Abstract: The process of domestication is likely to have led to the development of adaptive interspecific social abilities in animals. Such abilities are particularly interesting in less gregarious animals, such as cats. One notable social behaviour that cats exhibit in relation to humans is the slow blink sequence, which our previous research suggests can function as a form of positive emotional communication between cats and humans. This behaviour involves the production of successive half blinks followed by either a prolonged narrowing of the eye or an eye closure. The present study investigates how cat slow blink sequences might affect human preferences during the adoption of shelter cats.

Our study specifically tested (1) whether cats' propensity to respond to human-initiated slow blinking was associated with their speed of rehoming from a shelter environment, and (2) whether cats' anxiety around humans was related to their tendency to slow blink. Our experiments demonstrated that cats which slow blinked more readily were rehomed faster, and that nervous cats, who had been identified as needing desensitisation to humans, may be more responsive than a non-desensitisation group. These findings further our understanding of cat-human communication and how slow blinking behaviour may be used as an interspecific signalling mechanism.

Introduction

Human attitudes towards animals can be described in terms of two primary dimensions – affect and utility (Serpell, 2004). The domestication of *Felis catus*, the cat, is thought to originate in their use as a means of pest control (Driscoll et al., 2007). Thus, utility initially described early human motivations to tolerate a proximity to cats. However, over time the cat has integrated into the family home, becoming nearly as prevalent in households as the domestic dog (Murray, Gruffydd-Jones, Roberts, & Browne, 2015). Now, cats seem to play an increasingly significant affective role in our lives, even providing a supplementary source of emotional support to owners (Stammbach & Turner, 1999). This shift from co-existence with humans to companion raises interesting questions regarding the particular social behaviours in cats necessary for the formation and maintenance of the cat-human bond.

Despite previously being solitary animals, cats have become facultatively social during the process of domestication. They have been shown to use human given cues (Galvan & Vonk, 2016; Merola et al., 2015; Pongrácz & Szapu, 2018a) and adapt their own vocal communication in heterospecific interactions by using solicitation purrs that manipulate human propensity to attend to infant cries, in order to gain food and care (McComb et al., 2009). Social skills are advantageous to individuals (Preuschoft & van Schaik, 2000), in part due to signalling motivation to others, for example via emotional expression (Ekman, 1992a). Emotions therefore serve specific functions in social contexts, for example negative emotions such as fear can alert the signaller or other individuals in a group to an aversive situation. However, scientific study on positive emotional communication in animals remains relatively scant (Boissy et al., 2007). A proposed function of positive emotions in humans is to build on personal resources, including social relationships

(Fredrickson, 2001). This constructive function may extend to animals as well, since the degree to which cats display affection has been shown to be associated with owners' reported levels of attachment (Serpell, 1996). Thus, further investigation into cat-human positive emotional communication could shed light on the social function of positive emotions, specifically in the context of our relationship with felines.

One positive cat-human signal that has recently been documented scientifically is the slow blink sequence. Cat slow blink sequences involve narrowing of the eye aperture, specifically consisting of a series of shorter half blinks, followed by either a stable narrowing of the eye or a prolonged eye closure (see Figure 1). Cats appear to respond to similar eye narrowing movements initiated by humans, and tend to approach previously unfamiliar humans after such slow blink interactions (Humphrey et al., n.d.). The slow-blink has also been noted when a cat is seeking reassurance in a tense environment (Rodan, 2010). A survey into feline behaviour by the animal welfare charity, Cats Protection, found that 69% of the 1,100 cat owners asked indicated that the slow-blink implies a relaxed cat (Cats Protection, 2013). In addition, eye narrowing in various species typically signals positive affect in the individual, as seen in the chimpanzee silent bared-teeth display or the human smile (Duchenne, 1862; Parr & Waller, 2006).

Figure 1. Still images captured of the cat slow blink sequence, starting from a neutral face followed by a half blink then eye narrowing.

Slow blinking in cats may have evolved in response to human preferences for positive-looking facial expressions. Humans are able to detect positive emotional faces using only upper facial cues (Becker, Anderson, Mortensen, Neufeld, & Neel, 2011), as well as indirectly through unfocused images (Becker et al., 2012; for a review see, Becker & Srinivasan, 2014). Happy faces are also attended to more than other emotional expressions (e.g. sadness and anger) even when limitations on attention are put in place (Srivastava & Srinivasan, 2010), and tend to lead to more positive inferences regarding other's interpersonal traits such as kindness and affiliation (Knutson, 1996; Otta, Abrosio, & Hoshino, 1996). Slow blinking in cats shares features with the human smile (i.e. narrowing of the eyes), and therefore may have evolved by exploiting human sensitivity for positive facial expressions. To examine the functional relevance of specific behaviours in companion animals to interactions with humans, preference tests can be used. Waller et al. (2013) tested whether dogs using a specific facial expression (AU101, the inner brow raiser) were preferred by humans via rate of rehoming in an animal shelter. In their study, adoption speed in a shelter environment was used as a proxy for selection of dogs over time, a measure which we will also use to explore human preference for adopting shelter cats.

In the current study we specifically aimed to investigate how human-cat slow blinking interactions affect the speed of adoption of cats in a shelter environment. We tested whether shelter cats responded more to experimenter-initiated slow blink interactions compared to a control trial in which the experimenter adopted a neutral facial expression. We also examined whether cats' responses were related to rehoming speed over time. Finally, we compared whether cats that had, on admission been assessed as showing more anxiety around humans, responded differently to slow blink interactions than those who were not deemed anxious. Cats' eye narrowing movements were

recorded using the Cat Facial Action Coding System (CatFACS; Caeiro et al., 2017), an anatomically based system for coding facial muscle movements. We predicted that cats would be more responsive to the experimenter's slow blinking, by also narrowing their eye aperture, compared to the neutral expression. We also predicted that cats that were more responsive to slow blinking would be rehomed sooner, and that propensity to slow blink would vary between anxious and non-anxious cats.

Materials and Methods

Subjects

Cats were recruited from the National Cat Adoption Centre (NCAC) in Sussex. Data collection took place over 10 days between 27th June 2017 and 18th July 2017. Twenty-four cats in total were filmed. Six cats were removed from the final analysis due to problems with engaging the cat in the slow blinking interaction or lack of visibility when coding the videos as a result of the cat turning away from the experimenter or leaving the inside enclosure. Of the 18 remaining cats, 9 were female and 9 were male. All cats were neutered, and had no medical issues. Adult cats that were ≥ 1 year old were included in the study, and ages ranged from 1 to 16 years (M = 6.62, SD = 4.56).

Staff members at the Cats Protection site observe cats on admission to check for signs of anxiousness (e.g. hiding, reluctance to eat or drink). Anxious cats are placed on a desensitisation programme in which Cats Protection employees and volunteers spend time in contact with a cat to enhance the cat's confidence around humans. The final sample included 8 cats in the desensitisation group and 10 in the non-desensitisation group.

Experimental Procedure

Cats were housed in a homing wing of the NCAC, consisting of parallel rows of pens. The dimensions of each pen were 84cm x 84cm x 84cm inside, with a larger partially outdoor enclosure at the back. Cats also have visible access to the wing inside via a glass screen door. Video footage of inside the cat's pen was obtained using a Panasonic HC-V270 placed 60cm away from the screen door. A GoPro HERO4 camera was also used to capture inside the pen to increase the likelihood of recording the cat's eye movements. Another GoPro HERO4 camera was placed outside of the pen directly in front of the female experimenter (FS; see Figure 2). Once cameras were in place, cats were given 5 minutes to habituate to the presence of the equipment without the experimenter present. Each cat participated in four trials (2 experimental and 2 control), counterbalanced by condition. The first two trials were not included in the analyses but were used to allow the cats to habituate to the conditions.
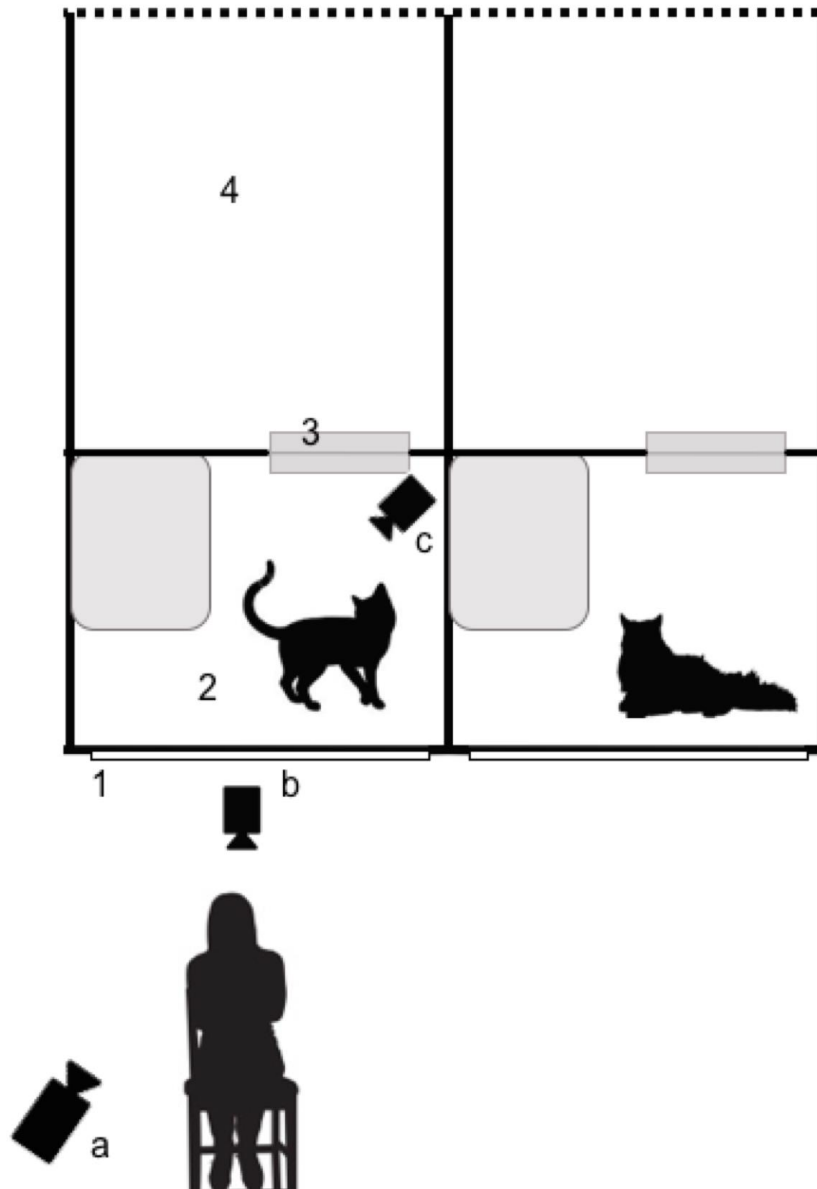
Figure 2: Experimental set-up (1 = Pen door, 2 = Indoor pen, 3 = Cat Flap, 4 = Back

enclosure; a = Panasonic HC-V270, b and c = GoPro HERO4).

In the slow blinking trial, the experimenter sat in front of the screen door and attempted

to engage the cat in an interaction by slowly narrowing and closing her eyes toward the

cat in order to initiate a slow blinking interaction. Where appropriate, the experimenter

called the cat's attention back to the interaction when the cats' gaze diverted from the

experimenter. The slow blink stimulus was then repeated several times throughout the trial. Control trials had the experimenter seated in the same position as the slow blink trials, however the experimenter averted her gaze slightly to the left of the pen at human eye level whilst still facing the cat. The experimenter could blink as normal (< 500ms). This eye position was chosen as previous trials revealed that cats may perceive staring as threatening (Humphrey et al., submitted). All trials lasted for 60 s and between testing different subjects the inside camera was disinfected using Anistel® for both infectious disease control and to remove possible effects of scent.

Behavioural and Statistical Analyses

Experimenter and cat eye narrowing movements in trials 3 and 4 were blind coded from videos on an Apple Mini Mac computer using Sportscode Gamebreaker Plus® 10.3 (www.hudl.com) software. Eye narrowing movements were derived from CatFACS (Caeiro et al., 2017) as well as adapted coding schemes used for slow blink research (see Table 1; (Humphrey et al., n.d.). Eye responses that may have occurred due to the experimenter calling the cat's attention were controlled for by excluding any cat eye movements made within half a second of an experimenter's call, in the absence of an experimenter eye closure. Coders were certified in CatFACS (TH and FS) and inter-rater reliability tests between TH and FS using identical codes found a Cronbach's alpha of 0.9.

Table 1: Cat and Human Eye Movements and corresponding FACS action units. See
CatFACS.com Paulekman.com for descriptions and visual presentations of these
actions.

Code Name	Facial Action Unit	Description of Code
Cat Half Blink	AU 147	One or both of the eyelids (upper or lower) moves towards the other without ever closing the eye. It may occur in only one eye. It may occur in a succession of movements or one movement only.
Cat Eye Closure	AU 143	The upper and lower eyelids move towards each other and cover the eye completely. The eye has to remain closed for more than half a second. It may occur in only one eye.
Cat Eye Narrowing		The upper and lower eyelids are held half closed. **This is a prolonged version of AU147.**
Cat Eye Closures due to Movement		When a cat closes its eyes due to rubbing against a surface, scratching, yawning or any other movement that would naturally cause the eyes to narrow or close.
Human Eye Closure	AU 43	The upper and lower eyelids move towards each other and cover the eye completely. The eye has to remain closed for more than half a second.

Human Eye Narrowing	The upper and lower eyelids are held half closed. This is a prolonged version of AU42 – Slit.

Data consisted of the number of instances and duration of individual eye movements (half-blink (a), eye closure (b) and eye narrowing (c)) as well as cat looking behaviour. Cat's individual eye movements were also summed (a + b + c) to create a total cat eye movement score. A total response latency measure was calculated for each cat's slow blinking trial by summing all of the latencies to the start of the cat's eye movement that occurred within 10 s of the experimenter's eye movement (note that here that a larger score would indicate a lower total response latency). Slow blinks given by the experimenter that were either not responded to or responded to after 10 s by cats were assigned a latency of 10.1. All latencies and non-responses were then summed together for each cat. Adoption rates were measured as days before the cat was reserved to be rehomed, with a maximum date of 132 days.

All analyses were conducted with IBM SPSS Statistics 24 software. Wilcoxon tests were used to examine differences in the cat's specific eye narrowing movements (half blink, eye narrowing, and eye closure) and looking behaviour between the slow blink stimulus and the neutral condition. Spearman's rank correlations assessed the relationship between the cat's specific eye narrowing movements and days before cats were reserved for rehoming. Mann-Whitney U tests were calculated to compare the response latency scores, eye movements and looking behaviours of anxious cats that had been selected for a desensitisation treatment at the shelter and cats that did not require desensitisation treatment. All analyses used two-tailed tests.

Ethical Statement

This study was conducted in accordance with the Association for the Study of Animal Behaviour (ASAB) guidelines for the use of animals in research and was approved by both the University of Sussex Animal Ethical Review Committee (ERC), reference number: Non-ASPA – Nov2013; and Cats Protection.

Results

Effects of Human-Initiated Slow Blinking

The number of cat half-blinks were significantly higher in the slow blinking trials (M = 4.22, $\pm$ 3.93 (SD)) compared to the control trials (M = 1.89, $\pm$ 2.52 (SD)), Z = -2.01, p = 0.04. There were also significantly more instances of eye narrowing in the slow blink stimulus condition (M = 3.39 $\pm$ 2.45 (SD)) compared to the neutral condition (M = 2.17 $\pm$ 2.26 (SD)), Z = -2.03, p = 0.04. The number of total eye movements were significantly higher in the slow blink stimulus condition (M = 8.89 $\pm$ 5.58 (SD)) compared to the neutral condition, Z = -2.31, p = 0.02, (see Figure 3). No significant difference was found for the number of cat eye closures between slow blinking (M = 1.28 $\pm$ 1.64 (SD)) and control trials (M = 1.06 $\pm$ 1.16 (SD)), Z = -0.69, p = 0.49. The number of instances where cats looked at the experimenter during trials approached significance with more looking in slow blinking trials (M = 2.94 $\pm$ 2.04 (SD)) than control trials (M = 1.72 $\pm$ 1.84 (SD)), Z = -1.79, p = 0.07.
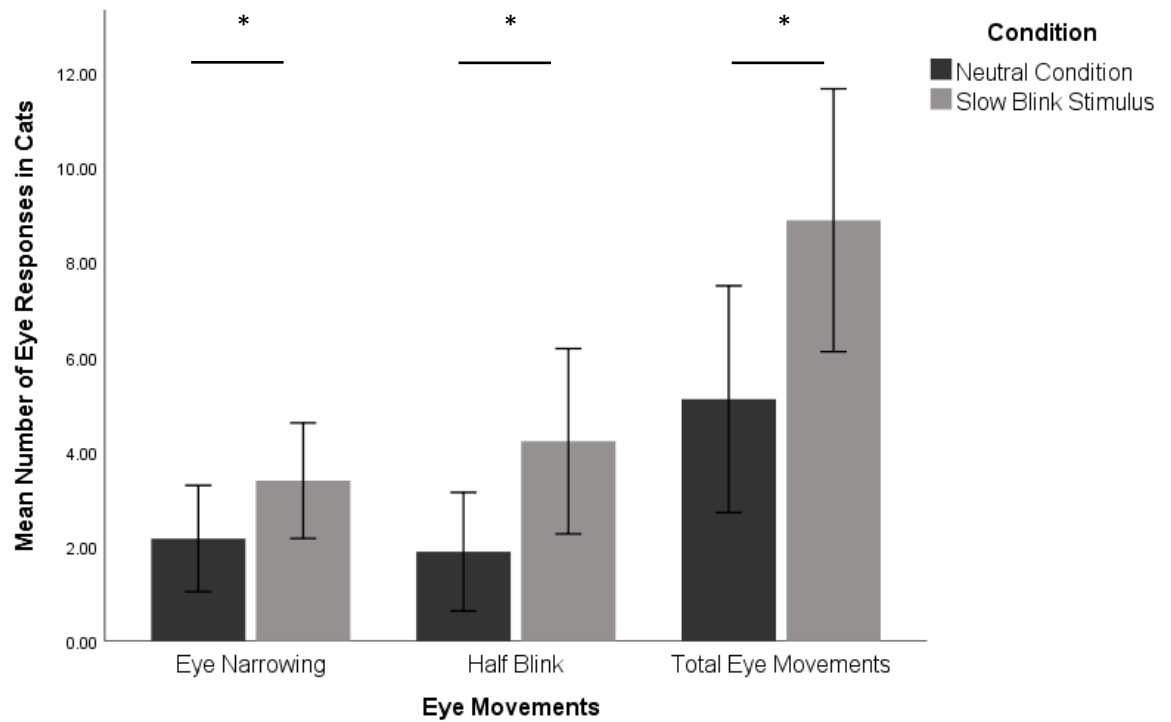
Figure 3: Mean number of instances of cat eye narrowing, half-blinks, and total eye movements in the control versus slow blinking trials (N = 18). Error bars represent 95% confidence intervals.

