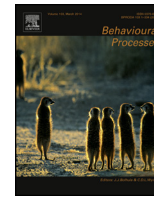
Behavioural Processes 141 (2017) 342–350

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Facial correlates of emotional behaviour in the domestic cat (*Felis catus*)

Valerie Bennett[a], Nadine Gourkow[b], Daniel S. Mills[a,*]

[a] Joseph Banks Laboratories, School of Life Sciences, University of Lincoln, Lincoln, Lincs LN6 7DL UK
[b] University of Queensland, Gatton Qld 4343, Centre for Animal Welfare and Ethics, The Whitehouse Building 8143, Australia

ARTICLE INFO

Article history:
Received 4 November 2016
Received in revised form 3 March 2017
Accepted 15 March 2017
Available online 21 March 2017

Keywords:
Cat
Emotion
Face
Fear
Frustration
Leyhausen

ABSTRACT

Leyhausen's (1979) work on cat behaviour and facial expressions associated with offensive and defensive behaviour is widely embraced as the standard for interpretation of agonistic behaviour in this species. However, it is a largely anecdotal description that can be easily misunderstood. Recently a facial action coding system has been developed for cats (CatFACS), similar to that used for objectively coding human facial expressions. This study reports on the use of this system to describe the relationship between behaviour and facial expressions of cats in confinement contexts without and with human interaction, in order to generate hypotheses about the relationship between these expressions and underlying emotional state. Video recordings taken of 29 cats resident in a Canadian animal shelter were analysed using 1-0 sampling of 275 4-s video clips.

Observations under the two conditions were analysed descriptively using hierarchical cluster analysis for binomial data and indicated that in both situations, about half of the data clustered into three groups. An argument is presented that these largely reflect states based on varying degrees of relaxed engagement, fear and frustration. Facial actions associated with fear included blinking and half-blinking and a left head and gaze bias at lower intensities. Facial actions consistently associated with frustration included hissing, nose-licking, dropping of the jaw, the raising of the upper lip, nose wrinkling, lower lip depression, parting of the lips, mouth stretching, vocalisation and showing of the tongue. Relaxed engagement appeared to be associated with a right gaze and head turn bias. The results also indicate potential qualitative changes associated with differences in intensity in emotional expression following human intervention. The results were also compared to the classic description of "offensive and defensive moods" in cats (Leyhausen, 1979) and previous work by Gourkow et al. (2014a) on behavioural styles in cats in order to assess if these observations had replicable features noted by others. This revealed evidence of convergent validity between the methods However, the use of CatFACS revealed elements relating to vocalisation and response lateralisation, not previously reported in this literature.

1. Introduction

Emotions are responses to specific, personally salient events, factors of importance to the individual, and so can be expected to involve specific neurophysiological responses for each type of emotion, which may be aroused in different contexts according to that individual (Ledoux, 1998; Fox, 2008). What one individual finds fearful another may not, but when fearfully aroused, both individuals will show a similar response. A primary function of emotional responses is to mobilise an organism in response to unexpected change and so they involve relatively innate, species-typical behavioural and physiological responses (Lang et al., 1993; Fox, 2008). It has been argued that in mammals there are a number of fundamental but relatively neurobiologically 'discrete' emotional (affective) systems associated with complex motor responses such as fear, frustration/rage and social panic, which serve specific adaptive functions associated with particular contexts (Ekman, 1992; Panksepp, 1998; Panksepp and Biven, 2012). Fear is aroused by the anticipation or presence of an aversive stimulus, whilst rage/frustration is triggered by the denial of a valued incentive and/or where expectations are not met, and social panic arises when an individual is separated from important sources of safety and security (Panksepp, 1998; Panksepp and Biven, 2012). These responses to certain situations cause changes in arousal, behavioural tendency and communicative signals (Scherer, 1984),

* Corresponding author.
E-mail address: dmills@lincoln.ac.uk (D.S. Mills).

http://dx.doi.org/10.1016/j.beproc.2017.03.011
0376-6357/

and the study of emotion may focus on one or more of these components (Fox, 2008). For example, in humans, Ekman and Friesen (2003) showed that the emotions of anger (rage), fear and disgust are spontaneously expressed as a result of activation of the autonomic nervous system, emphasising the role of autonomic arousal in their spontaneous expression. By contrast, studies such as those in people with facial paralysis which have focused on their difficulty in developing or maintaining personal relationships (Ross, 1981), emphasise the role of communication (via the face) in the emotional responses associated with the development/regulation of interpersonal relationships.

The face is widely used to assess emotional expression, but especially the expression of pain in individuals who cannot speak, for example some of the elderly and neonates (Rinn, 1984) and, more recently, non-human animals such as the mouse (Langford et al., 2010), rat (Sotocinal et al., 2011), horse (Dalla Costa et al., 2014), rabbit (Hampshire and Robertson, 2015), and cat (Holden et al., 2014). Darwin (1872) described facial expression of a wide range of emotions across species in his seminal text, 'The Expression of the Emotions in Man and Animals', in which he argued that the contraction of specific muscle groups creates spontaneous facial expressions. This idea has been pursued extensively in humans following the work of Hjortsjö (1969) and Ekman and Friesen (1976) to objectively measure facial movement. By contrast, scientific interest in facial expressions of emotions other than pain has received remarkably patchy attention in the non-human animal-related literature, despite its clear importance to understanding the effective functioning of individuals. A potential exception to this is recent interest in this phenomenon in dogs (e.g. Guo et al., 2009; Bloom and Friedman, 2013; Albuquerque et al., 2016; Somppi et al., 2016).

Historically, general ethograms of emotional expression typically include a name for the behaviour being expressed, a description of its appearance, any accompanying vocalisation and perhaps information on how the behaviour is used or perceived socially by conspecifics (e.g. see Parr et al., 2007). Whilst there is little disagreement that the use of such ethograms has advanced our understanding of animal behaviour, there is justifiable concern over the subjective elements of this process (Ekman and Friesen, 1978). This includes the interpretation of meaning and the impressions of an observer in their report of the important facial features in emotionally ambiguous contexts.