Tests also indicated that the duration of cat half-blinks, and the duration cats looked at the experimenter were significantly longer in the slow blinking trials (Half blink: M = 2.69 ± 2.83 (SD); Looking behaviour: M = 26.19 ± 20.20 (SD)) compared to the control trials (Half blink: M = 1.06 ± 1.37 (SD), Z = -2.27, p = 0.02; Looking behaviour: M = 11.67 ± 14.99 (SD), Z = -2.55, p = 0.01). The duration of cat eye narrowing approached significance between the slow blinking condition (M = 10.58 ± 11.68 (SD)) and the control condition (M = 8.42 ± 12.44 (SD)), Z = -1.71, p = 0.09. Finally, no significant differences were found between the slow blinking condition and the control condition in the durations of cat eye closure (Slow Blink: M = 10.90 ± 17.42 (SD); Control: M =

14.72 ± 22.45 (SD)) and total cat eye movements (Slow Blink: M = 24.17 ± 22.55 (SD); Control: 24.19 ± 24.54 (SD)), Z = -1.22, p = 0.22; Z = -0.07, p = 0.95, respectively.

Effects on time to rehome

At the time of analysis, 14 cats (of N = 18) had been reserved to be rehomed. There was a significant negative correlation between the duration of cat eye closures in the slow blinking trials and days before reserved (r = -0.56, p = 0.04; see Figure 4), thus as eye closure duration increased, cats took less time to rehome.
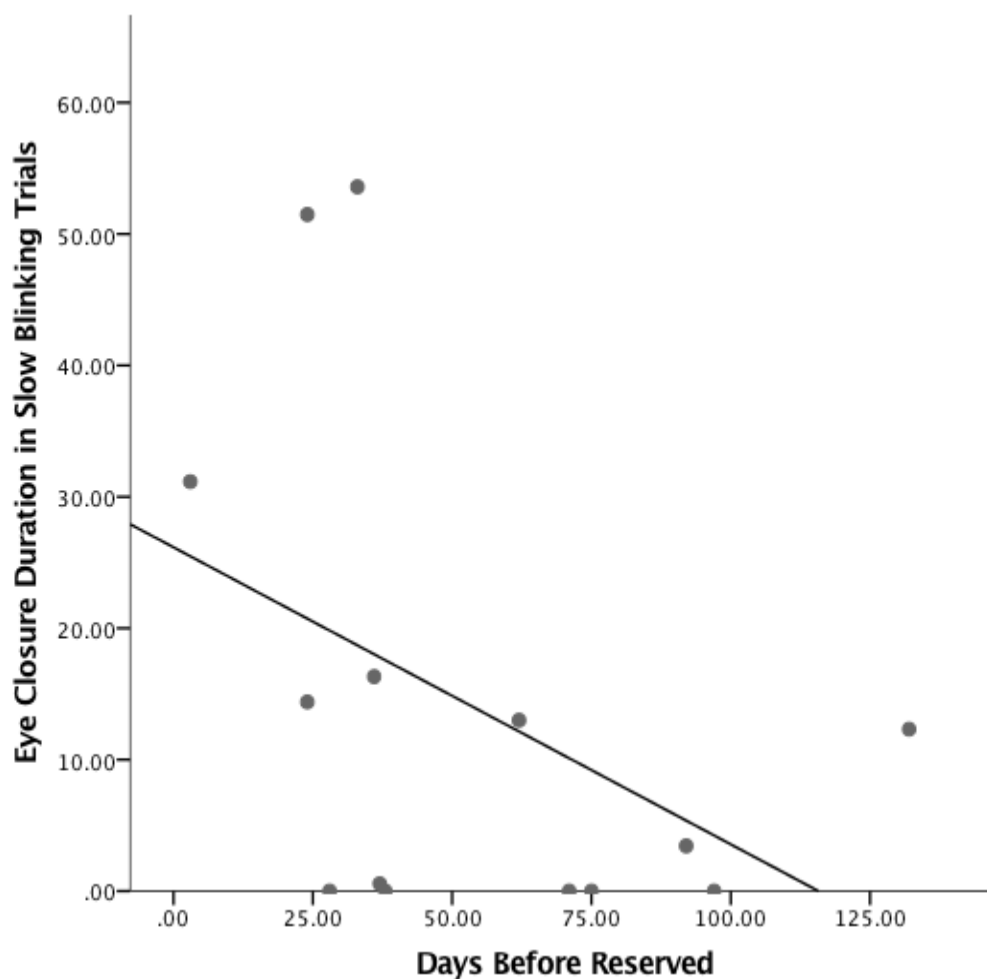
Figure 4: Relationship between duration of cat eye closures and days before cats were reserved for rehoming (N = 14).

A Spearman's correlation showed no significant relationship between the number of cat eye closures in the slow blinking condition and days before cats were reserved (r = -0.30, p = 0.30). No significant correlations with days before being reserved were found for total response latency (r = 0.08, p = 0.78), or the durations and number of cat half-blinks, eye narrowing, total eye movements and looking behaviour (Half blink frequency: r = 0.19, p = 0.51; duration: r = 0.23, p = 0.43; Eye narrowing frequency: r = 0.07, p = 0.81; duration: r = -0.19, p = 0.51; Total eye movements frequency: r = 0.13, p = 0.65; duration: r = -0.31, p = 0.28; Looking behaviour frequency: r = 0.15, p = 0.60; duration: r = 0.46, p = 0.10).

Comparison of desensitisation and non-desensitisation cats

The difference in the total response latency of desensitisation and non-desensitisation cats approached significance (U = 19.00, p = 0.06), with desensitisation cats being more responsive to slow blinking trials (M = 45.96 ± 29.66 (SD)) than non-desensitisation cats (M = 74.57 ± 33.55 (SD)). The duration of all cat eye movements also approached significance (U = 19.50, p = 0.07), with the desensitisation group showing cumulatively longer total eye movements (M = 34.35 ± 24.22 (SD)) than the non-desensitisation group (M = 16.03 ± 18.39 (SD)). No significant difference was found between desensitisation and non-desensitisation groups in duration or number of half blinks, eye narrowing, eye closure and looking behaviour (see Appendix 2 for statistical results).

Discussion

This study supports previous research showing that cats actively choose to engage in slow blinking with humans by responding with eye narrowing movements of their own. Our results offer additional insights into understanding how slow blinking functions in cat-human communication. Moreover, this study demonstrates for the first time that cats that responded to human slow blinking, specifically by using eye closures, were rehomed quicker than cats that closed their eyes less. This provides evidence that the use of slow blinking may have given cats a selective advantage during the domestication process. Furthermore, cats that were identified as more anxious around humans upon first arriving at the shelter had a tendency to be more responsive to human slow blinking.

Positive emotional expressions in other species, such as laughter and smiling in humans and primates, can help individuals to down-regulate negative affect in social interactions (Scott, Lavan, Chen, & McGettigan, 2014). In these instances, positive emotions serve a generalized purpose to enhance social affinity between partners. Slow blinking could share a similar social bonding function, and therefore the trend toward increased responsivity seen in the anxious cats in our study may have been used to mitigate cats' anxiety around humans. This could also explain the presence of half blinking in fearful contexts around humans in another feline facial behaviour study (Bennett et al., 2017). Such down-regulation in social contexts could also be considered a form of submissive behaviour. In fact, evidence indicates that displays typically seen in both positive and submissive contexts often share facial muscle movements (Waller & Micheletta, 2013). Thus, positive emotional signals may have derived from submissive displays and become more specialized as social complexity increased. Research on the similarities

between typical positive emotional expressions, including slow blinking in cats, and submissive displays generally would be a useful line of future study.

Similar to the results in our study, there is evidence that particular facial actions (inner brow raiser AU101) in dogs can increase the speed of their adoption in shelters (Waller et al., 2013). While it was suggested that this display may operate through enhancing paedomorphic facial features in dogs, it was also noted that the inner brow raise action may have been perceived as indicating sadness (the corresponding action in humans (AU 1) is an integral feature in typical sadness expressions). In the current study, eye closure movements in cats increased adoption speed. Narrowing of the eye aperture shares similar features with the human Duchenne smile – the genuine smile in humans (Duchenne, 1862). This is interesting as humans not only use the eyes to gauge the emotional state of others (Baron-Cohen et al., 1997), but also to gain purposeful social information (Perrett & Emery, 1994). Thus, the adopters may have responded more to cats who made eye narrowing movements as they appeared happier, and potentially friendlier to prospective adopters. Potential differences in the perceived emotion which effected rates of adoption between cats and dogs may also reflect common beliefs about cats' capacity for independence and dogs as "best friends" requiring close companionship.

The apparent response to eye closures by adopters, rather than other eye narrowing movements in this study (half blinking and eye narrowing) might be the result of eye closures lasting longer than the other eye narrowing movements (see Table 1). It is possible then that the salience of eye closures may affect potential adopters more than other eye narrowing movements. This is supported by the human literature which shows that gaze allocation is strongly influenced by dynamic facial movements (Buchan, Paré, & Munhall, 2007). Furthermore, the eyes play an important role in influencing human

behaviour in a number of contexts (Baron-Cohen et al., 1997; Ernest-Jones, Nettle, & Bateson, 2011; Perrett & Emery, 1994). For example, eyes that are made visually explicit can enhance the likelihood of altruistic behaviour in humans (Ernest-Jones et al., 2011). Humans may therefore be inadvertently influenced by eye closures more than other eye narrowing movements. Interestingly, however, cats do not appear to use eye closures more than other eye narrowing movements in their slow blink sequences. This suggests that eye closures, specifically, may not have undergone selective pressure by humans but rather the overall dynamic pattern of the slow blink sequence may have.

In another published study, no cat facial actions influenced adoption rates in a shelter environment (Caeiro et al., 2017), but cats' rubbing behaviour was related to faster speeds of rehoming. Interestingly, the authors also found that rubbing was correlated with half blinking and blinking in an exploratory factor analysis. Caeiro et al.'s (2017) study may not have provided sufficient opportunity for cats to display slow blinking behaviour as the human-cat paradigm used was non-communicative in nature. The social aspect of slow blinking may therefore explain the influence of eye narrowing movements on potential adopters. Adopters from previous studies when asked the reasons for choosing their pet often highlight the connection they felt towards the individual, e.g. "we clicked" and "the cat chose us" (Weiss, Miller, Mohan-Gibbons, & Vela, 2012). Since the slow blink is becoming increasingly recognised as a form of communication employed by cat owners and non-cat owners alike, these findings may have practical implications for shelters by introducing strategies to promote positive social interactions between potential adopters and shelter cats, particularly for cats that might be more likely to spend a longer time in care (e.g. inactive cats, Fantuzzi, Miller, & Weiss, 2010; or black cats, Kogan, Schoenfeld-tacher, & Hellyer, 2013).

Our study shows that cats participate in slow blinking interactions with humans, and that this interaction can lead to faster rehoming rates for shelter cats. Additionally, we demonstrate a trend which suggests that nervous cats are more responsive to slow blinking, supporting evidence that positive emotional signals share common features with submissive displays, and that certain positive emotional expressions may have resulted from cues of submission. Increased knowledge about feline behaviour acts as a protective factor against relinquishment of cats (Salman et al., 1998). Thus, better understanding of human-cat communication, such as the slow blink, is fundamental to the welfare of cats. Future studies should further explore the function of slow blinking in cats in a variety of emotional contexts. Further research could also examine how the use of slow blinking may enhance cat-human attachment.

References

Baron-Cohen, S., Wheelwright, S., & Jolliffe, T. (1997). Is there a "language of the eyes"? Evidence from normal adults, and adults with autism or Asperger Syndrome. *Visual Cognition*. https://doi.org/10.1080/713756761

Becker, D. V., Anderson, U. S., Mortensen, C. R., Neufeld, S. L., & Neel, R. (2011). The face in the crowd effect unconfounded: Happy faces, not angry faces, are more efficiently detected in single- and multiple-target visual search tasks. *Journal of Experimental Psychology: General*. https://doi.org/10.1037/a0024060

Becker, D. V., Neel, R., Srinivasan, N., Neufeld, S., Kumar, D., & Fouse, S. (2012). The vividness of happiness in dynamic facial displays of emotion. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0026551

Becker, D. V., & Srinivasan, N. (2014). The vividness of the happy face. *Current Directions in Psychological Science*. https://doi.org/10.1177/0963721414533702

Bennett, V., Gourkow, N., & Mills, D. S. (2017). Facial correlates of emotional behaviour in the domestic cat (*Felis catus*). *Behavioural Processes*. https://doi.org/10.1016/j.beproc.2017.03.011

Boissy, A., Manteuffel, G., Jensen, M. B., Moe, R. O., Spruijt, B., Keeling, L. J., … Aubert, A. (2007). Assessment of positive emotions in animals to improve their welfare. *Physiology and Behavior*. https://doi.org/10.1016/j.physbeh.2007.02.003

Buchan, J., Paré, M., & Munhall, K. (2007). Spatial statistics of gaze fixations during dynamic face processing. *Social Neuroscience*. https://doi.org/10.1080/17470910601043644

Caeiro, C. C., Burrows, A. M., & Waller, B. M. (2017). Development and application of

CatFACS: Are human cat adopters influenced by cat facial expressions? *Applied Animal Behaviour Science*. https://doi.org/10.1016/j.applanim.2017.01.005

Cats Protection. (2013). Moggies remain a mystery to many, suggests survey. Retrieved July 11, 2017, from http://www.cats.org.uk/news/behaviour--survey

Driscoll, C. A., Menotti-Raymond, M., Roca, A. L., Hupe, K., Johnson, W. E., Geffen, E., … Macdonald, D. W. (2007). The near eastern origin of cat domestication. *Science*. https://doi.org/10.1126/science.1139518

Duchenne, B. de. (1862). The mechanism of human facial expression. *RA Cuthbertson, Trans.*

Ekman, P. (1992). An argument for basic emotions. *Cognition and Emotion*. https://doi.org/10.1080/02699939208411068

Ernest-Jones, M., Nettle, D., & Bateson, M. (2011). Effects of eye images on everyday cooperative behavior: A field experiment. *Evolution and Human Behavior*. https://doi.org/10.1016/j.evolhumbehav.2010.10.006

Fantuzzi, J. M., Miller, K. A., & Weiss, E. (2010). Factors relevant to adoption of cats in an animal shelter. *Journal of Applied Animal Welfare Science*. https://doi.org/10.1080/10888700903583467

Fredrickson, B. L. (2001). The role of positive emotions in positive psychology: The broaden-and-build theory of positive emotions. *American Psychologist*. https://doi.org/10.1037/0003-066X.56.3.218

Galvan, M., & Vonk, J. (2016). Man's other best friend: domestic cats (*F. silvestris catus*) and their discrimination of human emotion cues. *Animal Cognition*. https://doi.org/10.1007/s10071-015-0927-4

Humphrey, T., Proops, L., Forman, J., Spooner, R., Wathan, J., & McComb, K. (n.d.). *The cat smile?: The role of cat eye narrowing movements in cat-human communication* (unpublished manuscript).

Knutson, B. (1996). Facial expressions of emotion influence interpersonal trait inferences. *Journal of Nonverbal Behavior*. https://doi.org/10.1007/BF02281954

Kogan, L. R., Schoenfeld-tacher, R., & Hellyer, P. W. (2013). Cats in animal shelters: Exploring the common perception that black cats take longer to adopt. *The Open Veterinary Science Journal*, *7*(2002), 18–22. https://doi.org/10.2174/1874318820130718001

McComb, K., Taylor, A. M., Wilson, C., & Charlton, B. D. (2009). The cry embedded within the purr. *Current Biology*. https://doi.org/10.1016/j.cub.2009.05.033

Merola, I., Lazzaroni, M., Marshall-Pescini, S., & Prato-Previde, E. (2015). Social referencing and cat–human communication. *Animal Cognition*. https://doi.org/10.1007/s10071-014-0832-2

Murray, J. K., Gruffydd-Jones, T. J., Roberts, M. A., & Browne, W. J. (2015). Assessing changes in the UK pet cat and dog populations: Numbers and household ownership. *Veterinary Record*. https://doi.org/10.1136/vr.103223

Otta, E., Abrosio, F. F. E., & Hoshino, R. L. (1996). Reading a smiling face: Messages conveyed by various forms of smiling. *Perceptual and Motor Skills*. https://doi.org/10.2466/pms.1996.82.3c.1111

Parr, L. A., & Waller, B. M. (2006). Understanding chimpanzee facial expression: Insights into the evolution of communication. *Social Cognitive and Affective Neuroscience*. https://doi.org/10.1093/scan/nsl031

Perrett, D. I., & Emery, N. J. J. (1994). Understanding the intentions of others from visual signals: Neurophysiological evidence. *Current Psychology of Cognition.* https://doi.org/10.1016/S0165-0173(02)00185-6

Pongrácz, P., & Szapu, J. S. (2018). Cats (*Felis silvestris catus*) read human gaze for referential information. *Intelligence*, (January), 0–1. https://doi.org/10.1016/J.INTELL.2018.11.001

Preuschoft, S., & van Schaik, C. P. (2000). Dominance and communication: Conflict management in various social settings. *Natural Conflict Resolution.*

Rodan, I. (2010). Understanding feline behavior and application for appropriate handling and management. *Topics in Companion Animal Medicine.* https://doi.org/10.1053/j.tcam.2010.09.001

Salman, M. D., New, Jr., J. G., Scarlett, J. M., Kass, P. H., Ruch-Gallie, R., & Hetts, S. (1998). Human and animal factors related to relinquishment of dogs and cats in 12 selected animal shelters in the United States. *Journal of Applied Animal Welfare Science.* https://doi.org/10.1207/s15327604jaws0103_2

Scott, S. K., Lavan, N., Chen, S., & McGettigan, C. (2014). The social life of laughter. *Trends in Cognitive Sciences.* https://doi.org/10.1016/j.tics.2014.09.002

Serpell, J. A. (2004). Factors influencing human attitudes to animals and their welfare. *Animal Welfare.*

Serpell, James A. (1996). Evidence for an association between pet behavior and owner attachment levels. *Applied Animal Behaviour Science.* https://doi.org/10.1016/0168-1591(95)01010-6

Srivastava, P., & Srinivasan, N. (2010). Time course of visual attention with emotional

faces. *Attention, Perception, and Psychophysics*.
https://doi.org/10.3758/APP.72.2.369

Stammbach, K. B., & Turner, D. C. (1999). Understanding the human-cat relationship: Human social support or attachment. *Anthrozoos*.
https://doi.org/10.2752/089279399787000237

Waller, B. M., & Micheletta, J. (2013). Facial expression in nonhuman animals.
Emotion Review. https://doi.org/10.1177/1754073912451503

Waller, B. M., Peirce, K., Caeiro, C. C., Scheider, L., Burrows, A. M., McCune, S., & Kaminski, J. (2013). Paedomorphic facial expressions give dogs a selective advantage. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0082686

Weiss, E., Miller, K., Mohan-Gibbons, H., & Vela, C. (2012). Why did you choose this pet?: Adopters and pet selection preferences in five animal shelters in the United States. *Animals*. https://doi.org/10.3390/ani2020144

Article III: Lateral paw use in cats predicts emotional communication with humans

Tasmin Humphrey, Hollie Panther, Leanne Proops, Karen McComb

Abstract

Emotional functioning in a range of species has been linked to brain and motor lateralisation. Paw preference therefore represents a potentially useful measure of lateralisation that can provide insights into the underlying emotional basis of certain animal behaviours. Slow blinking is a type of interaction between humans and cats that appears to have emotional significance (Humphrey et al., submitted). Both spontaneously, and in response to humans performing a slow blink, cats give a series of half blinks followed by either a prolonged narrowing of the eye or an eye closure. In order to throw light on the emotional mechanisms underlying cat slow blinking behaviour, the current study investigates its relationship with paw preferences. Strong paw preferences in cats were related to enhanced responding and greater synchrony during cat-human slow blink interactions. These findings provide additional support for the hypothesis that slow blink interactions are emotionally relevant cat-human displays.