Facial expressions associated primarily with emotional arousal are the result of relatively stereotyped movements of facial skin and underlying connective tissue due to contraction of facial muscles in certain combinations. Such contractions create folds, lines, and wrinkles in the skin and cause movements of facial landmarks such as the eyebrows and mouth corners (Rinn, 1984), as well as more obvious landmarks such as the ears and whiskers. Description in terms of specific muscle movement provides a more objective and direct representation of the actions of the nervous system than attempts at global description of the poses expressed at the level of the skin associated with their movement (e.g. a smile). Thus coding behavioural change from video is also preferable to using static images (Russell and Fernández-Dols, 1997). This focus on coding the dynamic activity of individual muscle groups which give rise to facial expressions (rather than trying to describe the static global result) is the underlying principle of the Facial Action Coding System (FACS), which was originally developed for use in humans (Hjortsjö, 1969; Ekman et al., 1978). As a result of its focus on muscle group activity it can measure all visually discernible facial movement and several categories of head and eye positions and movements, by reference to unique action units. FACS not only provides an objective coding method for quantifying facial movement but also allows the effects of individual variations in bone structure, fatty deposits and permanent wrinkles (e.g. due to racial features) to be eliminated from the data. Although freely available, the FACS method requires some pre-training and needs to be used with caution to avoid bias (e.g. Russell, 1994); accordingly the developers of the system hold a register of qualified users for quality control purposes. Using these essential principles and knowledge of species-specific facial anatomy, open access FACS have been developed for use with other species such as chimpanzees, macaques, hylobatids, orangutans, the domestic dog, (Parr et al., 2007; Vick et al., 2007; Parr et al., 2010; Waller et al., 2012) and, most recently, the domestic cat (Caeiro et al., 2013a; Caeiro et al., 2017). Fig. 1 shows an example of the coding that would be associated with the mouth opening gesture illustrated in this sequence of images.

The main point of reference for inferring many of the emotional states of the cat comes from Leyhausen's (1979) seminal treatise on cat social and predatory behaviour. Emotional states were inferred from careful observation of the relationships between behavioural and facial expression in these contexts. In his text, "attack" and "defense" are described as types of mood (p194), and although the English translation of the original German work may have changed the terminology somewhat, it should be recognised that these terms do not refer to an emotional predisposition (mood) in a normal psychobiological sense. Indeed, terminology which is intended to refer to the emotional basis of a behaviour (e.g. fear) is often confused with that used to describe the style of a behaviour (aggressive) or its motivation (e.g. defensive) and this can give rise to problems with its scientific and practical assessment (Mills and Ewbank, 2016). Because emotions are an internal state, behaviour is only an indirect measure of their occurrence, (even when it is a good correlate in tasks like cognitive bias testing (Mendl et al., 2009)), and so it is important to acknowledge the basis on which these states are being inferred; this will typically involve inductive reasoning. Specific inductive research methods feature prominently within qualitative research methodologies. They overtly acknowledge and accommodate the uncertainty of some knowledge (Creswell, 2013; Denzin and Lincoln 2011), and so can be particularly useful to increasing our understanding of (or more generally exploring) phenomena such as mood and other subjective experiences which cannot be known for sure. Such qualitative methods seek to describe and explore the depth of phenomenon rather than test a specific hypothesis using a hypothetico-deductive experimental method. Indeed the original work of Leyhausen (1979) may be considered a form of qualitative research since it used naturalistic observation alongside reference to brain stimulation studies in the laboratory setting in order to make its inferences about the underlying motivational/emotional state of the cats. Results were purely narrative and do not appear to have been derived statistically. They must therefore be considered anecdotal description, and therefore provide a relatively low level of scientific evidence for the phenomenon (Hoppe et al., 2009). Nonetheless these observations continue to be widely reproduced with their interpretation in many standard texts on cat behaviour e.g. Bradshaw et al. (2012), Turner and Bateson (2000). More recently Gourkow et al. (2014a,b), Gourkow and Phillips (2015, 2016) provided objective quantifiable evidence of the behavioural styles of cats that might relate to their emotional predisposition. They identified that cats, following initial introduction to a shelter (Gourkow et al., 2014a,b), tended to show one of three groups of behaviour: either one related to hiding, flat postures, freezing, startling, crawling and retreat from humans; or one related to normal patterns of feeding, grooming, sleeping and locomotion, sitting at the front of the cage while calmly observing activities, sleeping or resting while lying on their side, rubbing on cage items and friendly behaviour towards humans; or one related to persistent meowing, scanning, pacing and pushing, bouts of destructive behaviour, escape attempts and redirected aggression. From the affective neuroscience perspective described by Panksepp (1998), these might broadly relate to FEAR, SEEKING and RAGE. They could therefore

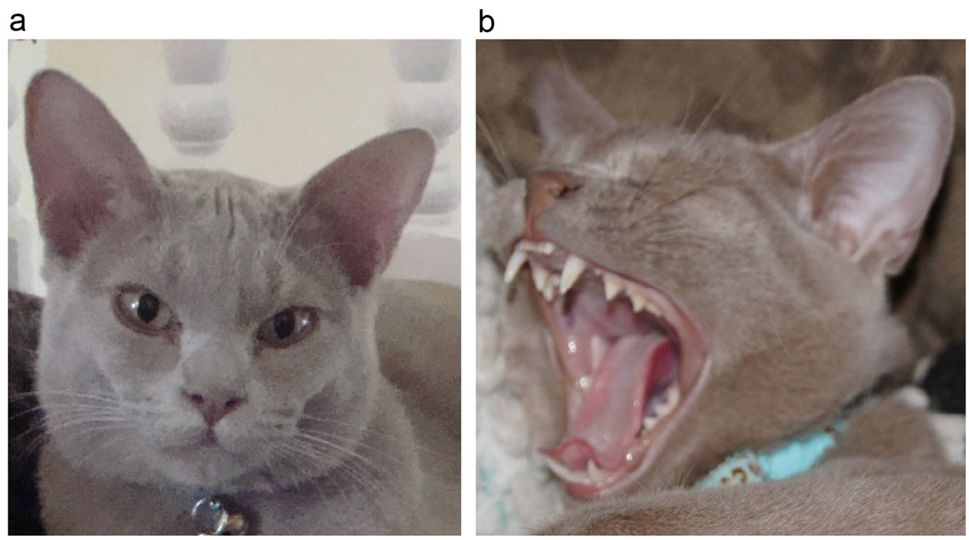


Fig. 1. (a, b) Example comparison of global coding versus FACS coding. Using global coding the mouth in Fig. 1a might be described as neutral and in Fig. 1b as a "Yawn", "Open mouth" or similar. In FACS coding reference is made to the observed differences between the two images by reference to the underlying action units. In this case involves raising of upper lip (AU109 + 110), lower lip depression (AU116) and mouth stretching (AU27). Images taken from CATFacs.com with permission.