Introduction

In animals, motor and brain lateralisation is associated with social behaviour (Ghirlanda & Vallortigara, 2004), where the right hemisphere is linked to avoidance/withdrawal, and the left hemisphere is linked to approach behaviour (Vallortigara & Rogers, 2005). Such evidence suggests that both of the cerebral hemispheres play a role in emotional processing, and indeed lateral biases in animals has been associated with a range of emotional contexts and behaviours. For example, Westergaard, et al. (2003) found that free-ranging rhesus macaques with a right hand preference were less submissive and would receive fewer aggressive attacks by conspecifics, but would spend more time in grooming interactions with others. In addition, tail-wagging in dogs when they view familiar and unfamiliar others shows lateral biases which depend on the affective appraisal of the other (Quaranta, Siniscalchi & Vallortigara, 2007). Similarly, lateral gaze biases in dogs and horses have been found in response to the presentation of conspecific and human emotion faces (Racca, Guo, Meints & Mills, 2012; Smith, Proops, Grounds, Wathan & McComb, 2016).

Observable biological indices of emotion such as lateralised behaviour are crucial to affective research in non-human animals. In the absence of verbal report, understanding whether behaviours in animals are a display of emotion requires verification against a range of other known emotional indicators. Nevertheless, our current understanding of emotional signalling in animals contains substantial gaps, particularly in the area of positive emotions (Boissey et al., 2007; Seligman & Csikszentmihalyi, 2000). This is important as the presence of positive emotions shows that an animal is flourishing, rather than simply receiving a level of care in which there is no explicit suffering (Lawrence, 1987).

Descriptions of a range of positive emotional indicators are particularly significant for domestic species, who regularly interact with and are under the care of humans. There are an estimated 8 million domestic cats in the UK, residing in 17% of households (Pet Food Manufacturing Association, 2016). Despite the popularity of the cat as a companion animal, research on cats' social and cognitive abilities is sparse. However, one specific cat behaviour that has recently been empirically explored is the slow blink sequence (Humphrey et al., submitted). The cat slow blink sequence consists of a series of eye narrowing movements, typically involving half blinks followed by eye narrowing and/or closure of the eyes. These eye narrowing movements can be elicited during cat-human interactions where the human initiates a slow eye closure toward the cat. Slow blink sequences also appear to be perceived as positive by both parties; cats are more likely to approach an unfamiliar human after a slow blink interaction (Humphrey et al., submitted), and cats who make salient responses to slow blink interactions with humans are rehomed quicker (Humphrey et al. in prep.). However, further investigations are required to explore how the slow blink is related to emotional functioning in cats.

Paw preference, like hand preference in humans and non-human primates, is another measure of hemispheric asymmetry. McDowell, Wells, Hepper and Dempster (2016) investigated the relationship between paw preference and temperament in the domestic cat. Paw preference was assessed by observing the paw cats used to reach for treats in a food puzzle game over multiple trials. The researchers found that paw-preferent cats (with either a left or right paw preference) were more affectionate, friendly and obedient, and less aggressive than their ambi-lateral counterparts. In dogs, ambi-lateralisation is also linked to more reactivity to noise in comparison with significant paw preference (Branson & Rogers, 2006). This suggests that not only is the specific

asymmetric specialisation important but also the presence of a lateralisation may provide important clues to the emotional relevance of particular behaviours.

The present study examines whether lateralisation is associated with the responses of cats during a human-initiated slow blink interaction. Extending McDowell, Wells, Hepper and Dempster's (2016) study on lateralisation and temperament in cats, our study explores whether paw-preferent cats are more responsive in slow blink interactions with humans than ambi-lateral cats. As well as inducing cat slow blinking using our previously established human slow blink protocol, we also included a parallel protocol where the experimenter turned their head away from the cat at the end of each slow blink presentation, mimicking a natural response observed in cats to prolonged human eye contact and potentially providing more opportunity for them to engage.

Methods

Subjects

A total of 33 cats were recruited, 11 cats were excluded due to their lack of motivation to participate in the food puzzle task, two did not participate during the slow blink trials, and one due to a technical fault with the camera footage. Nineteen cats were included in the final analysis, who ranged in age from 2 to 17 years old ($M = 7.63$, $SD = 4.21$). Of these cats 12 were male and 7 were female; all cats were spayed/neutered. Two cats were not allowed outdoors, whilst the rest of the cats had indoor and outdoor access. Ten cats from our sample had been rescued. None of the cats were familiar with the experimenter (HP) and cats had no visual or auditory impairments. Eight cats were lateralised (5 right paw-preferent and 3 left paw-preferent) and 11 cats were ambi-lateral.

Paw Preference Test

The paw preferences of the cats were measured using the Catit Senses Food Maze (Catit, United Kingdom). This is a three-storey tower with holes on each level in which food can be reached by the cats or moved down through the levels to eventually fall into a tray at the bottom. The same food puzzle has been used successfully to measure paw preference in cats in a previous study (McDowell Wells, Hepper & Dempster, 2016). The cat watched treats (Dreamies, Mars Petcare, United Kingdom) being placed at the top of the maze. No time limit was given to retrieve the treats and cats completed a minimum of 20 trials. As required (i.e. once the number of treats in the maze was low), treats were replenished. A trial was considered to be any attempt made by the cat to retrieve treats from the puzzle, with a new trial commencing when the paw was removed from the tower. The paw used, whether successful or not in retrieving the food, was recorded.

Slow Blink Stimuli

Two variations of slow blink stimuli were used in this study. The first slow blink condition, hereafter known as the Standard Slow Blink (SSB), involved the experimenter performing full eye closures and eye narrowing at the cat. This SSB stimulus has effectively been used to elicit slow blink sequences in cats in previous research (Humphrey et al., submitted). The second variation of the slow blink stimulus (the Slow Blink with Breaks; SBB) consisted of the same eye narrowing movements by the experimenter as in the SSB condition, but the experimenter turned their head away from the cat at the end of each slow blink eye closure. The experimenter continued the SSB or SBB stimuli for the duration of the trial, with attention-getting noises (e.g.

calling the subject's name) being made in order to return the cat's attention to the direction of the experimenter where necessary.

Procedure

All tests took place in the owners' homes to ensure the subjects were as comfortable as possible. Two cameras were used, one facing the cat to capture its responses, and another facing the experimenter. Cameras were set up on tripods and positioned as soon as possible after the experimenter's arrival, in order to give cats time to habituate to their presence. Once cats appeared calm, the food puzzle was set up and paw preferences were recorded. During this time, demographic information about the cats was collected from the owners. Then, four 60s trials were conducted, with counterbalancing between trial types (i.e. SSB and SBB). Four trials were conducted as a pilot study had revealed that cats may need time to ease into the slow blink interactions with an unfamiliar human. Consequently, the last 2 of the 4 trials were coded.

Data Analysis

Laterality Index (LI). For each cat, a directional laterality index (see Wells, 2003; Smith, Proops, Grounds, Wathan, & McComb, 2016) was calculated, to quantify each cat's paw preference on a continuum from -1 (strong right paw-preferent) through 0 (ambi-lateral), to +1 (strong left paw-preferent). The LI was calculated by dividing the difference between number of left-paw and right-paw attempts by their sum, i.e.: (L-R)/ (L+R). Cats who scored between -.33 and +.33 were considered ambi-lateral (Pike & Maitland, 1996).

Behavioural Coding

Eye movements of the cat and the experimenter in the last 2 trials were blind coded from videos on a Mini Macintosh computer using Sportscode Gamebreaker Plus® 10.3

(www.hudl.com) software. Analysis of the facial actions of cats were undertaken by a trained Cat Facial Action Coding System (CatFACS) observer (TH; Caeiro, Waller & Burrows, 2013). The additional codes, Eye Narrowing and Look Away, were employed to fit the purpose of the present study (see Table 1). The code for Eye Narrowing has been used in previous research on slow blinking (Humphrey et al., submitted.).

Table 1. Cat and Human Eye Movements and corresponding FACS action units. See CatFACS.com and Paulekman.com for descriptions and visual presentations of these actions, as well as Humphrey et al. (submitted).

Code Name	Facial Action Unit	Description of Code
Cat Half Blink	AU 147	One of the eyelids (upper or lower) moves towards the other without ever closing the eye. It can occur in only one eye. It can occur in a succession of movements or one movement only.
Cat Eye Closure	AU 143	The upper and lower eyelids move towards each other and cover the eye completely. The eye has to remain closed for more than half a second. It can occur in only one eye.

Cat Eye Narrowing		The upper and lower eyelids are held half closed. This is a prolonged version of AU147.
Cat Look away		When the cat distinctly moves their gaze and head away from the experimenter (left or right). Ends when the cat's head and gaze returns to face the experimenter.
Cat Eye Closures due to Movement		When a cat closes its eyes due to rubbing against a surface, scratching, yawning or any other movement that would naturally cause the eyes to narrow or close.
Human Eye Closure	AU 43	The upper and lower eyelids move towards each other and cover the eye completely. The eye has to remain closed for more than half a second.

| Human Eye Narrowing | The upper and lower eyelids are held half closed. This is a prolonged version of AU42 – Slit. |
| Human Look away | When the experimenter begins to turn their head away from the position of the cat. This ends when the experimenter's head returns to face the cat. (Performed only in SBB trials). |

Statistical Analysis

Data consisted of the rates at which cats made individual eye movements (half blink (a), eye closure (b) and eye narrowing (c)) and looking away behaviour in each trial type. Cat's individual eye movements were also summed (a + b + c) to create a total cat eye movement score. All analyses were conducted using IBM SPSS Statistics 24 software. Data were assessed to see if they met parametric assumptions, and parametric and non-parametric tests were chosen accordingly. All of the analyses in this study used two-tailed tests. Non-parametric Wilcoxon tests were used to investigate differences in the rates of eye narrowing movements and looking away behaviour by cats between the two trial types (SSB and SBB), and Mann Whitney U tests were used to examine differences

between directional biases (left and right paw-preference) or lateralisation (paw-preferent and ambi-lateral cats).

Synchrony between the cat and the experimenter during the slow blink interactions was calculated using cross-correlations (Feldman, 2007). The data was binned into 2-second intervals then cross-correlation functions (CCFs) were produced by analysing the associations between the two series (experimenter and cat) at different time lags for each trial. The maximum number of lags we used in this analysis was 5; this represents a maximum 10-second total lag time (5 x 2 seconds) between the onset of the experimenter and cat's eye movements. To assess whether cat and experimenter eye movements were synchronised, and potentially communicative in nature, synchronous coherence was calculated for both types of slow blink trials (SSB and SBB). We adopted Feldman's (2007) definition of coherence, by selecting the largest cross-correlation coefficient for each dyad, which shows the strength of the correlation between the two time series at any time lag in that interaction. An independent samples T-test and Mann-Whitney test were then used to examine the differences in synchrony between the paw-preferent and ambi-lateral cats for the SSB and the SBB conditions.

Ethics

This research adheres to the Association for the Study of Animal Behaviour Guidelines for the Use of Animals (Animal Behaviour, 2006, 71, 245–253) and all experimental protocols were approved by the University of Sussex Ethical Review Committee (ERC), reference number: Non-ASPA – Nov2013. Consent for participation was gained from cat owners and no participants were under the age of 18.

Results

No significant differences were found in the rates of eye closure, eye narrowing, half blinking, total eye movements or look away behaviour between left and right paw-preferent cats across both trial types, thus all data from all paw-preferent cats are pooled for further analysis (Eye closure: $U = 7.00$, $p = 0.87$; Eye narrowing: $U = 6.00$, $p = 0.66$; Half blinks: $U = 7.00$, $p = 0.88$; Total eye movements: $U = 7.00$, $p = 0.88$; Look away: $U = 3.00$, $p = 0.18$).

Slow Blink and Lateralisation

SBB condition. Paw-preferent cats had significantly higher rates of half blinks and total eye movements compared to ambi-lateral cats (Half-blinks: $U = 11.00$, $p = 0.005$; Total eye movements: $U = 19.00$, $p = 0.04$; see Figure 1). There was no significant difference between the rates of eye closure and eye narrowing across the paw-preferent and ambi-lateral cats (Eye closure: $U = 38.00$, $p = 0.66$; Eye narrowing: $U = 34.50$, $p = 0.44$). No significant difference was found in the rate of look away behaviour between paw-preferent and ambi-lateral cats (Look Away: $U = 30.00$, $p = 0.27$).
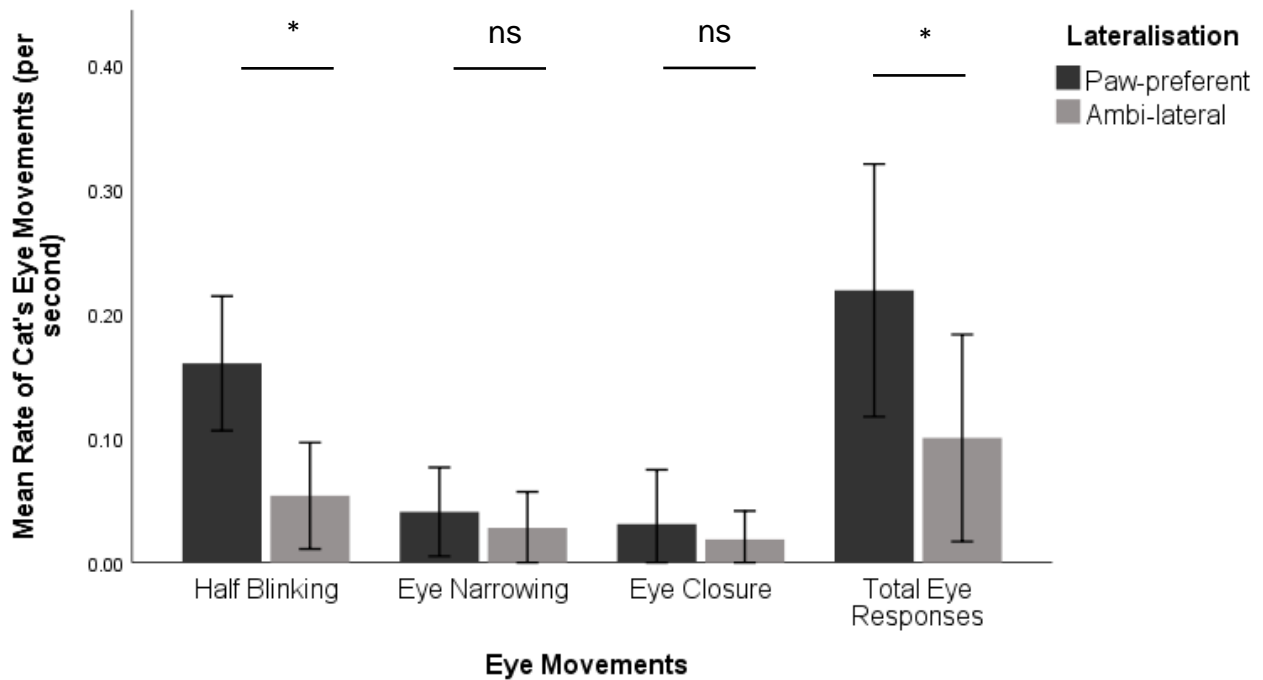
Figure 1. Mean rate of cats' eye movements (half blinks, eye narrowing, eye closure and total eye movements) during the SBB condition by lateralisation type. Error bars represent 95% Confidence Intervals.

SSB condition. The rates of total eye movements between paw-preferent and ambi-lateral cats did not significantly differ (U = 32.00, p = 0.35). There was also no significant difference between the rates of half-blinks, eye closures or eye narrowing in paw-preferent versus ambi-lateral cats (Half-blinks: U = 30.00, p = 0.27; Eye closure: U = 39.00, p = 0.72; Eye narrowing: U = 40.00, p = 0.78). Finally, there was no significant difference between the rates of look away behaviour of the paw-preferent versus ambi-lateral cats (U = 35.00, p = 0.49).

Table 2. Mean rates (per second) ± Standard deviations for subjects' eye movements and looking away behaviour across conditions.

	Half Blinks	Eye Narrowing	Eye Closure	Total Movements	Look Away
Lateralised Subjects					
Left Preferent	0.13 ± 0.04	0.03 ± 0.03	0.04 ± 0.07	0.20 ± 0.14	0.10 ± 0.04
Right Preferent	0.12 ± 0.06	0.04 ± 0.02	0.02 ± 0.02	0.17 ± 0.06	0.06 ± 0.02
SBB condition					
Paw-preferent	**0.16 ± 0.07**	0.04 ± 0.04	003 ± 0.05	**0.22 ± 0.12**	0.09 ± 0.05
Ambi-lateral	**0.05 ± 0.06**	0.03 ± 0.04	0.02 ± 0.03	**0.10 ± 0.12**	0.07 ± 0.05
SSB Condition					
Paw-preferent	0.09 ± 0.06	0.02 ± 0.03	0.02 ± 0.04	0.14 ± 0.10	0.06 ± 0.04
Ambi-lateral	0.06 ± 0.06	0.03 ± 0.04	0.03 ± 0.06	0.12 ± 0.15	0.08 ± 0.04

Synchronous Coherence and Lateralisation

SBB condition. No significant difference was found in the degree of synchrony between the ambi-lateral and paw-preferent cats (paw-preferent: M = 0.56 ± 0.15 (SD), and ambi-lateral: M = 0.40 ± 0.27 (SD), U = 31.00, p = 0.28).

SSB condition. Paw-preferent cats were significantly more synchronised with the experimenter in this condition than the ambi-lateral cats (paw-preferent: M = 0.61 ± 0.16 (SD); ambi-lateral: M = 0.43 ± 0.23 (SD); $t_{1,17}$ = 1.96, p = 0.044).

Discussion

Our results produce two new findings which suggest that lateralisation is related to cats' slow blink responses. Firstly, cats categorised as paw-preferent on a food puzzle task delivered a higher rate of eye responses in the slow blink condition with breaks in eye contact compared to cats who did not present a lateral paw bias. Secondly, the slow blink sequences of paw-preferent cats were more synchronised with the experimenter's slow blinks than the ambi-lateral cats, in trials that did not involve a break. Our study not only supports and extends previous research regarding the contribution of lateralisation to emotional functioning in cats (McDowell et al., 2016), but also corroborates our previous findings on cat-human slow blinking as emotionally relevant behaviour (Humphrey et al., submitted).

Left and right paw-preferent cats did not differ significantly in their eye responses to the slow blink interactions in the current study. This is consistent with the hypothesis that lateralisation itself may be more important than directional asymmetries (McDowell, Hepper, Wells & Dempster, 2016; McGrew & Marchant, 1999; Vallortigara & Rogers, 2005). Vallortigara and Rogers (2005) argue that the selective advantages to population-level directional asymmetries (e.g. a species being predominantly right-handed) may be due to predation pressure on individuals to align their asymmetries with others in their group. The authors give the example of escape responses displayed in schooling fish, where groups of fish who collectively flee to the right after detecting a predator will increase their individual fitness. Since cats are facultatively social and lone hunters, the direction of paw used in reaching for food is unlikely to have undergone such social selection, although future studies should confirm this.

In our study cats who were strongly lateralised were more in sync with the experimenters during the SSB trials. Such enhanced synergy during cat-human interactions by paw-preferent cats may explain why owners report strongly paw-preferent cats as being more affectionate, friendly and obedient than ambi-lateral cats (McDowell, Hepper, Wells & Dempster, 2016). Behavioural synchrony between human social partners similarly increases interpersonal affiliation (Hove & Risen, 2009). In addition, prospective guide dogs with a strong paw-preference are more confident and relaxed than ambi-lateral dogs (Batt, Batt, Baguley & McGreevy, 2009). Rather interestingly, paw-preferent cats during the SBB condition were not significantly more in sync with the experimenters. Here, the effect of lateralisation on cat-human behavioural synchrony may have been interrupted by the use of breaks in the SBB condition, where synchronised slow blinking between the experimenter and the cat may not have had the opportunity to be established before the interaction was 'broken off'.