be interpreted as providing some evidence of the behaviours that might be associated with these affective predispositions within a shelter setting. However, unlike Leyhausen (1979) no descriptions of the facial expressions of the cats were made in this latter work. Facial features have the potential to provide important initial cues for the assessment of cats that may predict their subsequent behaviour (Leyhausen, 1979). Despite the considerable advances in ethological methods since Leyhausen's time his reports and interpretations of the behaviour of cats, appear to have remained largely unchallenged and undeveloped. Therefore the aim of this research was to undertake a detailed ethological description of the behaviour and facial expression of cats in cages under two conditions, one when they were filmed from a distance and one when a human approached and interacted with them. We use inductive methods in order to evaluate the relationship between the patterns of signs shown in these circumstances and potential emotional states in cats. In order to more specifically assess the potential relationship between these signs and their underlying emotion, we were interested in the statistical clustering of behaviour and facial expressions, rather than anecdotal observations (as per Leyhausen, 1979) or the clustering of behaviours into particular styles for a given individual (as per Gourkow et al., 2014a) rather than a temporary state within it. By observing cats in two conditions, one on their own in a cage, which appears to have the potential to invoke exploration, fear and frustration, the other involving interaction with a human, which might be expected to intensify these states, and comparing our results to those previously described, we also aimed to be able to comment on both the reliability of the grouping of responses as potential indicators of emotional arousal and their potential change with emotional intensity. The hypotheses generated here lay the foundation for future quantitative experimental evaluations.

2. Material and methods

2.1. Design

This was an inductive, qualitative research study (Creswell, 2013) examining the behaviour of cats in a previously undertaken study. As such the emphasis was on detailed description and inductive reasoning from these observations rather than deduction from an experiment designed to test a specific hypothesis. Video recordings taken by Gourkow as part of her previously reported work (Gourkow et al., 2014b) were used. These featured 29 (15 female, 14 male) cats resident in a Canadian animal shelter in two conditions, one in which no human interaction occurred, and one with human interaction.

All cats were housed individually in a stainless steel cage (76 cm × 76 cm × 71 cm) furnished with a litter box and non-absorbent cat litter; stainless steel bowls for food and water and a towel for bedding. Food was provided twice a day and water was available *ad libitum*. Cages were cleaned daily by removing all waste, changing bedding and wiping walls with a clean cloth soaked in water. Windows provided natural light. An ambient temperature of $20 \pm 2°$c was maintained.

Video footage of the cats was obtained in the same way in both conditions using a video camera (Sony CCD25 M crystal-view super Hi-Res ICR IR Camera SLED w/9–22 mm vari-focal lens, Microtech Advanced Technologies Ltd), set up 1 m from the cages, set to record continuously. Data were extracted from the first 10 min of recording in each hour. Twenty seven cats provided data from when they were alone in the cage, and 28 provided data relating to their response to interaction (26 cats were common to both situations).

2.2. Human interaction protocol

Interactions lasted 10 mins and involved a human standing by the cat's cage and calling their name; opening the cage door; stroking the cat, either by hand or with a stick. Cats were initially interacted with for 1 min by stroking the cheek, under the chin, and between the ears; with continuous vocal interaction. This was followed by 1 min of withdrawal, during which time the experimenter closed the cage door and stood to the side of the cage out of view, but observing the cat on a computer screen. If the cat stretched his/her neck with attention oriented towards front left of the cage (the location of the experimenter) within 1 min, the interaction was initiated immediately. If not, interaction was initiated at the end of the 1 min interruption. This cycle continued for the 10 min period. For cats who were not overtly aggressive, including those who were simply avoidant, interaction was with the hand. If the cat was aggressive during greeting (growling and/or hissing, with or without paw strike), the interaction was done with the aid of an extendable stick with a round rubber tip (Target stick, The Clicker Company, Canada:www.clickercompany.com). The door remained closed; the tool was slid through the bars along the floor and raised up to the cat's chin initially, then over the cheeks and between the ears (see Gourkow et al., 2014b for further details).

2.3. Behavioural and facial observations

The behaviour and facial features of subjects were coded from the 10 min video recordings, using clips that showed both the cat's face and general behaviour during the clip. 1-0 behavioural sampling was used to note the occurrence of both a facial and behavioural event during each observation period.

For general behaviours, the ethogram, defining location (6 categories), posture (11 categories) and behaviour (23 categories) previously used by Gourkow (Gourkow et al., 2014a) was adapted for use. To this list of 40 items one further behavioural category was added: "yowl/growl", defined as "a growling or wailing sound emitted from a closed or open mouth". The following four subjective rating variables were also added to the coding system to assess the cats' response to humans; 'neutral', 'friendly', 'aggressive' and 'retreat'.

Facial analysis was undertaken by a trained CatFACS observer (VB) independent of the researcher (NG) involved in gathering the data, by reference to the 48 distinct action units described in this system (http://www.catfacs.com/Caeiro et al., 2013b). A second CatFACS certified observer analysed 25% of the video clips in order to determine the level of inter-observer reliability.

Gross behavioural changes can involve a greater degree of inertia than facial expressions, due to both the amount of mass being displaced and the functional role of the two types of emotional response, with facial expression allowing rapid initial assessment of the individual before closer interaction and the potential provocation of an overt behavioural response (Frith, 2009). To accommodate this potential lack of synchrony between facial and behavioural events which is well recognised in cats (Leyhausen, 1979), we analysed video clips relating to gross behaviour (including posture and location) and facial response over different time periods within suitable four second clips, following pilot studies. Facial coding focused on the changes occurring in first two seconds while behaviour analysis extended over the whole of the four second period. A sampling duration of two seconds was long enough to facilitate the observation of an acceptable amount of facial change for our purposes, without too high a risk of including facial changes associated with several events within a single clip; with four seconds providing a similar balance for behavioural observations. In order to impart a degree of independence between samples, we decided *a priori*, that clips needed to be separated by a minimum of three seconds to be considered suitable for the descriptive analysis undertaken, having carefully considered the potential impact of pseudoreplication on the inferential context of the work (Hurlbert, 1984; Schank and Koehnle, 2009).

Finally, in order to explore the validity of our results we used CatFACS to code Leyhausen's (1979) facial ethogram of 'defensive and offensive moods in cats', using the neutral face as the point of reference for facial change. Similarity would demonstrate convergent validity and increase the robustness of our findings.

2.4. Statistical analysis

Inter-observer reliability was assessed using Cohen's Kappa coefficient. Data consisted of binomial scores relating to the presence or absence of the behaviour within a given clip. For each of the two conditions, events occurring in less than 10% of observation periods were excluded from analysis. In order to examine which events reliably grouped together, the data for each of the two conditions (no interaction vs interaction) were then subjected to hierarchical cluster analysis using between groups linkage on the basis of a Jaccard measure of distance for binary variables (Finch, 2005). Dendrograms were inspected to determine the number of clusters, and non-clustering variables excluded from interpretation. These analyses were conducted using SPSS Statistics 22 (IBM).