The use of frequent breaks in eye contact appears to be important for positive cat-human interactions. For example, cats are more likely to reduce their proximity to unfamiliar men and look at them for longer when the men had looked away after initial eye contact with the cat (Goodwin and Bradshaw, 2007). Paw-preferent cats in our study displayed an increased rate of half blinks and total eye movements in the trials involving a break in eye contact by the experimenter in comparison with ambi-lateral cats, an effect which did not appear in the Standard Slow Blink trials. This suggests that such breaks in eye contact may be an essential part of cats' responses to slow blinking, and may more generally facilitate communication with cats. Further research should aim to explore the effects of incorporating respites during human-cat interactions, which may help alleviate feline stress in veterinary and shelter environments.

The results of the current study offer further evidence of the potential emotional significance of human-initiated slow blink interactions for cats, and provide some insight into the underlying cognitive mechanisms related to such interactions. Our findings also add to our understanding of which movements are important during slow blink interactions. Future research should aim to explore the use of breaks in eye contact in other contexts with cats, as this could be a useful technique for owners or veterinary staff to optimise communication with their cat, as well as promote more positive cat-human interactions.

References

Batt, L. S., Batt, M. S., Baguley, J. A., & McGreevy, P. D. (2009). The relationships between motor lateralization, salivary cortisol concentrations and behavior in dogs. *Journal of Veterinary Behavior: Clinical Applications and Research*. https://doi.org/10.1016/j.jveb.2009.02.001

Boissy, A., Manteuffel, G., Jensen, M. B., Moe, R. O., Spruijt, B., Keeling, L. J., … Aubert, A. (2007). Assessment of positive emotions in animals to improve their welfare. *Physiology and Behavior*. https://doi.org/10.1016/j.physbeh.2007.02.003

Branson, N. J., & Rogers, L. J. (2006). Relationship between paw preference strength and noise phobia in *Canis familiaris*. *Journal of Comparative Psychology*. https://doi.org/10.1037/0735-7036.120.3.176

Caeiro, C. C., Burrows, A. M., & Waller, B. M. (2017). Development and application of CatFACS: Are human cat adopters influenced by cat facial expressions? *Applied Animal Behaviour Science*. https://doi.org/10.1016/j.applanim.2017.01.005

Feldman, R. (2007). On the origins of background emotions: From affect synchrony to symbolic expression. *Emotion*. https://doi.org/10.1037/1528-3542.7.3.601

Ghirlanda, S., & Vallortigara, G. (2004). The evolution of brain lateralization: A game-theoretical analysis of population structure. *Proceedings of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rspb.2003.2669

Goodwin, D., & Bradshaw, J. (1997). Gaze and mutual gaze: its importance in cat/human and cat/cat interactions. *International Society of Anthrozoology*. Boston.

Hove, M. J., & Risen, J. L. (2009). It's all in the timing: Interpersonal synchrony increases affiliation. *Social Cognition*. https://doi.org/10.1521/soco.2009.27.6.949

Humphrey, T., Proops, L., Forman, J., Spooner, R., Wathan, J., & McComb, K. (n.d.). *The cat smile?: The role of cat eye narrowing movements in cat-human communication* (unpublished manuscript).

Humphrey, T., Stringer, F., Proops, L., & McComb, K. (n.d.). *Shelter cats that slow blink are adopted more quickly* (unpublished manuscript).

McDowell, L. J., Wells, D. L., Hepper, P. G., & Dempster, M. (2016). Lateral bias and temperament in the domestic cat (*Felis silvestris*). *Journal of Comparative Psychology*. https://doi.org/10.1037/com0000030

McGrew, W. C., & Marchant, L. F. (1999). Laterality of hand use pays off in foraging success for wild chimpanzees. *Primates*. https://doi.org/10.1007/BF02557586

Pet Food Manufacturing Association (2016). *A Brave New World 2017. PFMA Annual Report & Brexit Manifesto.* Retrieved 19/04/2017 from http://www.pfma.org.uk/_assets/docs/annual-reports/PFMA-Annual-Report-2016.pdf

Pike, A. V. L., & Maitland, D. P. (1997). Paw preferences in cats (*Felis silvestris catus*) living in a household environment. *Behavioural Processes*. https://doi.org/10.1016/S0376-6357(96)00758-9

Quaranta, A., Siniscalchi, M., & Vallortigara, G. (2007). Asymmetric tail-wagging responses by dogs to different emotive stimuli. *Current Biology*. https://doi.org/10.1016/j.cub.2007.02.008

Racca, A., Guo, K., Meints, K., & Mills, D. S. (2012). Reading faces: Differential lateral gaze bias in processing canine and human facial expressions in dogs and 4-year-old children. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0036076

Seligman, M. E. P., & Csikszentmihalyi, M. (2014). Positive psychology: An introduction. *Flow and the Foundations of Positive Psychology: The Collected Works of Mihaly Csikszentmihalyi*. https://doi.org/10.1007/978-94-017-9088-8_18

Smith, A. V., Proops, L., Grounds, K., Wathan, J., & McComb, K. (2016). Functionally relevant responses to human facial expressions of emotion in the domestic horse (*Equus caballus*). *Biology Letters*. https://doi.org/10.1098/rsbl.2015.0907

Vallortigara, G., & Rogers, L. J. (2005). Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences*. https://doi.org/10.1017/S0140525X05000105

Wells, D. L. (2003). Lateralised behaviour in the domestic dog, *Canis familiaris*. *Behavioural Processes*. https://doi.org/10.1016/S0376-6357(02)00161-4

Westergaard, G. C., Chavanne, T. J., Lussier, I. D., Houser, L., Cleveland, A., Suomi, S. J., & Higley, J. D. (2003). Left-handedness is correlated with CSF monoamine metabolite and plasma cortisol concentrations, and with impaired sociality, in free-ranging adult male rhesus macaques (*Macaca mulatta*). *Laterality*. https://doi.org/10.1080/713754484

Article IV: Comparative expressions in a 'positive' emotional state in cats, dogs and horses

Humphrey, T., Proops, L., & McComb, K.

Abstract

There are multiple mechanisms that contribute to the experience of emotion, including behavioural, physiological, neural and cognitive components. Observations of singular components therefore inevitably provide a limited view of emotional experiences. Understanding fully how animals express emotions is fundamental to reliable and valid evaluations of welfare. We investigated both the behavioural and physiological responses of three companion species (cats, dogs, and horses) during a putatively positive human-animal interaction. We measured eye narrowing movements and eye surface temperature in a baseline compared to a stroking condition where the subjects were stroked by either their owner or an experimenter. Eye temperatures of cats and dogs, but not horses, significantly increased in the stroking condition compared to baseline, and could reflect positive emotional fever. Thus, we suggest that a positive emotional response can potentially be measured by eye temperature. During stroking, differing patterns of eye narrowing movements were observed for dogs and horses, with horses displaying a trend towards a greater number of and longer half blinks and dogs displaying faster eye closures compared to the baseline. In addition, our results demonstrate an association between eye narrowing movements and eye temperature. However, the direction of this relationship was species-dependent. These findings highlight the importance of using species-specific behavioural indicators of emotion in

animal welfare assessments, and the complexity of using thermography to assess emotional valence or arousal across species at this early stage in thermography research in animals.

Introduction

Emotions are considered to vary on two intrinsic axes; emotional valence (positive or negative), and arousal level (degree of excitation; Mendl, Burman, & Paul, 2010). Understanding how animals experience emotions is key to improving animal welfare (Proctor, 2012), and it is now widely recognised that the experience of positive emotions is an important indicator of good welfare (Boissy et al., 2007; Mellor, 2012). However, the experience of emotions is a multi-component process, involving behavioural expressions, physiological changes, and subjective feelings (Scherer, 2005). Thus, when measuring an individual's emotional response it is important to look at various components in order to understand the experience in more detail. Emotional responses produce corresponding physiological changes that can be objectively measured, which is of particular importance when attempting to assess emotions in non-human animals, given their inability to directly communicate subjective states with us. However many physiological measures, such as heart rate or skin conductance measurements, involve physical contact with the individual which may disrupt how they experience emotional events. Physiological responses are also particularly sensitive to changes in arousal, and may reflect these changes more readily than changes in valence. This is particularly problematic in the study of positive emotions. Thermal imaging provides a non-invasive method of capturing such experiences, allowing us to naturally observe how animals respond to emotional states.

Despite the relevance of thermal imaging for the study of positive emotions, this method has predominantly been used to investigate negative states, in particular those induced by stress (e.g. in primates, Kano, Hirata, Deschner, Behringer, & Call, 2016; Kuraoka & Nakamura, 2011; Nakayama, Goto, Kuraoka, & Nakamura, 2005; in birds, Ikkatai & Watanabe, 2015; Jerem, Herborn, McCafferty, McKeegan, & Nager, 2015; in cats, Mazzotti & Boere, 2009; in horses, Valera et al., 2012; in dogs, Travain et al., 2015; and in rabbits, Ludwig, Gargano, Luzi, Carenzi, & Verga, 2007). For example, Ikkatai & Watanabe (2015) investigated the eye temperature responses of laboratory-housed budgerigars under a stressful handling condition. The researchers found that eye temperature increased in response to stress and that eye surface temperature correlated with core body temperature. Likewise, the temperature of the nasal region in monkeys decreases during the presentation of a threat (Kuraoka & Nakamura, 2011; Nakayama et al., 2005). Physical and emotional stress in animals activates the 'fight or flight' response. This response causes a temporary rise in core body temperature, and a corresponding reduction in temperature at the extremities, as blood is directed toward the muscles and peripheral vasoconstriction occurs, preparing the body for action.

To date, only three studies have examined the thermal responses of animals in positive emotional states compared to an emotionally neutral state (Moe, Stubsjøen, Bohlin, Flø, & Bakken, 2012; Proctor & Carder, 2015b; Travain et al., 2016). Moe et al. (2012) found that comb surface temperature in laying hens decreased during the anticipation and consumption of a food reward. In dogs, Travain et al. (2016) found that eye temperature significantly increased when the dogs received positive stimulation through food treats. These results show the same thermal responses as negative stimuli, which suggests that changes in peripheral and body temperatures may be due to a sensitivity to high arousal contexts in comparison to the low arousal, control conditions used in these

studies, potentially masking the effects of emotional valence. Research which controls

arousal state to explore the thermal changes associated with positive valence is

unfortunately limited. Proctor & Carder (2015b) used stroking with the aim of inducing

a low arousal, positive emotion in cows and found a decrease in nasal temperature.

However, although the cows were habituated to human contact and the study

procedures, the extent to which the cows found such stimuli pleasant is uncertain,

particularly given that the authors reported the cows walking away or being distracted

during the habituation period. It is also possible that the stroking produced a positive,

high arousal state, rather than the intended low arousal state. Nasal temperature can also

be effected by nose licking or drinking by the individual. The researchers did account

for this by omitting temperature readings within 30 seconds of such activity (Proctor &

Carder, 2015b), yet residual temperature changes may still have occurred. Eye

temperature therefore may be a better measure of thermal responses to emotional stimuli

as it is correlated with core body temperature. No research that we are aware of has

investigated the relationship between eye temperature and a low arousal, positive

emotional state in animals.

Another useful measure for inferring emotions is through facial expressions (Ekman,

1993; Tate, Fischer, Leigh, & Kendrick, 2006). Facial expressions of emotion are

considered to be universal in humans (Ekman, 1997) and the antecedents of such

muscle movements are found across mammalian species (Waller & Micheletta, 2013).

As such, researchers have aimed to explore the facial actions which correlate with

emotions in animals (Bennett et al., 2017; Parr, Waller, Vick, & Bard, 2007). Measures,

such as the Facial Action Coding System (FACS) which is based on the underlying

facial musculature, have been created in a range of species to aid such investigations by

enabling objective observations to be made (Caeiro, Burrows, & Waller, 2017; Caeiro,

Waller, Zimmermann, Burrows, & Davila-Ross, 2013; Parr, Waller, Burrows, Gothard, & Vick, 2010; Vick, Waller, Parr, Smith-Pasqualini, & Bard, 2006; Waller, Lembeck, Kuchenbuch, Burrows, & Liebal, 2012; Wathan, Burrows, Waller, & McComb, 2015). However, finding consistent specific facial indicators of emotion across species has proven less straightforward. For example, previous research on farm animals shows that relaxed ear postures are associated with some positive emotional states (Proctor & Carder, 2014; Reefmann, Bütikofer Kaszàs, Wechsler, & Gygax, 2009; Reefmann, Wechsler, & Gygax, 2009), yet in horses alert, forward facing ears are seen in the high arousal context of positive anticipation (Wathan, Proops, Grounds, & McComb, 2016). This highlights again how differences in arousal, as well as valence, are important to consider when exploring the facial actions that correlate with emotion and the extent to which specific facial actions are shown to communicate emotions comparably across species. This line of research has relevance for both the scientific understanding of evolutionary continuities in facial expression, as well as for establishing tools to review animal welfare.

Recent studies on dogs, horses and, to a lesser extent, cats collectively indicate that these species provide opportunities for understanding correlates of emotion. These three species are able to discriminate between human emotion faces (Galvan & Vonk, 2016; Müller et al., 2015; Smith et al., 2016), and respond to them in appropriate ways (dogs: Merola, Prato-Previde, Lazzaroni, & Marshall-Pescini, 2014; horses: Smith et al., 2016). Dogs and horses also discriminate between the emotions of conspecific faces (Albuquerque et al., 2016; Wathan et al., 2016). Furthermore, humans appear to be accurate in the identification of canine facial expressions of emotion, irrespective of whether they own dogs (Schirmer, Seow, & Penney, 2013). These studies suggest possible continuities in the expression of emotions between humans and companion

animals. Indeed, the key feature in the human Duchenne smile (the genuine smile) is narrowing of the eyes, which discriminates it from other forms of smiling (Duchenne, 1862). Positive emotional facial expressions in horses include a similar decrease in the size of the eye aperture (Hintze et al., 2016). In addition, slow blinking in cats involves a sequence of short and longer eye narrowing movements and appears to be a form of positive emotional communication between cats and humans (Humphrey et al., submitted). Relaxed narrowing of the eye aperture could be an important indicator of positive emotions across species (as opposed to, and distinct from, the orbital tightening observed in negative states and documented in Grimace Scales of pain devised for a range of mammalian species where other muscles around the eyelid are activated (horses: Dalla Costa et al., 2014; sheep: Häger et al., 2017; mice: Langford et al., 2010; rabbits: Leach, 2012; rats: Sotocinal et al., 2011; and pigs: Viscardi, Hunniford, Lawlis, Leach, & Turner, 2017).

In the current study, we aim to test the behavioural and physiological responses of three model companion species (cats, dogs and horses) to a positively valenced emotional state. We recorded eye temperature and eye narrowing movements before, during and after a stroking stimulus. Stroking is a prevalent positive stimulus in human-animal interactions among companion animals, which has known emotional and biological benefits, such as reduced heart rate (cats: Gourkow, Hamon, & Phillips, 2014; horses: Hama, Yogo, & Matsuyama, 1996; dogs: Handlin et al., 2011). Gentle stroking also helps alleviate anxiety, as shelter cats who receive a stroking intervention four times a day over a period of 10 days show higher indicators of contentment and marked health benefits (Gourkow et al., 2014) .

The existing literature makes it difficult to predict the direction of changes in eye temperature in response to stroking sessions, since the evidence focuses on different

species, stimuli and regions of interest (ROI). However, we predicted that there would be comparable changes in eye temperature across all three species. In addition, we predicted that such eye temperature changes would correlate with eye narrowing movements in the study species.

Methods

Subjects

26 domestic cats (N= 16 males and 10 females), 25 horses (N= 17 males and 8 females), and 26 dogs (N= 18 males and 8 females) were included in this study. Horses were recruited from two riding schools in Sussex. The cats were kept as pets in thirteen different households, and had both in- and outdoor access. The dogs were also kept as pets in 16 different households. Cats ranged in age from $1 – 18$ years (M = 7.76 ± 4.38 (S.D)). Dogs' ages ranged from 5 months – 11 years (M = 5.44 ± 3.36). Horses ranged in age from $7 – 29$ years (M = 16.23 ± 5.93). To be included in the study, all of the subjects were required to be comfortable around unfamiliar humans, specifically the horses who needed to be comfortable with unfamiliar handlers. One dog and 1 cat were excluded because of technical issues with the camera equipment, and 2 dogs, 3 cats and 3 horses were excluded because they did not settle during the trials (i.e. were moving/walking).

Procedure

Before the start of the trials, an acclimatisation period took place where subjects were kept indoors or in stables for at least 5 minutes prior to testing. This allowed the animal to adjust to its environment and relax. During the acclimatisation period the experimenter asked cat or dog owners demographic questions about their pets. For the

horses, demographic data was collected separately from testing days. After acclimatisation, a functional infrared thermal imaging (fITI) camera (T450sc, FLIR) and a video camera (Panasonic HC-X920) were placed on tripods and recorded the faces of the animals at a distance of approximately 1m from the subject. Each subject took part in two successive 5-min sessions: (1) a baseline condition, during which no contact was made with the subject; (2) a stroking condition, where the animal was stroked in their preferred areas for 2-min then recorded for 3-min post-stroking to measure any delayed responses.

All individuals were filmed in their home environment. Stroking involved full hand contact across the body (in cats and dogs) and/or gentle scratching by humans. Cats and dogs were stroked by their owners, who were instructed to focus on a known preferred area whilst avoiding contact with the facial area. Cats and dogs were not restrained at any point throughout the acclimatisation period and trials, and therefore were able to move. If subjects left the testing area during trials, the trial was terminated. Cats and dogs were not fed during the trials. Horses were stroked by one of the experimenters, who focused on the preferred area outlined in Figure 1 (Feh & de Mazierès, 1993), again avoiding the facial area. Horses wore a head collar and experimenters loosely held a lead rope. As with the other subjects, horses were able to pull away from the testing area, terminating the trial. Horses had access to hay as part of their usual stable environment during the trials. Humans who stroked the subjects were present at all times. As all of the horses used in the present study were from riding schools, they were accustomed to being around unfamiliar humans. Ambient temperature, humidity, and light levels of the rooms or stables were also recorded.
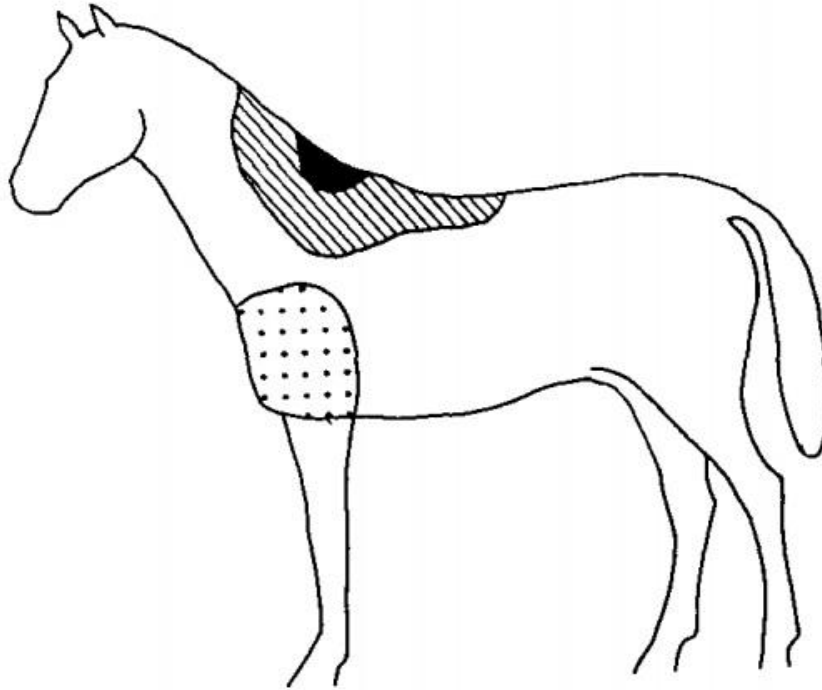
Figure 1. Preferred grooming sites of horses. The area in black indicates the most preferred grooming site, with the striped area indicating a less preferred grooming site. The dotted area indicates a non-preferred grooming site.

Note. From "Grooming at a preferred site reduces heart rate in horses." by C., Feh & J., De Mazieres, *in Animal Behaviour,* 1993. Copyright 1993 by Elsevier Ltd.

Thermal Coding

Analysis of the thermal data was conducted using FLIR ResearchIR Software (www.flir.co.uk). Eye temperatures were measured at 30 s (+/- 10 s) intervals throughout both parts of the session using ROI polygons covering the eye aperture of the subject (see Figure 2 for example images). Within an interval (including +/- 10 s), if a frame was unable to capture a stable image of the ROI then values would be omitted for that time point. In order to ensure that we acquired reliable temperature values, we measured the maximum temperature in the eye ROI for all species. This accounted for movement of the subjects between frames that an average temperature reading of the

ROI would obscure (Kano et al., 2016), and ensured that temperature readings were from the eye rather than the skin around the eye. We also ensured that the coordinates of the maximum temperature readings within an ROI of successive frames did not vary significantly and that temperature readings did not differ by over 1°C between 30 s intervals, and if this occurred a value of zero would be reported. Finally, an average temperature from the interval readings of each trial was calculated to give a temperature value for each subject per condition.

Behavioural Coding

All videos were coded using the species-relevant Facial Action Coding System manuals (FACS; (Cat: Caeiro, Burrows, & Waller, 2017; Dog: Waller et al., 2013; Horse: Wathan, Burrows, Waller, & McComb, 2015). FACS is an objective coding system used to measure facial movements, based on underlying musculature. FACS was originally developed for humans, however a FACS manual has now been produced for each species in the current study. A qualified Cat-, Dog-, and Equi-FACS coder (TH) coded the frequency and duration of eye narrowing movements (half blink: CatFACs AU 147 and EquiFACs AU47; eye closures: AU 143). An additional code, 'eye narrowing' was included across all three species to account for instances where the eyelid was held partially closed for at least 2 frames (0.08 seconds) rather than returning to the neutral eyelid position in a continuous movement. Behavioural responses during the last two minutes of the baseline condition and the first two minutes of the stroking trials were coded using Sportscode Gamebreaker Plus (www.sportstec.com) software. Blind coding was unavailable for the experiment due to the set order and visual nature of the conditions.
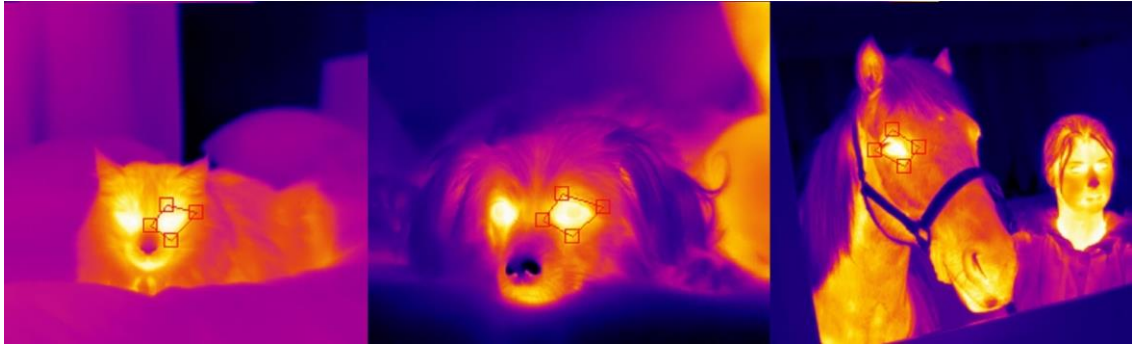
Figure 2. Thermograms displaying example polygons used to measure temperatures of the ROI. Left – right: cat, dog and horse in the neutral condition.

Statistical Analysis

Eye temperature changes between the baseline and the stroking condition were examined using Wilcoxon tests for each species. The frequencies and durations of instances where dogs, cats and horses produced specific eye narrowing movements (half blink, eye narrowing, and eye closure) were also analysed. The three specific eye movements were summed to form a total eye movements composite variable. Non-parametric Wilcoxon tests were used to analyse the differences in the frequency and durations of specific eye movements and total eye movements between the baseline condition and the stroking condition for each species type. Finally, Spearman's rho correlations were used to analyse any relationships that may exist between the physiological and behavioral measures (eye temperature and eye narrowing movements) in the baseline and stroking conditions. All analyses used two-tailed tests.

Results

Thermal analysis

In the cats and dogs, a significant increase in eye temperature was found between the baseline condition (Cats: M = 36.47 ± 0.64 (SD); Dogs: M = 36.89 ± 0.55 (SD)) and the stroking condition (Cats: M = 36.68 ± 0.62 (SD); Dogs: M = 37.05 ± 0.44 (SD)), Cats: Z = 3.01, p = 0.003 and Dogs: Z = 3.25, p = 0.001. There was no significant difference in eye temperature between the baseline condition (M = 35.12 ± 0.65 (SD)) and stroking condition (M = 35.19 ± 0.61 (SD)) in the horses, Z = -0.76, p = 0.45 (see Figure 3; note that changes are minor as body temperature remains relatively stable so small fluctuations are pronounced).

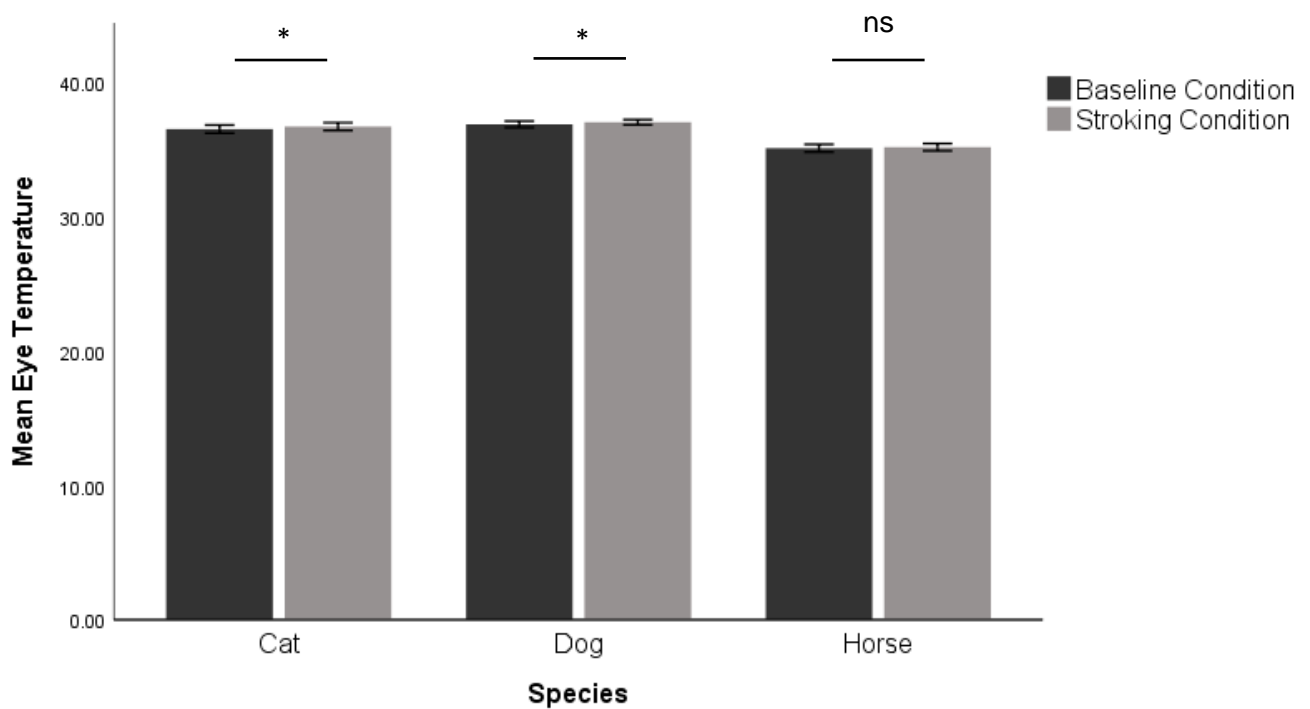*Figure 3. Mean eye temperature of cats, dogs and horses in the baseline versus stroking conditions. Error bars represent 95% confidence intervals.* *p < 0.05.
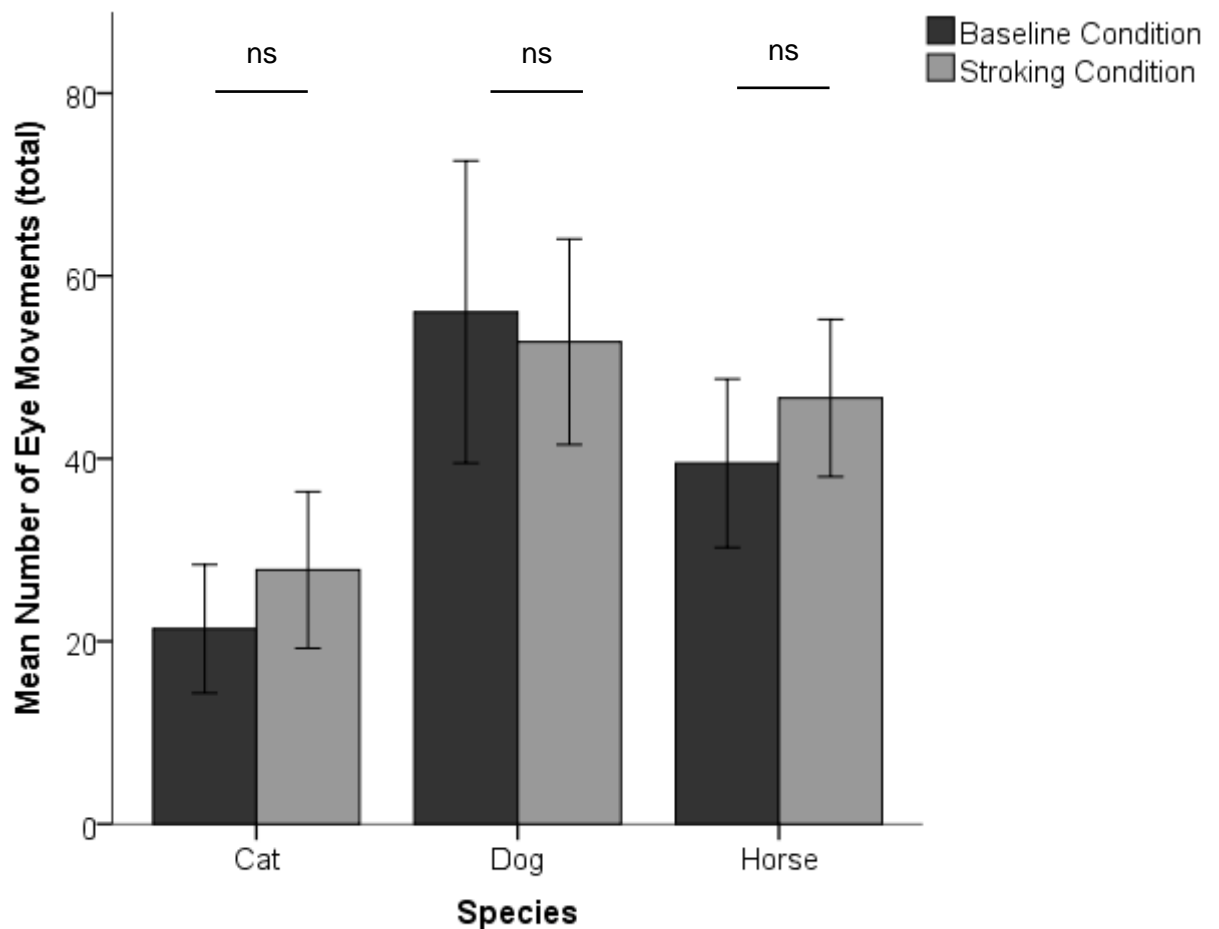
Behavioural analysis

Cats: There were no significant differences in the frequencies of half blinks, eye narrowing, eye closures or total eye movements between the baseline condition (Half blink: M = 9.55 ± 9.63 (SD); Eye narrowing: M = 8.46 ± 7.08 (SD); Eye closure: M = 3.36 ± 3.58 (SD); Total eye movements: M = 21.36 ± 15.89 (SD)) and the stroking condition (Half blink: M = 9.68 ± 8.00 (SD), Z = -0.37, p = 0.72; Eye narrowing: M = 13.77 ± 11.75 (SD), Z = -1.49, p = 0.14; Eye closure: M = 4.36 ± 5.88 (SD), Z = -0.84, p = 0.40; Total eye narrowing: M = 27.82 ± 19.32 (SD), Z = -1.30, p = 0.19). There were also no significant differences in the durations of cat's half blinks, eye narrowing, eye closures and total eye movements between the baseline condition (Half blink: M = 7.07 ± 7.91 (SD); Eye narrowing: M = 22.35 ± 21.26 (SD); Eye closure: M = 27.34 ± 33.64 (SD); Total eye movements: M = 56.75 ± 36.92 (SD)) and the stroking condition (Half blink: M = 5.77 ± 6.76 (SD), Z = -0.37, p = 0.71; Eye narrowing: M = 28.53 ± 25.93 (SD), Z = -1.25, p = 0.21; Eye closure: M = 16.07 ± 19.76 (SD), Z = -1.42, p = 0.16; Total eye movements: M = 50.37 ± 34.94 (SD), Z = -0.57, p = 0.57).

Dogs: The difference in the frequency of dogs' eye closures across conditions approached significance, but here with a trend towards more eye closures occurring in the baseline condition (M = 2.65 ± 3.98 (SD)) compared to the stroking condition (M = 1.04 ± 2.03 (SD), Z = -1.82, p = 0.07). There were no significant differences in the frequencies of dogs' half blinks, eye narrowing and total eye movements between the baseline condition (Half blink: M = 34.91 ± 28.70 (SD); Eye narrowing: M = 18.48 ± 16.05 (SD); Total eye movements: M = 56.04 ± 38.28 (SD)) and the stroking condition (Half blink: M = 36.96 ± 22.00 (SD), Z = -1.00, p = 0.32; Eye narrowing: M = 14.78 ± 12.14 (SD), Z = -1.33, p = 0.19; Total eye movements: M = 52.78 ± 26.04 (SD), Z = -0.61, p = 0.54). Dogs closed their eyes for significantly longer in the baseline condition

(M = 15.27 ± 26.23 (SD)) compared to the stroking condition (M = 2.71 ± 7.43 (SD), Z = -2.56, p = 0.01). The durations of total eye movements also approached significance in dogs, with a trend towards longer total eye movements in the baseline condition (M = 45.64 ± 31. 74 (SD)) than the stroking condition (M = 32.69 ± 24.67 (SD), Z = -1.83, p = 0.07). There were no significant differences in duration of half blinks and eye narrowing between the baseline condition (Half blink: M = 10.98 ± 8.38 (SD); Eye narrowing: M = 18.48 ± 16.05 (SD)) and the stroking condition (Half blink: M = 11.11 ± 8.20 (SD), Z = -0.15, p = 0.88; Eye narrowing: M = 18.88 ± 19.81 (SD), Z = -0.26, p = 0.79).

Horses: The frequency of the horses' half blinks and total eye movements approached significance, with a trend towards a greater number of eye movements occurring in the stroking condition (Half blink: M = 42.57 ± 19.28 (SD); Total eye movements: M = 47.52 ± 19.44 (SD)) compared to the baseline condition (Half blink: M = 31.33 ± 19.58 (SD), Z = -1.90, p = 0.06; Total eye movements: M = 37.71 ± 19.52 (SD), Z = -1.76, p = 0.08). There were no significant differences in the frequency of horses' eye narrowing or eye closures between the baseline condition (Eye narrowing: M = 5.91 ± 7.31 (SD); Eye closure: M = 0.48 ± 1.17 (SD)) and the stroking condition (Eye narrowing: M = 4.86 ± 5.70 (SD), Z = -0.85, p = 0.39; Eye closure: M = 0.10 ± 0.44 (SD), Z = -1.28, p = 0.20). The duration that horses half blinked approached significance, with longer half blinking in the stroking condition (M = 9.58 ± 5.01 (SD)) compared to the baseline condition (M = 7.33 ± 3.82 (SD), Z = -1.72, p = 0.09). No significant difference was found for the duration of horses eye narrowing, eye closures or total eye movements between the baseline condition and the stroking condition (Eye narrowing: M = 6.90 ± 10.09 (SD), Z = -0.59, p = 0.55; Eye closure: M = 0.08 ± 0.38 (SD), Z = -1.36, p = 0.17; Total eye movements: M = 16.56 ± 9.96 (SD), Z = -0.71, p = 0.48).

Figure 4. Mean number of eye movements (total) of cats, dogs and horses in the baseline versus stroking conditions. Error bars represent 95% confidence intervals.

Association between physiological and behavioural measures

Cats: There were no significant correlations between eye temperature and the frequency of half blinks, eye narrowing, eye closure and total eye movements in the baseline condition (Half blink: $r = -0.18$, $p = 0.42$; Eye narrowing: $r = 0.22$, $p = 0.33$; Eye closure: $r = 0.22$, $p = 0.33$; Total eye movements: $r = 0.15$, $p = 0.50$). The correlations between the durations of eye closures and total eye movements with eye temperature in the baseline condition approached significance (Eye closure: $r = 0.37$, $p = 0.09$; Total eye movements: $r = 0.39$, $p = 0.07$). No significant correlations were found between the durations of half blinking or eye narrowing and eye temperature in the baseline

condition (Half blink: r = -0.13, p = 0.55; Eye narrowing: r = 0.15, p = 0.51). In the stroking condition, no significant correlations were found between the frequencies of half blinks, eye narrowing, eye closure or total eye movements with eye temperature (Half blink: r = 0.33, p = 0.14; Eye narrowing: r = 0.14, p = 0.53; Eye closure: r = -0.16, p = 0.48; Total eye movements: r = 0.21, p = 0.35). There was a significant positive correlation between the duration of half blinking and eye temperature in the stroking condition (r = 0.47, p = 0.03). Thus, as half blink duration increased, there was a rise in cats' eye temperature. The correlations between the durations of eye narrowing, eye closure or total eye movements and eye temperature in the stroking condition were not significant (Eye narrowing: r = 0.31, p = 0.16; Eye closure: r = -0.12, p = 0.63; Total eye movements: r = 0.21, p = 0.35).