3. Results

3.1. Video analysis

In total, 275 video clips of facial (550 s) and behavioural (1100 s) observations were used for analysis. 112 clips were obtained from the videos of cats alone (with individual subjects providing between 1 and 17 clips), and 163 clips relating to interaction with a human (with a range of 1–15 clips per cat). Inter-observer reliability was acceptable (K = 0.86).

For the cluster analysis of variables when there was no interaction with the cat, 61 variables occurred in at least 10% of incidences, with 31 of these clustering into 3 distinct clusters (Fig. 2): one cluster of 13 variables, which appear to relate to frustration, one cluster of 10 variables that appear to relate to fear and one cluster of 8 variables that seem to relate to relaxed interest in the environment (low level SEEKING *sensu* Panksepp).

For the cluster analysis of variables associated with interaction with the human, 36 variables occurred in at least 10% of incidences, with 32 of these clustering into 3 distinct groups (Fig. 3). These seem to largely reflect and replicate the groups in the previous analysis, although the third relaxed cluster seems to now contain an element of caution. 16 variables make up the first and largest cluster with 10 variables in common between the two conditions, 6 variables make up the second cluster with 3 variables common to both conditions (freezing, hiding and lying in sternal recumbency with body flattened to the floor and neck retracted with head held low- ventral flat), 10 variables now make up the third cluster with four of these in common across the two conditions (ears forward, ears adducted, being at the front of the cage and lying sternally recumbent with a relaxed body – ventral high).

3.2. CatFACs analysis of Leyhausen

The results of the use of the CatFACS assess Leyhausen's (1979) facial ethogram of 'offensive and defensive' moods in cats, using the neutral face (A_0B_0) as the point of reference for facial change are shown in Fig. 4. In Leyhausen's text, he suggests that the top right image (A_2B_0) represents the "strongest threat of attack", and the bottom left (A_0B_2) "the greatest readiness for defense".

4. Discussion

This study describes for the first time the unique clustering of facial and behavioural features of confined cats, and their response to the approach of a human. Like Gourkow et al. (2014a), we found that the behaviour clustered into three groups, but whereas the latter study focused on the behavioural style of cats using factor analysis of frequency and duration data, this study focused on the grouping of behaviour across individuals using dichotomous scoring of the behaviour (present-absent) over a short period of time followed by a cluster analysis for binomial data. The similarity in the findings, facilitated by using in part the same ethogram, add greatly to the robustness of the associations described.

For example, in both the current study and that of Gourkow et al. (2014a) freezing, ventral flat posture, hiding and retreating were found to group together and we suggest these are all part of the typical fear response of cats. The initial fear response is characterized by behavioural inhibitory components and, as such, the animal is seen to freeze (Panksepp, 1998). Previous work has also demon-

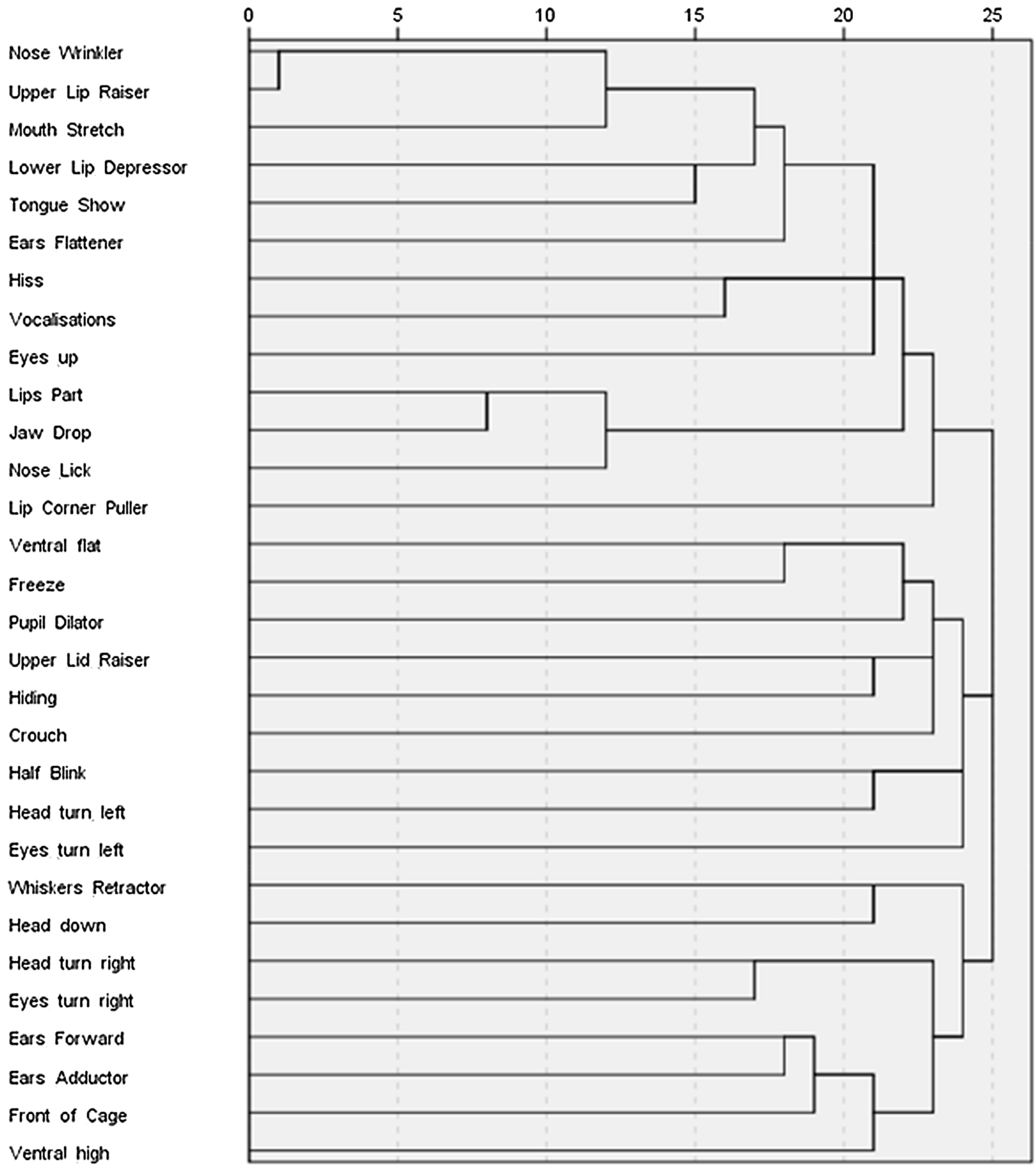


Fig. 2. Dendrogram showing the grouping of 31 variables (1-0 sampling) observed to occur in more than 10% of 112 observations of 27 cats contained with a cage without interaction from the observer. Observations cluster from left to right on the basis of an average linkage function. Many terms are largely self explanatory except ventral high which refers to the cat being at the front of the cage and lying sternally recumbent with a relaxed body, but see See Gourkow et al. (2014a) for full definition of terms.

strated that in circumstances such as hospitalization or animal shelter situations, cats tend to freeze before attempting to escape or hide (e.g. Tsyrlin et al., 1983; Carlstead et al., 1993; Kry and Casey, 2007). The current work, importantly adds facial actions to these behavioural elements. In the condition without human interaction, the CatFACS identifies several associations with this behaviour; the involvement of the ear rotator and pupil dilator seem to be most closely aligned to the central image (A_1B_1) in Leyhausen's facial ethogram, while the involvement of the ear rotator and upper lid raiser are features of the top right hand image (A_2B_0), which Leyhausen describes as the expression of the strongest threat to attack. Both this image and our own analysis indicate a bias in the gaze of the cat to the left in this expression, and a left gaze bias is associated with right hemispherical dominance for the processing of more negative stimuli across many species (Rogers, 2010). A left head turning bias has also been reported to occur in dogs in relation to negative visual stimuli (Siniscalchi et al., 2010), supporting the suggestion that this lateralisation is not coincidental; however,

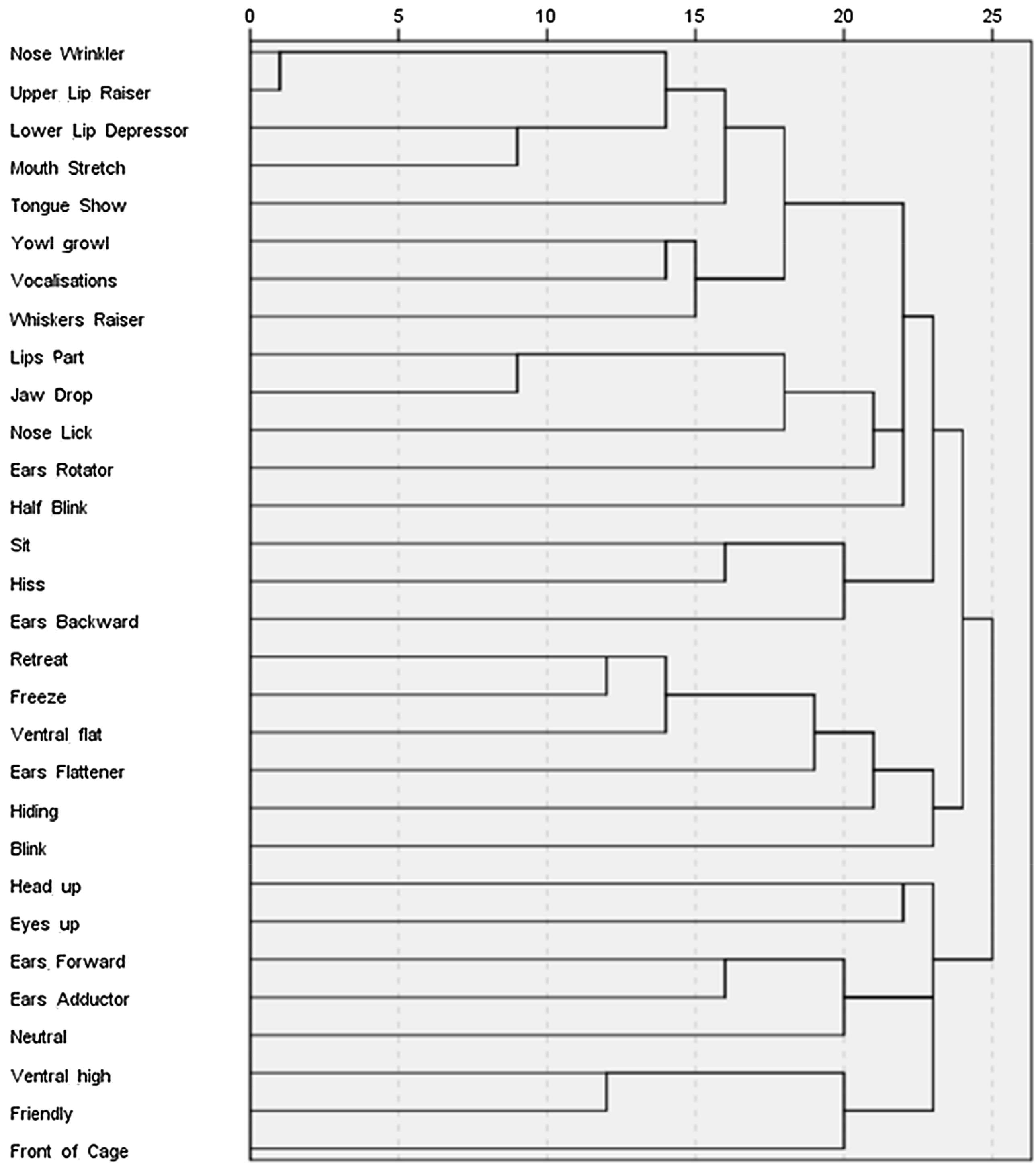


Fig. 3. Dendrogram showing the grouping of 32 variables (1-0 sampling) observed to occur in more than 10% of 163 observations of 28 cats contained with a cage with interaction from the observer. Observations cluster from left to right on the basis of an average linkage function. Many terms are largely self explanatory except ventral high which refers to the cat being at the front of the cage and lying sternally recumbent with a relaxed body, but see Gourkow et al. (2014a) for full definition of terms.

the loss of the bias in the interaction situation, might indicate that it is perhaps a feature more obvious in the less intimate situation, i.e that it is a cue that can be detected at a distance, which may be irrelevant when individuals are very close one another. The increased proximity and interaction with a human, as occurs in the second condition, appears to have a number of effects. The cat retreats and blinking is now associated with its response, as well as ear flattening. In contrast to Gourkow's findings (2014a), ear flattening is associated with the cluster that seems to reflect frustration in the non-interaction setting (see below), and its inclusion in the response alongside clear fear elements in this second condition is consistent with the involvement of an element of frustration in this second condition, as the retreat and hiding and freezing would not be expected to provide the animal with sufficient security, resulting in an element of frustration, in relation to access to safety. This suggestion is further supported by the cross reference to Leyhausen's ethogram. The facial description at this time, aligns most closely with features of the middle image of the first column in Ley-