Dogs; There were no significant correlations between the frequencies of half blinks, eye narrowing, eye closure or total eye movements and eye temperature in the baseline condition (Half blink: r = -0.33, p = 0.12; Eye narrowing: r = 0.05, p = 0.83; Eye closure: r = 0.27, p = 0.22; Total eye movements: r = -0.21, p = 0.34). There were also no significant correlations between the durations of half blinks, eye narrowing, eye closures or total eye movements and eye temperature in the baseline condition (Half blink: r = -0.19, p = 0.39; Eye narrowing: r = 0.15, p = 0.50; Eye closure: r = 0.34, p = 0.11; Total eye movements: r = 0.19, p = 0.40). In addition, during the stroking condition, no significant correlations were found between the frequencies of half blinks, eye narrowing, eye closure or total eye movements and eye temperature (Half blink: r = -0.27, p = 0.22; Eye narrowing: r = 0.13, p = 0.56; Eye closure: r = -0.10, p = 0.65; Total eye movements: r = -0.20, p = 0.35). The durations of half blinks, eye narrowing, eye closure or total eye movements were also not significantly correlated with eye temperature in the stroking condition (Half blink: r = -0.18, p = 0.42; Eye narrowing: r

= 0.24, p = 0.26; Eye closure: r = -0.17, p = 0.45; Total eye movements: r = 0.11, p = 0.62).

Horses: In the baseline condition, the correlation between the frequency of eye narrowing and eye temperature was positive and approached significance (r = 0.37, p = 0.095). There were no significant correlations between the frequencies of half blinking, eye closure or total eye movements and eye temperature in the baseline condition (Half blink: r = -0.09, p = 0.70; Eye closure: r = 0.02, p = 0.92; Total eye movements: r = -0.02, p = 0.93). The correlation between the duration of eye narrowing and eye temperature in the baseline condition was positive and approached significance (r = 0.39, p = 0.07). No significant correlations between the duration of half blinks, eye closure or total eye movements and eye temperature were found in the baseline condition (Half blink: r = -0.14, p = -.54; Eye closure: r = 0.03, p = 0.89; Total eye movements: r = 0.16, p = 0.49). However, in the stroking condition the frequency of half blinks negatively correlated with eye temperature (r = -0.50, p = 0.02). The frequency of total eye movements also negatively correlated with eye temperature in the stroking condition (r = -0.47, p = 0.03). Thus, the more half blinks and total eye movements that were produced by horses, the lower the temperature of their eyes. There were no significant correlations between the frequency of eye narrowing or eye closure and eye temperature in the stroking condition (Eye narrowing: r = 0.19, p = 0.40; Eye closure: r = 0.22, p = 0.32). The negative correlation between the duration of half blinks and eye temperature approached significance in the stroking condition (r = -0.41, p = 0.06). No significant correlations between the duration of eye narrowing, eye closure or total eye movements and eye temperature were found in the stroking condition (Eye narrowing: r = 0.22, p = 0.32; Eye closure: r = 0.22, p = 0.32; Total eye movements: r = 0.13, p = 0.55).

Discussion

Our comparative cross-species study examining the physiological and behavioural signals of a positive emotional state between cats, dogs and horses provides important new insights. The study demonstrated that cats and dogs show a similar increase in eye temperature in response to being stroked by their owner. However, the behavioural eye movements analysed in this study provided contrasting results in relation to species. Horses in the stroking condition tended to display more and longer eye movements. Cats, unexpectedly, did not produce significantly higher frequencies or durations of eye movements in the stroking condition, although the means were in the expected direction. However during the stroking condition, dogs showed a lower duration of eye closures and a trend toward shorter overall eye movements compared to the baseline condition. In addition, we demonstrated a coupling between the physiological and behavioural measures in the stroking condition in cats and horses, but the effects were in opposite directions. In the cats, longer half blinking was related to a higher eye temperature in the stroking condition, yet in horses, more half blinking and total eye movements were associated with a reduced eye temperature in the stroking condition. One explanation for this could be that the cats and horses in this study experienced different emotional states during the baseline condition and in response to stroking, specifically in regards to the level of arousal. Further studies could measure other physiological indicators of arousal in cats and horses to explore whether these domestic species experience human-initiated stroking in comparable ways.

Our study is the first to investigate how eye temperature varies during an apparently low arousal, positive emotional state. The cats' and dogs' eye temperatures increased in response to stroking. This rise in eye temperature may indicate emotional fever – a rise in core body temperature in response to an emotional stimulus, which has been

observed in a range of species (Andrews, 1983; Borsini, Lecci, Volterra, & Meli, 1989; Cabanac, 2005; Cabanac & Aizawa, 2000). Typically, emotional fever has been described during unpleasant or stressful events. However, Moe et al. (2012) suggests that emotional fever may also occur during positively valenced states, and therefore may be more indicative of emotional arousal rather than valence. This argument supports current evidence of thermal responses to positive emotions, which show a drop in peripheral temperature (Moe et al., 2012; Proctor & Carder, 2015b) and a rise in core body temperature in positive contexts (Travain et al., 2016). Furthermore, it is possible that stroking, relative to a relaxed, baseline condition, may have elicited more arousal in the animals. Interestingly, the horses in the current study did not show a significant thermal response to stroking in comparison to the baseline condition. This may be the result of three methodological limitations: (1) the use of experimenters to deliver the stroking stimulus may not have been substantially positive for the horses; (2) the larger body size of the horses, compared to the other two species, possibly resulted in the duration of the trials not being sufficient to generate or detect a change in eye temperature; and (3) the baseline condition may have been higher in arousal for the horse than the dogs and cats, leading to a drop in arousal during the stroking condition. Specifically, many of the horse subjects were grazing or vigilant during the baseline whereas many of the dogs and cats were resting. With regards to the second limitation, another study measured the eye temperatures of horses placed under different bridling conditions for a full 10 minutes per session, and found significant differences in the bridling conditions compared to baseline (McGreevy et al., 2012). Further validation is therefore required to determine the thermal responses of horses receiving grooming for longer time periods.

The behavioral measures in our study suggest eye movements should not be automatically used as a general indicator of positive emotion. Each species displayed a different pattern of eye behaviour between the baseline and stroking conditions. This could be due to individual differences in how stroking was perceived on an emotional level. However, the tendency to narrow the eye aperture during stroking, as seen in the increased half blinks in horses in the present study, is in line with previous research on horses during human-initiated grooming (Hintze et al., 2016), as well as in other species (cows: Proctor & Carder, 2015a; and sheep: Reefmann, Wechsler, & Gygax, 2009). Conversely, dogs appear to have closed their eyes more during the baseline condition. These eye closures could conceivably be due to the relaxed nature of the baseline condition leading dogs to adopt a resting sleep-like state with more eye closures during this part of the trial. Alternatively, these findings potentially suggest that eye narrowing movements may not be key to the expression of positive emotion in dogs. The latter possibility receives some support from studies which demonstrate that humans are unable to differentiate between dogs' baseline and positive facial expressions using the eye region alone (Schirmer et al., 2013). It is important to note that the cats in our study did not show any significant differences in eye movements between conditions. The absence of greater frequencies or durations of eye movements in cats is surprising given our research on slow blinking as a positive emotional signal in human-cat interactions (Humphrey et al., submitted). However, the stroking stimulus in this study was non-communicative as owners were sat beside, rather than facing, their animal and were not explicitly instructed on whether to maintain attention to the subject. It is possible that this affected the facial expressions produced by the subjects, as dogs are said to produce less facial expressions when a human is inattentive (Kaminski et al., 2017). It would

therefore be useful for future research to investigate the use of facial expressions by companion animals during differing levels of groomer attentiveness.

The eye movements of cats did correlate with their eye temperature responses. This suggests that eye movements could have been related to changes in emotional state in cats. A similar relationship between relative eye aperture and physiological changes has also been observed in sheep during positive stroking conditions (Reefmann et al., 2009). Interestingly, the reverse pattern was observed in the horses in our study, in which eye movements negatively correlated with eye temperature. This may be due to the lack of change in eye temperature in the horses over the length of the trial. Alternatively, the horses in this study may have been more aroused during the baseline condition. Horses tend to remain awake and more alert during baseline conditions than cats and dogs, and therefore the horses may have experienced a possible decrease in arousal during the stroking condition, whereas the cats and dogs may have been more aroused. This underlines how complex it is to systematically generate positive emotional responses while controlling for arousal levels across species.

Studying the expressions of positive emotions can be useful in the development of more comprehensive assessments of animal welfare (Boissy et al., 2007). Identifying indicators of emotion is particularly important in animals who are under human care as these individuals are set to benefit the most from good standards of welfare. Our study highlights species-level differences in the behavioral and physiological responses to a shared 'positive' emotional stimulus. In addition, how 'positive' emotional stimuli are perceived is considered to vary much more than the reactions to negative emotional stimuli (Reefmann et al., 2009), and it is as yet unclear whether actions such as stroking by humans have similarly positive effects on all species. Thus, further work is needed to

identify both appropriate stimuli and species-specific signatures of positive emotion

before practical applications to welfare can be established.

References

Albuquerque, N., Guo, K., Wilkinson, A., Savalli, C., Otta, E., & Mills, D. (2016). Dogs recognize dog and human emotions. *Biology Letters*. https://doi.org/10.1098/rsbl.2015.0883

Andrews, R. V. (1983). Hyperthermic reactions of voles to novel and repetitive psychogenic stimuli. *Comparative Biochemistry and Physiology -- Part A: Physiology*. https://doi.org/10.1016/0300-9629(83)90424-3

Bennett, V., Gourkow, N., & Mills, D. S. (2017). Facial correlates of emotional behaviour in the domestic cat (*Felis catus*). *Behavioural Processes*. https://doi.org/10.1016/j.beproc.2017.03.011

Boissy, A., Manteuffel, G., Jensen, M. B., Moe, R. O., Spruijt, B., Keeling, L. J., … Aubert, A. (2007). Assessment of positive emotions in animals to improve their welfare. *Physiology and Behavior*. https://doi.org/10.1016/j.physbeh.2007.02.003

Borsini, F., Lecci, A., Volterra, G., & Meli, A. (1989). A model to measure anticipatory anxiety in mice? *Psychopharmacology*. https://doi.org/10.1007/BF00444693

CABANAC, M. (2005). Emotion and phylogeny. *The Japanese Journal of Physiology*. https://doi.org/10.2170/jjphysiol.49.1

Cabanac, M., & Aizawa, S. (2000). Fever and tachycardia in a bird (*Gallus domesticus*) after simple handling. *Physiology and Behavior*. https://doi.org/10.1016/S0031-9384(00)00227-4

Caeiro, C. C., Burrows, A. M., & Waller, B. M. (2017). Development and application of CatFACS: Are human cat adopters influenced by cat facial expressions? *Applied Animal Behaviour Science*. https://doi.org/10.1016/j.applanim.2017.01.005

Caeiro, Cátia C., Waller, B. M., Zimmermann, E., Burrows, A. M., & Davila-Ross, M. (2013). OrangFACS: A muscle-based facial movement coding system for orangutans (*Pongo spp.*). *International Journal of Primatology*. https://doi.org/10.1007/s10764-012-9652-x

Dalla Costa, E., Minero, M., Lebelt, D., Stucke, D., Canali, E., & Leach, M. C. (2014). Development of the horse grimace scale (HGS) as a pain assessment tool in horses undergoing routine castration. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0092281

Duchenne, B. de. (1862). The mechanism of human facial expression. *RA Cuthbertson, Trans.*

Ekman, P. (1993). Facial expression and emotion. *American Psychologist*. https://doi.org/10.1037/0003-066X.48.4.384

Ekman, P. (1997). Universal facial expressions of emotion: an old controversy and new findings. *Nonverbal Communication*. https://doi.org/10.1098/rstb.1992.0008

Feh, C., & de Mazierès, J. (1993). Grooming at a preferred site reduces heart rate in horses. *Animal Behaviour*. https://doi.org/10.1006/anbe.1993.1309

Galvan, M., & Vonk, J. (2016). Man's other best friend: domestic cats (*F. silvestris catus*) and their discrimination of human emotion cues. *Animal Cognition*. https://doi.org/10.1007/s10071-015-0927-4

Gourkow, N., Hamon, S. C., & Phillips, C. J. C. (2014). Effect of gentle stroking and vocalization on behaviour, mucosal immunity and upper respiratory disease in anxious shelter cats. *Preventive Veterinary Medicine*. https://doi.org/10.1016/j.prevetmed.2014.06.005

Häger, C., Biernot, S., Buettner, M., Glage, S., Keubler, L. M., Held, N., … Bleich, A. (2017). The sheep grimace scale as an indicator of post-operative distress and pain in laboratory sheep. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0175839

Hama, H., Yogo, M., & Matsuyama, Y. (1996). Effects of stroking horses on both humans' and horses' heart rate responses. *Japanese Psychological Research*. https://doi.org/10.1111/j.1468-5884.1996.tb00009.x

Handlin, L., Hydbring-Sandberg, E., Nilsson, A., Ejdebäck, M., Jansson, A., & Uvnäs-Moberg, K. (2011). Short-term interaction between dogs and their owners: Effects on oxytocin, cortisol, insulin and heart rate-an exploratory study. *Anthrozoos*. https://doi.org/10.2752/175303711X13045914865385

Hintze, S., Smith, S., Patt, A., Bachmann, I., & Würbel, H. (2016). Are eyes a mirror of the soul? What eye wrinkles reveal about a horse's emotional state. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0164017

Humphrey, T., Proops, L., Forman, J., Spooner, R., Wathan, J., & McComb, K. (n.d.). *The cat smile?: The role of cat eye narrowing movements in cat-human communication* (unpublished manuscript).

Ikkatai, Y., & Watanabe, S. (2015). Eye surface temperature detects stress response in budgerigars (*Melopsittacus undulatus*). *NeuroReport*. https://doi.org/10.1097/WNR.0000000000000403

Jerem, P., Herborn, K., McCafferty, D., McKeegan, D., & Nager, R. (2015). Thermal imaging to study stress non-invasively in unrestrained birds. *Journal of Visualized Experiments*. https://doi.org/10.3791/53184 <http://dx.doi.org/10.3791/53184>) (PMID:26575985)

Kaminski, J., Hynds, J., Morris, P., & Waller, B. M. (2017). Human attention affects facial expressions in domestic dogs. *Scientific Reports*. https://doi.org/10.1038/s41598-017-12781-x

Kano, F., Hirata, S., Deschner, T., Behringer, V., & Call, J. (2016). Nasal temperature drop in response to a playback of conspecific fights in chimpanzees: A thermo-imaging study. *Physiology and Behavior*. https://doi.org/10.1016/j.physbeh.2015.11.029

Kuraoka, K., & Nakamura, K. (2011). The use of nasal skin temperature measurements in studying emotion in macaque monkeys. *Physiology and Behavior*. https://doi.org/10.1016/j.physbeh.2010.11.029

Langford, D. J., Bailey, A. L., Chanda, M. L., Clarke, S. E., Drummond, T. E., Echols, S., … Mogil, J. S. (2010). Coding of facial expressions of pain in the laboratory mouse. *Nature Methods*. https://doi.org/10.1038/nmeth.1455

Leach, M. (2012). Rabbit grimace scale (RbtGS) manual. *PloS One*. https://doi.org/10.1371/journal.pone. 0044437

Ludwig, N., Gargano, M., Luzi, F., Carenzi, C., & Verga, M. (2007). Technical note: Applicability of infrared thermography as a non invasive measurement of stress in rabbit. *World Rabbit Science*.

Mazzotti, G. A., & Boere, V. (2009). The right ear but not the left ear temperature is related to stress-induced cortisolaemia in the domestic cat (*Felis catus*). *Laterality*. https://doi.org/10.1080/13576500802344420

McGreevy, P., Warren-Smith, A., & Guisard, Y. (2012). The effect of double bridles and jaw-clamping crank nosebands on temperature of eyes and facial skin of

horses. *Journal of Veterinary Behavior: Clinical Applications and Research*. https://doi.org/10.1016/j.jveb.2011.08.001

Mellor, D. J. (2012). Animal emotions, behaviour and the promotion of positive welfare states. *New Zealand Veterinary Journal*. https://doi.org/10.1080/00480169.2011.619047

Mendl, M., Burman, O. H. P., & Paul, E. S. (2010). An integrative and functional framework for the study of animal emotion and mood. In *Proceedings of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rspb.2010.0303

Merola, I., Prato-Previde, E., Lazzaroni, M., & Marshall-Pescini, S. (2014). Dogs' comprehension of referential emotional expressions: Familiar people and familiar emotions are easier. *Animal Cognition*. https://doi.org/10.1007/s10071-013-0668-1

Moe, R. O., Stubsjøen, S. M., Bohlin, J., Flø, A., & Bakken, M. (2012). Peripheral temperature drop in response to anticipation and consumption of a signaled palatable reward in laying hens (*Gallus domesticus*). *Physiology and Behavior*. https://doi.org/10.1016/j.physbeh.2012.03.032

Müller, C. A., Schmitt, K., Barber, A. L. A., & Huber, L. (2015). Dogs can discriminate emotional expressions of human faces. *Current Biology*. https://doi.org/10.1016/j.cub.2014.12.055

Nakayama, K., Goto, S., Kuraoka, K., & Nakamura, K. (2005). Decrease in nasal temperature of rhesus monkeys (*Macaca mulatta*) in negative emotional state. *Physiology and Behavior*. https://doi.org/10.1016/j.physbeh.2005.03.009

Parr, L. A., Waller, B. M., Burrows, A. M., Gothard, K. M., & Vick, S. J. (2010). Brief communication: MaqFACS: A muscle-based facial movement coding system for

the rhesus macaque. *American Journal of Physical Anthropology*.
https://doi.org/10.1002/ajpa.21401

Parr, Lisa A., Waller, B. M., Vick, S. J., & Bard, K. A. (2007). Classifying chimpanzee
facial expressions using muscle action. *Emotion*. https://doi.org/10.1037/1528-
3542.7.1.172

Proctor, H. (2012). Animal sentience: Where are we and where are we heading?
Animals. https://doi.org/10.3390/ani2040628

Proctor, H. S., & Carder, G. (2014). Can ear postures reliably measure the positive
emotional state of cows? *Applied Animal Behaviour Science*.
https://doi.org/10.1016/j.applanim.2014.09.015

Proctor, H. S., & Carder, G. (2015a). Measuring positive emotions in cows: Do visible
eye whites tell us anything? *Physiology and Behavior*.
https://doi.org/10.1016/j.physbeh.2015.04.011

Proctor, H. S., & Carder, G. (2015b). Nasal temperatures in dairy cows are influenced
by positive emotional state. *Physiology and Behavior*.
https://doi.org/10.1016/j.physbeh.2014.11.011

Reefmann, N., Bütikofer Kaszàs, F., Wechsler, B., & Gygax, L. (2009). Ear and tail
postures as indicators of emotional valence in sheep. *Applied Animal Behaviour
Science*. https://doi.org/10.1016/j.applanim.2009.02.013

Reefmann, N., Wechsler, B., & Gygax, L. (2009). Behavioural and physiological
assessment of positive and negative emotion in sheep. *Animal Behaviour*.
https://doi.org/10.1016/j.anbehav.2009.06.015

Scherer, K. R. (2005). What are emotions? and how can they be measured? *Social*

Science Information. https://doi.org/10.1177/0539018405058216

Schirmer, A., Seow, C. S., & Penney, T. B. (2013). Humans process dog and human facial affect in similar ways. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0074591

Smith, A. V., Proops, L., Grounds, K., Wathan, J., & McComb, K. (2016). Functionally relevant responses to human facial expressions of emotion in the domestic horse (*Equus caballus*). *Biology Letters*. https://doi.org/10.1098/rsbl.2015.0907

Sotocinal, S. G., Sorge, R. E., Zaloum, A., Tuttle, A. H., Martin, L. J., Wieskopf, J. S., … Mogil, J. S. (2011). The rat grimace scale: A partially automated method for quantifying pain in the laboratory rat via facial expressions. *Molecular Pain*. https://doi.org/10.1186/1744-8069-7-55

Tate, A. J., Fischer, H., Leigh, A. E., & Kendrick, K. M. (2006). Behavioural and neurophysiological evidence for face identity and face emotion processing in animals. *Philosophical Transactions of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rstb.2006.1937

Travain, T., Colombo, E. S., Grandi, L. C., Heinzl, E., Pelosi, A., Prato Previde, E., & Valsecchi, P. (2016). How good is this food? A study on dogs' emotional responses to a potentially pleasant event using infrared thermography. *Physiology and Behavior*. https://doi.org/10.1016/j.physbeh.2016.03.019

Travain, T., Colombo, E. S., Heinzl, E., Bellucci, D., Prato Previde, E., & Valsecchi, P. (2015). Hot dogs: Thermography in the assessment of stress in dogs (*Canis familiaris*)-A pilot study. *Journal of Veterinary Behavior: Clinical Applications and Research*. https://doi.org/10.1016/j.jveb.2014.11.003

Valera, M., Bartolomé, E., Sánchez, M. J., Molina, A., Cook, N., & Schaefer, A. (2012). Changes in eye temperature and stress assessment in horses during show jumping competitions. *Journal of Equine Veterinary Science*. https://doi.org/10.1016/j.jevs.2012.03.005

Vick, S., Waller, B. M., Parr, L. A., Smith-pasqualini, M., & Bard, K. (2006). ChimpFACS - The chimpanzee facial action coding system. *Interchange*.