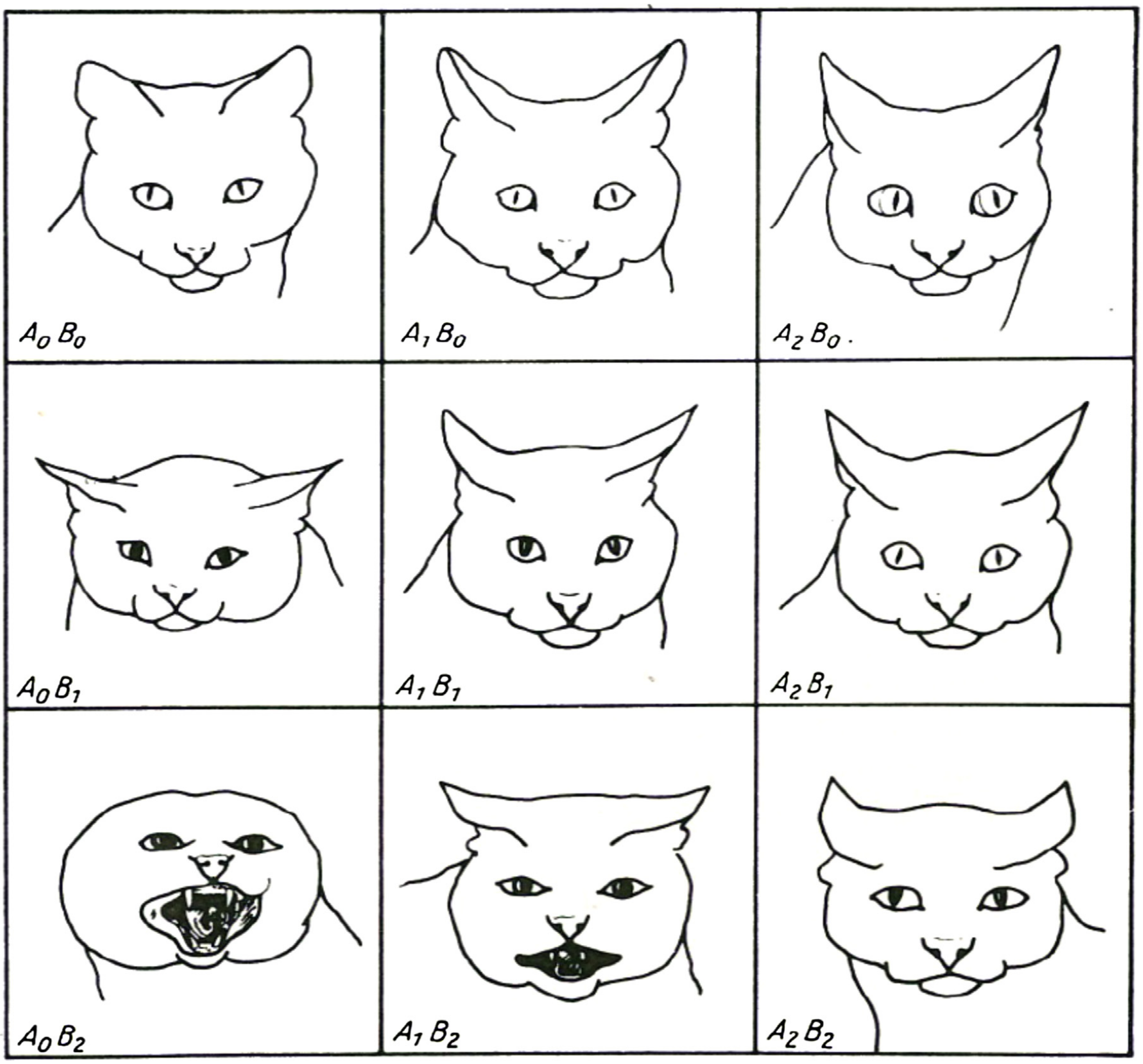


Fig. 4. Leyhausen's facial expressions of offensive and defensive mood (taken from Leyhausen 1979) coded using CatFACS. A_0B_0: neutral face used for reference; A_1B_0: Upper lid raiser (AU105), Ears adductor (EAD 102), Ears rotator (EAD104), A_2B_0: Upper lid raiser (AU105), Eyes left (AD61), Ears rotator (EAD 104), A_0B_1: Pupil dilator (AD68), Ears flattener (EAD103); A_1B_1: Pupil dilator (AD68), Ears flattener (EAD103), Ears rotator (EAD104); A_2B_1: Ears flattener (EAD103), Ears Rotator (EAD104); A_0B2: Lower lip depressor (AU116), tongue show (AD19), Lips part (AU125), Jaw drop (AU126), Mouth stretch (AU27), Vocalisations (AD50), Eyes up (AD63) Pupil dilator (AD68), Ears flattener (EAD103), Nose wrinkler (AU109), Upper lip raiser (AU110); A_1B_2: Tongue show (AD19), Lips part (AU25), Jaw drop (AU26), Pupil dilator (AD68), Ears flattener (EAD103); A_2B_2: Eyes up (AD63), Pupil dilator (AD68), Ears flattener (EAD103), Ears rotator (EAD104). See CatFACS.com for videos and descriptions of these actions.

hausen's ethogram (A_0B_1), which seems to be the prelude to a more overt threat (bottom left image, A_0B_2). The body posture also seems to align with that indicated by Leyhausen at this time (Leyhausen 1979; Fig 17-3 A_0B_1 and A_0B_2 p194).

The largest cluster groups together hissing, nose-licking, dropping of the jaw, the raising of the upper lip, nose wrinkling, lower lip depression, parting of the lips, mouth stretching, vocalisation and showing of the tongue. This has many similarities to the facial image at the bottom of the first column (A_0B_2) described by Leyhausen (1979) and indicates high arousal associated with repulsion. Without human interaction, the gaze of the eyes are directed upwards, ears flattened and lip corners retracted, and these elements disappear with interaction, to be replaced by half blinking, the ears rotated and back, the whiskers raised and yowling/growling appears. Interestingly, the rotation of the ears and half blink are both elements identified with the potential expression of fear described above.

Intense fear is commonly characterised by flight (Panksepp, 1998). If, as Panksepp (1998) postulates, the fear and frustration circuits are intimately related, this overlap is not surprising especially if hiding or flight is thwarted, alongside the opportunity to avoid bodily harm, however this is not to say they result in the same behavioural display. The fearful cat that is thwarted from escape can only defend itself and so will display aggressive behaviours such as biting and scratching alongside defensive postures, which would not be expected in the simply frustrated cat. It is perhaps notable that there are few behavioural categories aligned consistently with the facial expression in this cluster, except sitting. Leyhausen (1979) noted that the expression of posture and facial expression that he describes in his offensive and defensive moods do not necessarily coincide, except in extremis. In this latter situation both facial and behavioural responses are less variable and coincide, whereas when the animal is less intensively aroused facial expressions are much more labile and responsive than overt behaviour. By contrast, Gourkow et al. (2014a) identified a behaviour grouping that included physically aggressive displays involving biting and paw swiping, which may reflect a more intensive response if the facial features described here are ignored. Such overt aggressive behaviour may not be evident in this study as the interaction was not designed to be so intrusive or aversive, however the absence of consistently associated overt behavioural signs of withdrawal leads us to speculate that these collections of signs may both reflect frustration. In the current study the absence of overt behavioural correlates may simply reflect the variety of contexts in which this occurred, and in humans, frustration can be one of the hardest emotions for automatic systems to detect from body posture (D'Mello and Graesser, 2009); by contrast Gourkow et al. (2014a) focused on identifying groupings of cats who shared certain behavioural characteristics, one group tended to push and persistently attempt to escape from the cage, while another group were aggressive. Rather than identifying specific signs of frustration, this latter study may be largely describing particular contexts that might lead to frustration due to the cat's temperament; by contrast, our study potentially identifies useful facial markers of specific states. Other than the overt hiss, and facial processes involved in expressing this, it seems flattening of the ears may be a useful marker of frustration. This would then suggest that descent from the neutral face of the cat described by Leyhausen (1979) may actually reflect at least in part, increasing frustration.

The third cluster in the situation without human interaction appears to describe a cat engaged with its environment in a relaxed way with ears forward and adducted, and the cat at the front of the cage in sternal recumbency with a relaxed body, the whiskers are retracted and head down. Interestingly, there is also a noticeable laterality to the facial posture of the cats with a right gaze and head turn noted around this time. During interaction, the head and eyes become raised and there is a noticeable shift in this laterality to the left. The cat remains friendly or neutral to the interaction, but these changes might indicate that the cat has a greater attentional focus on the person, and approaches them with a degree of trepidation. This shows some commonality with the third component described by Gourkow et al. (2014a) which appeared to describe a relaxed cat at the front of its cage.

Cat faces are variable in form, for example Siamese versus Persian breeds, and are often covered in hair (with the exception of breeds such as the Sphinx). This can make distinguishing the nuances of facial expression in cats, in general, challenging, since there is no clear nor consistent neutral face; a problem that has been found in other species (Parr et al. (2007) and Bloom and Friedman (2013)). This would be problematic if facial coding was based on static or standard morphometric features, but is overcome by basing facial action coding on the observed movements, regardless of the preceding reference point. Thus CatFACS allows the coding of facial changes regardless of breed or starting point. Leyhausen's (1956) facial ethogram of "offensive and defensive moods" has been widely seen as the definitive guide to understanding cat expression, but he did not record movements of the eyes (such as blinking), lips or tongue, which are noted here. It therefore seems that the development and use of CatFACS provides a new opportunity to review and elucidate his original quite prescient findings.

Note

The behavioural units described here are all taken from the catFACS, videos and descriptions of which are freely accessible from www.catfacs.com.

References

Albuquerque, N., Guo, K., Wilkinson, A., Savalli, C., Otta, E., Mills, D., 2016. Dogs recognize dog and human emotions. Biol. Lett. 12, p.20150883.

Bloom, T., Friedman, H., 2013. Classifying dogs' (*Canis familiaris*) facial expressions from photographs. Behav. Proc. 96, 1–10.

Bradshaw, J.W.S., Casey, R.A., Brown, S.L., 2012. The cat: domestication and biology. Behav. Domest. Cat (Ed. 2), p 99.

Caeiro, C.C., Waller, B.M., Burrows, A.M., Zimmerman, E., Davila-Ross, M., 2013a. OrangFACS: A muscle-based coding system for orangutan facial movements. Int. J. Primatol. 34, 115–129.

Caeiro, C.C., Waller, B.M., Burrows, A.M., 2013b. CatFACS: The Cat Facial Action Coding System Manual. Department of Psychology, University of Portsmouth, UK, Retrieved from www.CatFACS.com.

Caeiro, C.C., Burrows, A.M., Waller, B.M., 2017. Development and application of CatFACS: Are human cat adopters influenced by cat facial expressions? Appl. Anim. Behav. Sci., http://dx.doi.org/10.1016/j.applanim.2017.01.005.

Carlstead, K., Brown, J.L., Strawn, W., 1993. Behavioural and physiological correlates of stress in laboratory cats. Appl. Anim. Behav. Sci. 12, 143–158.

Creswell, J.W., 2013. Research Design: Qualitative, Quantitative, and Mixed Methods Approaches. Sage Publications.

D'Mello, S., Graesser, A., 2009. Automatic detection of learner's affect from gross body language. Appl. Artif. Intell. 23, 123–150.

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 9, p.e92281.

Darwin, C., 1872. The Expression of the Emotions in Man and Animals. University of Chicago Press, USA, reprinted 1965.

Denzin, N.K., Lincoln, Y.S., 2011. The Sage Handbook of Qualitative Research. Sage.

Ekman, P., 1992. Are there basic emotions? Psychol. Rev. 99 (3), 550–553.

Ekman, P., Friesen, W.V., 1976. Measuring facial movement. Environ. Psychol. Nonverbal Behav. 1, 56–75.

Ekman, P., Friesen, W.V., 2003. Unmasking the Face: A Guide to Recognizing Emotions from Facial Clues. ISHK, USA.

Ekman, P., Friesen, W.V., Hager, J.C., 1978. Facial action coding system (FACS). A technique for the measurement of facial action. Consulting, Palo Alto, 22.

Finch, H., 2005. Comparison of distance measures in cluster analysis with dichotomous data. J. Data Sci. 3, 85–100.

Fox, E., 2008. Emotion Science: Cognitive and Neuroscientific Approaches to Understanding Human Emotions. Palgrave Macmillan.

Frith, C., 2009. Role of facial expressions in social interactions. Phil. Trans. R. Soc. B 364, 3453–3458.

Gourkow, N., Phillips, C.J., 2015. Effect of interactions with humans on behaviour, mucosal immunity and upper respiratory disease of shelter cats rated as contented on arrival. Prev. Vet. Med. 121, 288–296.