Viscardi, A. V., Hunniford, M., Lawlis, P., Leach, M., & Turner, P. V. (2017). Development of a piglet grimace scale to evaluate piglet pain using facial expressions following castration and tail docking: A pilot study. *Frontiers in Veterinary Science*. https://doi.org/10.3389/fvets.2017.00051

Waller, B. M., Lembeck, M., Kuchenbuch, P., Burrows, A. M., & Liebal, K. (2012). GibbonFACS: A muscle-based facial movement coding system for hylobatids. *International Journal of Primatology*. https://doi.org/10.1007/s10764-012-9611-6

Waller, B. M., & Micheletta, J. (2013). Facial expression in nonhuman animals. *Emotion Review*. https://doi.org/10.1177/1754073912451503

Waller, B. M., Peirce, K., Caeiro, C. C., Scheider, L., Burrows, A. M., McCune, S., & Kaminski, J. (2013). Paedomorphic facial expressions give dogs a selective advantage. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0082686

Wathan, J., Proops, L., Grounds, K., & McComb, K. (2016). Horses discriminate between facial expressions of conspecifics. *Scientific Reports*. https://doi.org/10.1038/srep38322

Wathan, Jen, Burrows, A. M., Waller, B. M., & McComb, K. (2015). EquiFACS: The equine facial action coding system. *PLoS ONE*.

Acknowledgements

General Discussion

In this final chapter I will summarise the findings of this thesis, and discuss how they contribute to an understanding of emotional signalling in non-human animals. I will also include a discussion of the theoretical and practical implications of my research. Finally, I will suggest future research directions derived from this thesis.

1. Overview of main findings

This thesis provides the first scientific account of slow blinking behaviour in cats, a previously anecdotally observed cat behaviour (International Cat Care & Lincoln, n.d.; Cats Protection, 2017). In summary, the key features of a slow blink were described (i.e. half blinking, eye narrowing and eye closures) and slow blinking behaviour was investigated in exchanges between domestic cats and humans. Slow blinking appears to be a positive signal for cats, who are more likely to approach an unfamiliar human after a slow blink interaction than after viewing a neutral face (Article I) – and for humans, where cats who are more responsive to slow blinking are rehomed faster (Article II). Slow blinking is linked to degree of lateralised paw use, and therefore may reflect differences in cats' emotional functioning (Article III). Furthermore, the eye narrowing movements involved in slow blinking in cats do not occur to the same extent in non-visual communicative interactions with humans (Article IV). Collectively, these results suggest that slow blinking behaviour is a possible indicator of positive emotions in cats. Furthermore cats displayed slow blinking towards familiar and unfamiliar humans, suggesting it is a generalised behaviour rather than one reserved for the cat's primary carers.

Considering each chapter in turn, Article I introduces the cat slow blink sequence, describing the particular eye movements involved in slow blinking behaviour. This

article also investigates whether cats respond to human slow blinking behaviour with slow blink sequences of their own. Cats slow blinked in response to human-initiated slow blinks from both their owners and an unfamiliar experimenter. Furthermore, Article I produces evidence which shows that cats perceive slow blinking positively, as cats were more likely to approach an unfamiliar experimenter after a slow blink interaction compared to a neutral face. This provides the first indication that slow blinking is a potential indicator of positive emotion in cats.

Article II expands upon the findings of Article I by examining the consequences of slow blinking in relation to human responses to cats. More specifically, Article II revealed that giving salient responses to human-initiated slow blinking led shelter cats to be rehomed faster, which indicates that slow blinking could provide cats with a selective advantage in cat-human relationship development and, more generally, in the domestication process. In addition, the evidence that cats who were assessed as nervous around humans upon arrival at the shelter had a greater propensity to respond to human slow blinking points toward the additional use of slow blinking by cats as a submissive response.

In accordance with the conclusions from Article I, Article III supports the relevance of slow blinking as an emotionally relevant behaviour. In Article III the degree of cats' motor lateralisation is examined through the identification of cats' paw preferences. This study used the same paradigm to study lateral bias in cats as McDowell, Wells, Hepper, & Dempster (2016), who found that having a significant paw preference, either left or right, predicted more more affectionate, friendly, confident, obedient, active and less aggressive temperament in cats. In our study, cats with a strong paw preference produced a higher rate of slow blink responses to human-initiated slow blinking compared to cats without a lateral paw-preference. Moreover, paw-preferent cats

showed increased slow blinking synchronisation with an unfamiliar human experimenter during slow blink interactions in comparison to ambi-lateral cats. It was also the case that paw-preferent cats produced a higher rate of slow blink responses when the experimenter's slow blinking incorporated a head turn, creating a natural break in the interaction. This effect was not observed in slow blink trials that did not include a break, which suggests that breaks are important in slow blink interactions. It has also been reported that cats show a preference for being in contact with unfamiliar men when that person breaks away from initial eye contact with the cat (Goodwin & Bradshaw, 1997). This suggests that cat-human interactions can be facilitated by the use of breaks in eye contact in general.

Finally, Article IV investigated the use of eye narrowing movements in another potentially positive context – receiving stroking/grooming from a human – and across other domestic species, specifically dogs and horses. Article IV also attempted to investigate the physiological signatures of positive emotion through measuring the eye temperature responses of cats, dogs, and horses during a baseline condition and during the animals receiving stroking by a human (hypothesised positive stimulus). Cats and dogs both showed an increase in eye temperature in response to being stroked, whereas the eye temperature of horses did not significantly change. Eye narrowing movements in response to stroking differed by species. Cats did not show any significant differences in eye responses to stroking compared to the baseline, although the mean frequencies and durations were in the expected direction. Nonetheless, higher eye temperatures were linked to longer durations of half blinking in cats. Horses showed a greater frequency and a longer duration of eye movements in response to stroking, although these behavioural responses were related to lower eye temperatures. Dogs produced shorter eye movements and had a tendency to produce less eye movements in

response to human stroking, which was not linked to their physiological response. This study emphasises the importance of considering species-specific differences in the study of positive emotions and suggests that domestic animals may perceive stimuli, commonly considered to be positive, in unique ways and may produce individualised responses. The valence and arousal states of members of each species in the baseline and stroking conditions are also hard to determine, rendering the results hard to interpret as both these factors could have contributed to the findings. In addition, stroking is a non-visual communicative human-animal interaction. Thus, this study suggests that eye narrowing may be specifically used to signal information to others in visual communicative positive human-animal interactions.

2. Positive emotional signalling in domestic animals

The articles presented in this thesis produce several strands of evidence to suggest that cats are able to produce specific signals of positive emotions to humans. The results also indicate that animals' behavioural expressions are communicative and to some degree, intentional.

Humans show eye narrowing movements in positive emotional expressions, as described in the Duchenne smile (Duchenne, 1862). Eye narrowing movements may therefore be a universal indicator of positive emotion across mammals. Indeed cats and humans share basic underlying mammalian facial musculature (Caeiro et al., 2017; Ekman & Friesen, 1971b), and therefore may use these muscles in similar ways. However in Article IV, cross-species comparisons found that dogs, as well as to some extent cats, do not produce these eye narrowing movements in a non-visual communicative positive emotional context. One explanation for the results in Article IV is that eye narrowing movements are used in intentional emotional communication in

these species, and therefore serve a social function. However, eye narrowing movements were found in the horses of this study, as well as in the literature on cows (Proctor & Carder, 2015a), horses (Hintze et al., 2016) and sheep (Reefmann, Wechsler, et al., 2009) in the same non-visual communicative positive context (receiving stroking by a human). Arguably, the latter species experience less frequent and intimate human-animal interactions in their day-to-day lives than dogs and cats. Thus, eye narrowing may be generalised in these ungulates to include non-communicative positive contexts with humans, whereas eye narrowing movements may have become more specialised in domestic species that regularly interact with humans. Universality of emotional expressions using the eyes is apparently present in negative emotional cues also, where increased eye whites indicate fear in a variety of species (Handelman, 2012; Hardee, Thompson, & Puce, 2008; Lee et al., 2013; Siniscalchi et al., 2018b; Susskind & Anderson, 2010). This is in line with evolutionary accounts of emotional expressions (Darwin, 1872). Further research investigating the use of eye narrowing movements as a signal of positive emotion should explore whether this is a truly universal cue in mammals, and its function as a communicative signal in certain human-animal interactions.

The domestic animals tested in this thesis all had a history of living with humans which will have shaped their behaviour in a range of ways. One could argue that the responses cats made in Articles I, II and III may be due to the subjects having learnt that humans have a positive response to slow blinking, as demonstrated via rates of rehoming in Article II. If this were the case, we would expect to find younger cats producing fewer slow blink responses than older cats. However, in Article I cats' age was not related to their response frequency. Furthermore, although cats underwent a habituation period, no cats were intentionally rewarded for responding to slow blinking. Thus, learning is

unlikely to strongly account for the high number of slow blinking responses by cats to human-initiated slow blinking, although this explanation cannot be ruled out.

Another point to consider is how domestication has affected the ways in which animals signal emotions to humans. Researchers argue that during the process of domestication, animals have been selected for specialised socio-cognitive abilities that facilitate human-animal communication (Hare, Brown, Williamson, & Tomasello, 2002). Miklósi et al. (2003) investigated the interspecific communicative abilities of dogs and wolves, and attributed dogs' superior ability to communicate with humans to their propensity to look at human faces. This behaviour affects how domestic animals signal to humans as well as their human-reading ability. For instance, dogs are sensitive to a humans' attentional states (Call et al., 2003), and consequently adapt the number of facial expressions they produce (Kaminski et al., 2017). The emotional signalling observed in this thesis therefore may have been due at least in part to human selection of higher socio-cognitive functioning in the study species through the process of domestication.

Alternatively, some researchers argue that domestic animals' enhanced communicative abilities with humans may be a by-product of their greater sociality, rather than from specific socio-cognitive skills selected by humans (Hare et al., 2005). Indeed, domestic guinea pigs display less aggressive behaviour and more positive social behaviour towards humans than their wild ancestor, the cavy (Künzl & Sachser, 1999). Furthermore, foxes that have been bred for increased sociality with humans show comparable abilities in using human gestures to domestic dogs, and are more skilled than foxes who have not been bred for greater sociality (Hare et al., 2005). Although cats are ancestrally non-social and less social overall than many other domestic species, making cats an interesting study species. This thesis focused on the positive emotional signals of domestic animals with humans. However, it would be useful to examine

whether such signals are present in non-domestic species, as well as in enculturated captive animals.

The reduction of aggression observed in domestic species (Künzl & Sachser, 1999; Plyusnina, Solov'Eva, & Oskina, 2011) is likely to have also led to greater submissive behaviour. Non-aggressive individuals are considered to adopt passive coping strategies when faced with threatening situations, where the aim is to reduce the emotional influence of the stress (Benus, Bohus, Koolhaas, & van Oortmerssen, 1991). In Article II, cats who were identified as anxious around humans upon arrival at the shelter had a greater propensity to be more responsive to human slow blinking than the non-anxious cats. This finding could suggest that in addition to slow blinking being a positive signal, this behaviour may also be used in appeasement. The latter could explain why one key feature of the slow blink, half blinking, has been shown to occur in cats in another study during fearful interactions with humans (Bennett et al., 2017). Cats may use slow blinking in potentially threatening situations with humans as a way to interrupt prolonged eye contact. Indeed staring is often perceived as threatening in a range of species (Emery, 2000), and therefore slow blinking may act to disrupt and decrease the emotional intensity of the situation.

The use of positive emotional signals to de-escalate stressful social situations is also shown in human smiling (Scott et al., 2014) and in the primate silent bared teeth display (Bout & Thierry, 2005; de Waal & Luttrell, 1985; Waller & Dunbar, 2005). Such displays could serve a general function of signalling socially affiliative intent by the sender, which explains why they are observed in both affiliative contexts and aggressive or threatening contexts. Signalling social affinity to others is adaptive as it enhances social cohesion and reduces the risk of aggression between individuals. This indicates that certain positive emotional signals may have evolved from submissive displays in

socially complex species as a result of sharing the same adaptive function. The idea that slow blinking signals social affinity is further substantiated by the fact that cats who interacted with an unfamiliar human that slow blinked at them were more likely to approach the human, as seen in Article I. Furthermore, the hypothesis that positive emotional expression enhances social affinity is in line with the 'Broaden and Build' theory of positive emotions, where positive emotions are said to broaden thought-action repertoires in the individual and build on their personal resources (Fredrickson, 2001). Here, the positive emotional signalling discussed in this thesis can be considered to build an individual cat's social resources.

3. General and Animal Welfare Implications

Identifying indicators of positive emotions in animals has useful implications for animal welfare. Animal welfare science has recently shifted its focus to incorporate the promotion of positive emotional states as well as advancing reductions in negative emotions in animals (Mellor & Beausoleil, 2015). Such a shift would allow assessments to move beyond the mere identification of compromises to welfare to detecting areas for welfare enhancement (Mellor & Beausoleil, 2015). Animals under human care are at risk of experiencing inadequate environmental conditions, such as a lack of space, enrichment and opportunities to socialise, which can lead to poor wellbeing in the individual. However, under favourable conditions, animals are given the opportunity to experience positive emotions which can result in lasting benefits to an individual's overall perception of their environment (Brydges et al., 2010; Douglas et al., 2012; Yeates & Main, 2008), as well as provide circumstances to build relationships (as seen in play behaviour: Palagi, Cordoni, & Borgognini Tarli, 2004). These outcomes consequently have positive effects on handling and management of such animals by humans. Slow blinking may enhance feline welfare in the home environment by

promoting opportunities for cats to engage in positive interactions. Slow blinking may also represent an immediate, non-invasive and cost-efficient indicator to assess the presence of positive emotions in cats – although the use of slow-blinking in submissive situations by anxious cats underlines that this relationship is likely to be complex. Further research is therefore needed to validate the use of slow blinking as a welfare indicator.

This thesis provides evidence of the applied relevance that slow blinking has for cats in the shelter environment. Adopters often refer to cats' emotional traits, such as 'friendly' and 'happy', as motives for selecting cats (Gourkow & Fraser, 2006). Better quality social interactions in shelter cats can also reduce the length of time individuals spend in the shelter environment (Gouveia, Magalhães, & de Sousa, 2011). In addition, once cats have been adopted, socialisation and other factors affecting the social bond between adopters and cats will influence retention in the home (Neidhart & Boyd, 2002). Introducing strategies that promote opportunities for social bonding, such as slow blinking, between potential adopters and shelter cats could therefore improve adoption rates. Indeed, prospective adopters spend a greater length of time viewing cats that are housed at eye level (Fantuzzi et al., 2010). Thus, this study along with the evidence provided in the current thesis emphasise the importance of strategic enclosure placement that provide enhanced opportunities for adopters and shelter cats to engage in positive social interactions involving eye movements, which may be an important factor for increased adoption success and reduced overpopulation, as well as enhancing retention rates in the home. As such, it would be useful for future studies to investigate how slow blink interactions affect the cat-human bond, particularly with respect to how such interactions impact levels of cat and owner attachment.

The results of this thesis may also have applications for training methods for cats. To date, animal training methods have largely been explored in domestic dogs (Hiby, Rooney, & Bradshaw, 2004) and horses (McLean & Christensen, 2017), and a lack of understanding exists regarding cat training as demonstrated by the scarcity of web-based feline behaviour training classes. However, recent research revealed that social interaction with humans was cats' preferred stimulus followed by food (Vitale Shreve, Mehrkam, & Udell, 2017). This suggests that cat-human interactions could be a useful reinforcement tool in cat training. The present thesis showed that slow blinking is perceived positively in cats, which suggests that slow blinking could also act as an effective positive reinforcer. Cat training could potentially be used to prevent behaviour problems (Seksel, 2008), which lead to increased rates of relinquishment in cats (Neidhart & Boyd, 2002).

4. Future Research

Given the above, an important area for future research would be to explore the use of slow blinking as an assessment marker in animal welfare evaluations, at the same time identifying contexts where cats might also use slow blinking in environments with compromised welfare. Investigating the latter confound would be particularly important given that anxious cats in a shelter environment slow blink more than non-anxious cats (as seen in Article II). Such research could involve testing the presence of cat slow blink responses to experimenter-initiated slow blinking under different welfare conditions, such as enriched environmental stimulation or increased opportunities to socialise.

In addition, since slow blinking appears to be perceived as positive in both cats and humans, how slow blink interactions affect the cat-human bond should be an important area for future research. Such studies could instruct cat owners to either take part in a

slow blinking intervention or ask owners to not interact with their cats via slow blinking for a number of weeks. Cat-human attachment in the different conditions could be assessed using subjective owner reports, such as the Lexington Attachment to Pets Scale (Garrity, Stallones, Marx, & Johnson, 1989), as well as an adapted version of Ainsworth's Strange Situation Test for cats (Edwards, Heiblum, Tejeda, & Galindo, 2007).

Although it is beyond the scope of this thesis, it would also be useful for future studies to explore whether slow blinking is present in cat-cat interactions, as well as in the social interactions of other felid species. The presence of this behaviour in other felids would suggest that slow blinking evolved in a common ancestor of the Felidae family, and is an inherent part of felids' behavioural repertoire. This would also suggest that emotional signalling pre-dates domestication in cats. Furthermore, if slow blinking is part of the cat's behavioural repertoire, it would be interesting to explore whether slow blinking is used in contexts of reconciliation or as an appeasement behaviour between group-living feral cats. These investigations could use the post-conflict matched-control (PC-MC) method previously established in the research on reconciliation in primates (Kappeler & van Schaik, 1992; Veenema, Das, & Aureli, 1994), which systematically compares post-conflict behaviour against behaviour not affected by conflict (the baseline; Arnold & Aureli, 2007). Here, rates of slow blinking that occurs in epochs after a conflict could be compared with rates of slow blinking that occurs in epochs in the absence of any conflict.

Article IV showed that the three domestic study species may be experiencing a positive interaction with humans (stroking) in different ways. This demonstrates the difficulty in reliably inducing a specific emotion in animals. Article IV was also limited by the inability to validate the presence of a neutral emotional state in the control condition.

The use of emotionally 'neutral' states for control conditions in emotion research is key to provide a comparison group for the emotion under study. However, achieving a truly neutral emotional state is challenging. Here, the more reliable and valid option to study emotions may be to ensure that the change in valence and arousal are in the expected direction. For example, the dogs in article IV may actually have been in a contented, relaxed state (positive valence, low arousal) during the control condition and stroking may have simply produced a higher arousal state for the dog, which was not the intended intervention given the study hypotheses. The use of manipulation checks may help to overcome this limitation by ensuring that the intended emotional state is present after each condition. Manipulation checks of emotional states in humans can include either physiological measures or behavioural observations (Gerrards-Hesse, Spies, & Hesse, 1994), which could be applied to future studies on emotional signalling in animals.