Gourkow, N., Phillips, C.J., 2016. Effect of cognitive enrichment on behavior: mucosal immunity and upper respiratory disease of shelter cats rated as frustrated on arrival. Prev. Vet. Med. 131, 103–110.

Gourkow, N., Lavoy, A., Dean, G.A., Phillips, C.J.C., 2014a. Associations of behaviour with secretory immunoglobulin A and cortisol in domestic cats during their first week in an animal shelter. Appl. Anim. Behav. Sci. 150, 55–64.

Gourkow, N., Hamon, S.C., Phillips, C.J., 2014b. Effect of gentle stroking and vocalization on behaviour: mucosal immunity and upper respiratory disease in anxious shelter cats. Prev. Vet. Med. 117, 266–275.

Guo, K., Meints, K., Hall, C., Hall, S., Mills, D., 2009. Left gaze bias in humans: rhesus monkeys and domestic dogs. Anim. Cognition 12, 409–418.

Hampshire, V., Robertson, S., 2015. Using the facial grimace scale to evaluate rabbit wellness in post-procedural monitoring. Lab. Anim. 44, 259.

Hjortsjö, C.H., 1969. Man's Face and Mimic Language. Studen litteratur.

Holden, E., Calvo, G., Collins, M., Bell, A., Reid, J., Scott, E.M., Nolan, A.M., 2014. Evaluation of facial expression in acute pain in cats. J. Small Anim. Pract. 55, 615–621.

Hoppe, D.J., Schemitsch, E.H., Morshed, S., Tornetta, P., Bhandari, M., 2009. Hierarchy of evidence: where observational studies fit in and why we need them. J. Bone Joint Surg. Am. 91 (Suppl. 3), 2–9.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54, 187–211.

Kry, K., Casey, R., 2007. The effect of hiding enrichment on stress levels and behaviour of domestic cats (Felis sylvestris catus) in a shelter setting and the implications for adoption potential. Anim. Welf. 16, 375–383.

Lang, P.J., Greenwald, M.K., Bradley, M.M., Hamm, A.O., 1993. Looking at pictures: affective facial, visceral, and behavioral reactions. Psychophysiology 30, 261–273.

Langford, D.J., Bailey, A.L., Chanda, M.L., Clarke, S.E., Drummond, T.E., Echols, S., Glick, S., Ingrao, J., Klassen-Ross, T., LaCroix-Fralish, M.L., Matsumiya, L., 2010. Coding of facial expressions of pain in the laboratory mouse. Nat. Methods 7, 447–449.

Ledoux, j., 1998. The emotional brain: The mysterious underpinnings of emotional life. Simon and Schuster, New York.

Leyhausen, P., 1979. Cat Behavior: The Predatory and Social Behavior of Domestic and Wild Cats, 1st ed. Garland STPM Press, New York.

Mendl, M., Burman, O.H., Parker, R.M., Paul, E.S., 2009. Cognitive bias as an indicator of animal emotion and welfare: emerging evidence and underlying mechanisms. Appl. Anim. Behav. Sci. 118, 161–181.

Mills, D.S., Ewbank, R., 2016. Chapter 4. ISAE, ethology and the veterinary profession. In: Brown, J., Seddon, Y., Appleby, M. (Eds.), Animals and Us: 50 Years and More of Applied Ethology. Academic Publishers, Wageningen, pp. 66–81.

Panksepp, J., Biven, L., 2012. The Archaeology of Mind: Neuroevolutionary Origins of Human Emotions. WW Norton & Company.

Panksepp, J., 1998. Affective Neuroscience: The Foundations of Human and Animal Emotions. Oxford University Press, USA.

Parr, L.A., Waller, B.M., Vick, S.J., Bard, K.A., 2007. Classifying chimpanzee facial expressions using muscle action. Emotion 7, 172–181.

Parr, L.A., Waller, B.M., Burrows, A.M., Gothard, K.M., Vick, S.J., 2010. MaqFACS: a muscle-based facial movement coding system for the macaque monkey. Am. J. Phys. Anthropol. 143, 625–630.

Rinn, W.E., 1984. The neuropsychology of facial expression: a review of the neurological and psychological mechanisms for producing facial expression. Psychol. Bull. 95, 52–77.
Rogers, L.J., 2010. Relevance of brain and behavioural lateralization to animal welfare. Appl. Anim. Behav. Sci. 127, 1–11.
Ross, E.D., 1981. The aprosodias: functional-anatomical organization of the effective components of language in the right hemisphere. Arch. Neurol. 38, 561–569.
Russell, J.A., Fernández-Dols, J.M., 1997. The Psychology of Facial Expression. Cambridge University Press, Cambridge.
Russell, J.A., 1994. Is there universal recognition of emotion from facial expression? A review of methods and studies. Psychol. Bull. 115, 102–141.
Schank, J.C., Koehnle, T.J., 2009. Pseudoreplication is a pseudoproblem. J. Comp. Psychol. 123, 421–433.
Scherer, K.R., 1984. On the nature and function of emotion: a component process approach. In: Scherer, K., Ekman, P. (Eds.), Approaches to Emotion. Hillsdale, NJ: Erlbaum, pp. 293–317.
Siniscalchi, M., Sasso, R., Pepe, A.M., Vallortigara, G., Quaranta, A., 2010. Dogs turn left to emotional stimuli. Behav. Brain Res. 208, 516–521.
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 11 (1), p.e0143047.
Sotocinal, S.C., Sorge, R.E., Zaloum, A., Tuttle, A.H., Martin, L.J., Wieskopf, J.S., Mapplebeck, J.C.S., Wei, P., Zhan, S., Zhang, S., McDougall, J.J., King, O.D., Mogil, J.S., 2011. The Rat Grimace Scale: a partially automated method for quantifying pain in the laboratory rat via facial expressions. Mol. Pain 7, 1–10.
Tsyrlin, V.A., Brakov, M.F., Bershadksy, B.G., 1983. Possible mechanisms underlying the pressure responses evoked in conscious cats by emotional stress. Eur. J. Physiol. 398, 81–87.
Turner, D.C., Bateson, P., 2000. The Domestic Cat: The Biology of its Behaviour. Cambridge University Press, Cambridge, p. 74.
Vick, S.J., Waller, B.M., Parr, L.A., Smith Pasaqualini, M.C., Bard, K.A., 2007. A cross-species comparison of facial morphology and movement in humans and chimpanzees using the facial action coding system (FACS). J. Nonverbal Behav. 31, 1–20.
Waller, B.M., Kuchenbuch, P., Lembeck, M., Burrows, A.M., Liebal, K., 2012. GibbonFACS: a muscle based coding system for the hylobatids. J. Primatol. Int. 33, 809–821.