5. Conclusions

This thesis details an example of the cat's ability to engage in emotional communication with humans. The current research suggests that cats have the capacity to experience emotion and signal their intentions to others. Cats have demonstrated similar socio-cognitive skills to dogs in regards to communicative behaviour with humans (Merola et al., 2015; Miklósi et al., 2005). However the literature on cats' emotional abilities is scant (Bennett et al., 2017; Galvan & Vonk, 2016), despite owners often subjectively attributing a high number of both basic and complex emotions to cats (Martens, Enders-Slegers, & Walker, 2016; Pongrácz & Szapu, 2018b). Thus, researchers have called for further study of cat behaviour in a similar capacity to the research already conducted with dogs (Pongrácz & Szapu, 2018b). The current thesis not only supports claims of the cat's high level of social cognition, but should also stimulate further research into

cats' emotional abilities, including the cat's ability to produce as well as perceive emotions across the species barrier.

This thesis provides the first empirical evidence of cats engaging in slow blinking, a widely anecdotally acknowledged cat behaviour, during cat-human interactions. The findings reveal slow blinking to be a potential indicator of positive emotion, and extend our current understanding of the universality of emotional expressions, specifically the use of eye narrowing movements. The present thesis also offers initial insights into the link between submissive behaviour and positive emotions, and suggests areas for further research. The tools and methodologies developed and tested in this programme of research may be useful for future studies investigating animal emotion, as well as in empirical work with cats. Finally, this thesis may inform current practices and monitoring techniques of animal welfare, and promote positive welfare through enhanced human-animal interactions.

References

Arnold, K., & Aureli, F. (2007). Postconflict reconciliation. *Primates in Perspective*.
https://doi.org/10.1111/j.1540-4560.2008.00563.x

Bennett, V., Gourkow, N., & Mills, D. S. (2017). Facial correlates of emotional
behaviour in the domestic cat (*Felis catus*). *Behavioural Processes*.
https://doi.org/10.1016/j.beproc.2017.03.011

Benus, R. F., Bohus, B., Koolhaas, J. M., & van Oortmerssen, G. A. (1991). Heritable
variation for aggression as a reflection of individual coping strategies. *Experientia*.
https://doi.org/10.1007/BF01923336

Bout, N., & Thierry, B. (2005). Peaceful meaning for the silent bared-teeth displays of
mandrills. *International Journal of Primatology*. https://doi.org/10.1007/s10764-
005-8850-1

Brydges, N. M., Leach, M., Nicol, K., Wright, R., & Bateson, M. (2010).
Environmental enrichment induces optimistic cognitive bias in rats. *Animal
Behaviour*. https://doi.org/10.1016/j.anbehav.2010.09.030

Caeiro, C. C., Burrows, A. M., & Waller, B. M. (2017). Development and application of
CatFACS: Are human cat adopters influenced by cat facial expressions? *Applied
Animal Behaviour Science*. https://doi.org/10.1016/j.applanim.2017.01.005

Call, J., Bräuer, J., Kaminski, J., & Tomasello, M. (2003). Domestic dogs (*Canis
familiaris*) are sensitive to the attentional state of humans. *Journal of Comparative
Psychology*. https://doi.org/10.1037/0735-7036.117.3.257

International Cat Care., & University of Lincoln., (n.d.). Slow Blink. Retrieved from
https://icatcare.org/behaviour-described/maintenance/sedentary/slow-blink

Cats Protection. (2017). *The Behaviour Guide*. Retrieved from

https://www.cats.org.uk/uploads/documents/CP_Behaviour_Guide-web.pdf

Darwin, C. (1872). The Expression of Emotion in Man and Animals. *Animals*.

de Waal, F. B. M., & Luttrell, L. M. (1985). The formal hierarchy of rhesus macaques:

An investigation of the bared-teeth display. *American Journal of Primatology*.

https://doi.org/10.1002/ajp.1350090202

Douglas, C., Bateson, M., Walsh, C., Bédué, A., & Edwards, S. A. (2012).

Environmental enrichment induces optimistic cognitive biases in pigs. *Applied

Animal Behaviour Science*. https://doi.org/10.1016/j.applanim.2012.02.018

Duchenne, B. de. (1862). The mechanism of human facial expression. *RA Cuthbertson,

Trans.*

Edwards, C., Heiblum, M., Tejeda, A., & Galindo, F. (2007). Experimental evaluation

of attachment behaviors in owned cats. *Journal of Veterinary Behavior: Clinical

Applications and Research*. https://doi.org/10.1016/j.jveb.2007.06.004

Ekman, P., & Friesen, W. V. (1971). Facial action coding system: A technique for the

measurement of facial movement. *Journal of Personality and Social Psychology*.

https://doi.org/10.1037/h0030377

Emery, N. J. (2000). The eyes have it: The neuroethology, function and evolution of

social gaze. *Neuroscience and Biobehavioral Reviews*.

https://doi.org/10.1016/S0149-7634(00)00025-7

Fantuzzi, J. M., Miller, K. A., & Weiss, E. (2010). Factors relevant to adoption of cats

in an animal shelter. *Journal of Applied Animal Welfare Science*.

https://doi.org/10.1080/10888700903583467

Fredrickson, B. L. (2001). The role of positive emotions in positive psychology: The broaden-and-build theory of positive emotions. *American Psychologist*. https://doi.org/10.1037/0003-066X.56.3.218

Galvan, M., & Vonk, J. (2016). Man's other best friend: domestic cats (*F. silvestris catus*) and their discrimination of human emotion cues. *Animal Cognition*. https://doi.org/10.1007/s10071-015-0927-4

Garrity, T. F., Stallones, L. F., Marx, M. B., & Johnson, T. P. (1989). Pet ownership and attachment as supportive factors in the health of the elderly. *Anthrozoös*. https://doi.org/10.2752/089279390787057829

Gerrards-Hesse, A., Spies, K., & Hesse, F. W. (1994). Experimental inductions of emotional states and their effectiveness: A review. *British Journal of Psychology*. https://doi.org/10.1111/j.2044-8295.1994.tb02508.x

Goodwin, D., & Bradshaw, J. (1997). Gaze and mutual gaze: Its importance in cat/human and cat/cat interactions. *International Society of Anthrozoology*. Boston.

Gourkow, N., & Fraser, D. (2006). The effect of housing and handling practices on the welfare, behaviour and selection of domestic cats (*Felis sylvestris catus*) by adopters in an animal shelter. *Animal Welfare*.

Gouveia, K., Magalhães, A., & de Sousa, L. (2011). The behaviour of domestic cats in a shelter: Residence time, density and sex ratio. *Applied Animal Behaviour Science*. https://doi.org/10.1016/j.applanim.2010.12.009

Handelman, B. (2012). *Canine Behavior: A Photo Illustrated Handbook*. Wenatchee, WA, USA: Dogwise Publishing.

Hardee, J. E., Thompson, J. C. J. C., & Puce, A. (2008). The left amygdala knows fear:

Laterality in the amygdala response to fearful eyes. *Social Cognitive and Affective Neuroscience*. https://doi.org/10.1093/scan/nsn001

Hare, B., Brown, M., Williamson, C., & Tomasello, M. (2002). The domestication of social cognition in dogs. *Science*. https://doi.org/10.1126/science.1072702

Hare, B., Plyusnina, I., Ignacio, N., Schepina, O., Stepika, A., Wrangham, R., & Trut, L. (2005). Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. *Current Biology*. https://doi.org/10.1016/j.cub.2005.01.040

Hiby, E. F., Rooney, N. J., & Bradshaw, J. W. S. (2004). Dog training methods: Their use, effectiveness and interaction with behaviour and welfare. *Animal Welfare*.

Hintze, S., Smith, S., Patt, A., Bachmann, I., & Würbel, H. (2016). Are eyes a mirror of the soul? What eye wrinkles reveal about a horse's emotional state. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0164017

Kaminski, J., Hynds, J., Morris, P., & Waller, B. M. (2017). Human attention affects facial expressions in domestic dogs. *Scientific Reports*. https://doi.org/10.1038/s41598-017-12781-x

Kappeler, P. M., & van Schaik, C. P. (1992). Methodological and evolutionary aspects of reconciliation among primates. *Ethology*. https://doi.org/10.1111/j.1439-0310.1992.tb00948.x

Künzl, C., & Sachser, N. (1999). The behavioral endocrinology of domestication: A comparison between the domestic guinea pig (*Cavia aperea f. porcellus*) and its wild ancestor, the cavy (*Cavia aperea*). *Hormones and Behavior*. https://doi.org/10.1006/hbeh.1998.1493

Lee, D. H., Susskind, J. M., & Anderson, A. K. (2013). Social transmission of the sensory benefits of eye widening in fear expressions. *Psychological Science*. https://doi.org/10.1177/0956797612464500

Martens, P., Enders-Slegers, M. J., & Walker, J. K. (2016). The emotional lives of companion animals: Attachment and subjective claims by owners of cats and dogs. *Anthrozoos*. https://doi.org/10.1080/08927936.2015.1075299

McDowell, L. J., Wells, D. L., Hepper, P. G., & Dempster, M. (2016). Lateral bias and temperament in the domestic cat (*Felis silvestris*). *Journal of Comparative Psychology*. https://doi.org/10.1037/com0000030

McLean, A. N., & Christensen, J. W. (2017). The application of learning theory in horse training. *Applied Animal Behaviour Science*. https://doi.org/10.1016/j.applanim.2017.02.020

Mellor, D. J., & Beausoleil, N. J. (2015). Extending the "Five Domains" model for animal welfare assessment to incorporate positive welfare states. *Animal Welfare*. https://doi.org/10.7120/09627286.24.3.241

Merola, I., Lazzaroni, M., Marshall-Pescini, S., & Prato-Previde, E. (2015). Social referencing and cat–human communication. *Animal Cognition*. https://doi.org/10.1007/s10071-014-0832-2

Miklósi, Ádám, Kubinyi, E., Topál, J., Gácsi, M., Virányi, Z., & Csányi, V. (2003). A simple reason for a big difference: Wolves do not look back at humans, but dogs do. *Current Biology*. https://doi.org/10.1016/S0960-9822(03)00263-X

Miklósi, Ádam, Pongrácz, P., Lakatos, G., Topál, J., & Csányi, V. (2005). A comparative study of the use of visual communicative signals in interactions

between dogs (*Canis familiaris*) and humans and cats (*Felis catus*) and humans. *Journal of Comparative Psychology*. https://doi.org/10.1037/0735-7036.119.2.179

Neidhart, L., & Boyd, R. (2002). Companion animal adoption study. *Journal of Applied Animal Welfare Science*. https://doi.org/10.1207/S15327604JAWS0503_02

Palagi, E., Cordoni, G., & Borgognini Tarli, S. M. (2004). Immediate and delayed benefits of play behaviour: New evidence from chimpanzees (*Pan troglodytes*). *Ethology*. https://doi.org/10.1111/j.1439-0310.2004.01035.x

Plyusnina, I. Z., Solov'Eva, M. Y., & Oskina, I. N. (2011). Effect of domestication on aggression in gray Norway rats. *Behavior Genetics*. https://doi.org/10.1007/s10519-010-9429-y

Pongrácz, P., & Szapu, J. S. (2018). The socio-cognitive relationship between cats and humans – Companion cats (*Felis catus*) as their owners see them. *Applied Animal Behaviour Science*. https://doi.org/10.1016/j.applanim.2018.07.004

Proctor, H. S., & Carder, G. (2015). Measuring positive emotions in cows: Do visible eye whites tell us anything? *Physiology and Behavior*. https://doi.org/10.1016/j.physbeh.2015.04.011

Reefmann, N., Wechsler, B., & Gygax, L. (2009). Behavioural and physiological assessment of positive and negative emotion in sheep. *Animal Behaviour*. https://doi.org/10.1016/j.anbehav.2009.06.015

Scott, S. K., Lavan, N., Chen, S., & McGettigan, C. (2014). The social life of laughter. *Trends in Cognitive Sciences*. https://doi.org/10.1016/j.tics.2014.09.002

Seksel, K. (2008). Preventing Behavior Problems in Puppies and Kittens. *Veterinary Clinics of North America - Small Animal Practice*.

https://doi.org/10.1016/j.cvsm.2008.04.003

Siniscalchi, M., d'Ingeo, S., Minunno, M., & Quaranta, A. (2018). Communication in dogs. *Animals*. https://doi.org/10.3390/ani8080131

Susskind, J. M., & Anderson, A. K. (2010). Facial expression form and function. *Communicative & Integrative Biology*. https://doi.org/10.4161/cib.1.2.6999

Veenema, H. C., Das, M., & Aureli, F. (1994). Methodological improvements for the study of reconciliation. *Behavioural Processes*. https://doi.org/10.1016/0376-6357(94)90035-3

Vitale Shreve, K. R., Mehrkam, L. R., & Udell, M. A. R. (2017). Social interaction, food, scent or toys? A formal assessment of domestic pet and shelter cat (*Felis silvestris catus*) preferences. *Behavioural Processes*. https://doi.org/10.1016/j.beproc.2017.03.016

Waller, B. M., & Dunbar, R. I. M. (2005). Differential behavioural effects of silent bared teeth display and relaxed open mouth display in chimpanzees (*Pan troglodytes*). *Ethology*. https://doi.org/10.1111/j.1439-0310.2004.01045.x

Yeates, J. W., & Main, D. C. J. (2008). Assessment of positive welfare: A review. *Veterinary Journal*. https://doi.org/10.1016/j.tvjl.2007.05.009

Appendices

Appendix 1: The role of cat eye narrowing movements in cat-human communication

Supplementary Information

Experiment 1.

Instructions for owners:

<u>Verbal instructions</u>

With a positive yet calm expression, close your eyelids slowly and purposefully whilst drawing your cheeks upward. Try to slow this action down to around 2-3 seconds.

Be careful not to also lower your eyebrow or wrinkle your nose.

<u>Additional FACS instructions made available</u>

<u>AU 12</u> Pull the corners of your mouth up and backwards into a U shape (deepening the crease to the outside of the mouth) this will raise the adjacent skin upward.

     a. The cheeks are pushed upward which should also narrow the eye aperture

     b. The deepening of the crease below your eyes is more evident

    c. The skin below the lower eyelid bags

    d. Produces crow's feet at eye corners

AU 6 Ensure that the skin from the temple and cheeks is drawn toward the eye – as the outer band of muscle around the eye constricts (similar effects to that of AU12)

AU 7 Tense your eyelids but not enough to close your eyelids completely. Do it as weakly as you can.

[If you have difficulty, think about narrowing your eye aperture to a slit so that you can see your eyelashes. Be careful you are not also lowering your eyebrow (AU 4). Be careful you are not also wrinkling your nose (AU 9).]

More complex definition for those who find it difficult (to be spoken through by the experimenter)

AU 6: Concentrate on lifting your cheeks without actively raising up the lip corners (that is AU 12).

The muscle underlying AU 6 (like that responsible for AU 7) circles the eye orbit, but it has a larger circumference that extends into the eyebrow and below the lower eye furrow. Action Unit 6 pulls skin towards the eye.

1. Draws skin towards the eye from the temple and cheeks as the outer band of muscle around the eye constricts.

2. Raises the infraorbital triangle, lifting the cheek upwards.

3. Pushes the skin surrounding the eye towards the eye socket, which can narrow the eye aperture, bag or wrinkle the skin below the eye, and push the eye cover fold down and/or change its shape.

4. May cause crow's feet lines or wrinkles to appear, extending radially from the outer corners of the eye aperture.

5. Deepens the lower eyelid furrow. (Apparent in image w6 more than in 6.)

6. May lower lateral portion of the eyebrows to a small extent (in image w6 not 6).

7. A strong AU 6 may:

a. Make evident or deepen the nasolabial furrow.

b. Raise the outer portions of the upper lip to a small extent.

c. Make evident or deepen the infraorbital furrow, so that this wrinkle runs across the top of the infraorbital triangle in a straight or crescent-like shape.

AU 7: This movement is fairly easy to do. Tense your eyelids but not enough to close your eyelids completely. Do it as weakly as you can. If you have difficulty, think about narrowing your eye aperture to a slit so that you can see your eyelashes. Be careful you are not also lowering your eyebrow (AU 4). Be careful you are not also wrinkling your nose (AU 9). Be careful you are not also raising your cheeks (AU 6).

AU 12: This movement is an easy to do. Smile. Imitate image 12i. Holding a weak version on your face, slowly increase the extent of action and watch as your face begins to resemble 6+12ii and 6+12+25ii.

1. Pulls the corners of the lips back and upward (obliquely) creating a U shape to the mouth

2. Deepens the nasolabial furrow, pulling it laterally and up. The skin adjacent to the nasolabial furrow is raised up and laterally.

3. In a weak to moderate 12, there is some raising of the infraorbital triangle and there may be some deepening of the infraorbital furrow.

4. In a strong action, one or more of the following:

a. The infraorbital triangle push upwards is more evident.

b. The infraorbital furrow deepening is more evident.

c. Bags the skin below the lower eyelid.

d. Narrows the eye aperture by pushing up the cheek and skin below the lower lid.

e. Produces crow's feet at eye corners.

f. May raise and widen the nostrils.

g. May flatten and stretch the skin on the chin boss

Experiment 2.

Facial Expression Instructions for Experimenter

Slow Blink Stimulus

For the slow blink stimulus, purposefully and slowly lower your eyelids whilst drawing your cheeks upward, toward the eye.

Try to perform this expression slower than you usually would in a conversation (approximately 2-3 seconds). Be careful not to also lower your eyebrow or wrinkle your nose.

Neutral Face Control

For this action try to release from muscle tension in the face. To do this it may help to relax and calm your thoughts, as if in a meditative state. Gaze slightly to the side of the cat whilst keeping your face forward towards the cat.

Be careful not to hold the expression too strongly, to avoid looking stern whilst performing this facial expression.

Appendix 2: Shelter cats that slow blink are adopted more quickly

Statistical Analysis:

No significant difference was found between desensitisation and non-desensitisation groups in the duration (desensitisation: M = 2.39 ± 2.36; non-desensitisation: M = 2.93 ± 3.26; U = 33.00, p = 0.57) or number (desensitisation: M = 3.00 ± 2.98; non-desensitisation: M = 5.20 ± 4.47; U = 28.00, p = 0.32) of half blinks. There were no significant differences between the desensitisation and non-desensitisation groups in the duration (desensitisation: M = 12.78 ± 14.14; non-desensitisation: M = 8.82 ± 9.72; U = 31.00, p = 0.46) or number (desensitisation: M = 4.00 ± 2.88; non-desensitisation: M = 2.90 ± 2.08; U = 30.50, p = 0.41) of eye narrowing. The desensitisation groups also did not significantly differ in the duration (desensitisation: M = 16.73 ± 22.73; non-desensitisation: M = 6.24 ± 10.83; U = 30.00, p = 0.41) or number (desensitisation: M = 1.63 ± 1.92; non-desensitisation: M = 1.00 ± 1.41; U = 31.00, p = 0.46) of eye closures. No significant difference was found between desensitisation and non-desensitisation groups in duration (desensitisation: M = 31.02 ± 19.95; non-desensitisation: M = 22.33 ± 20.57; U = 29.00, p = 0.36) or number (desensitisation: M = 2.88 ± 2.10; non-desensitisation: M = 3.00 ± 2.11; U = 38.50, p = 0.90) of looking behaviours.