

Facial expression production and perception in non-human primates

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Abstract

Facial expressions are ubiquitous among primates and many clear similarities across species suggest a shared evolutionary history for these behaviours. Investigations of non-human primate facial expressions are therefore vital to understand the form and function of human facial behaviour. Methodological developments over the last two decades enable fine-grained quantitative comparisons across species and have demonstrated that similar processes underpin the perception of facial expressions in non-human primates as in humans. However, there is a tendency to focus on facial expression as a repertoire of discrete, prototypical expressions that does not always reflect naturalistic behaviour. In this Review, we review production and perception of non-human primate facial expressions, focusing on methodological approaches and how to address the challenges of studying dynamic facial expressions. Moving forward, methods that enable the study of dynamic and variable communicative exchange within social interaction might provide a better understanding of how facial expressions function and what (if anything) about facial expression is unique to humans.

Introduction

Humans produce abundant facial expression during social interaction: approximately 100 facial movements per minute¹. Some of these behaviours bear clear visual similarity to those produced by other primate species such as bonobos (*Pan paniscus*) and macaques (*Macaca spp.*)^{2,3} (Figure 1). Thus, investigations of the production and perception of non-human primate facial expressions (referring to changes in facial appearance deriving from facial muscle action, also termed facial displays or facial behaviours) have been fruitful not only to understand the behaviour of each species, but also to understand the evolution of human facial expression. By studying multiple primate species, researchers can better understand the selection pressures that have acted upon facial expression over time, and how and why primates (and humans in particular) have evolved such complex facial behaviour. On the whole, the facial musculature of humans and other primate species seems very similar⁴, even across species that are less closely related, which suggests that human facial expression has built on evolutionarily well preserved and ancient systems⁴. Any extreme complexity or mobility of human faces in comparison to other primates seems to be due to differences in the composition of the muscle fibres and/or connective tissue and not the basic structure of the muscles^{5,6}. The ground plan of anatomical structures is therefore common to many primate species which enables comparisons of facial expression between species⁷. For example, the social bonding function of the human smile⁸⁻¹⁰ has been illuminated by comparisons with the morphologically similar bared-teeth display in primate relatives,¹¹⁻¹⁴ which is used as a signal of benign intent. Identifying non-human primate homologues of other forms of human communication (such as language, gesture and non-linguistic vocalisation) can be more difficult and comparisons often focus on cognitive components rather than explicit similarity¹⁵ (with some interesting exceptions^{16,17}). Thus, non-human primate facial expressions offer a rare opportunity to learn more about the evolved nature of human facial expressions and about the evolution of communication systems more generally both across and within species. Despite advances in non-human primate facial expression research, there is still a longstanding debate over what (if any) information is

conveyed by facial expressions in humans and other species. There is a strong tradition of treating human and non-human primate facial expressions as emotional signals (an emotional framework), which rests on the assumption that there is a correspondence between the feeling state of the acting individual and the facial expression produced^{15,18,19}. However, some authors challenge this view, arguing that there is little evidence that facial expressions truly express emotion, even in humans²⁰⁻²². In some ways, this debate reflects a difference between two disciplines feeding into the topic of non-human primate facial expression: psychology and biology. Psychologists might lean towards a focus on internal states, and biologists more towards adaptive function. However, emotional terms abound even in the more biological non-human primate facial expression literature (for instance, terms such as 'fear grin') when the focus is on adaptive function²³ , and early work in the 19th century used internal states (such as disappointed and sulky) to describe a facial expression in a chimpanzee³. The central idea that emotions underpin facial expressions has been contested in human psychology, . For instance, a large-scale meta-analysis showed that a strong correlation between felt emotion, facial expression, and perception (by others) does not always exist²¹. The fact that facial expressions often appear when there is no corresponding feeling state suggests that facial expressions do not always actually express emotion, which challenges the dominant emotional framework. Therefore , we support the alternative view that facial expressions might be better conceptualised as predictors of potential action^{22,24,25} or tools for social influence²⁶, equipping expressive individuals with a social advantage²⁷(the predictive framework).

In the majority of early texts documenting non-human primate behaviour, facial expressions are described as archetypal behaviours that form part of the species' typical repertoire^{28,29}. However, what is often described as a facial expression in this work is in essence a peak intensity snapshot of a more elaborate and dynamic display. Static snapshots do not show how the expression might change before or after the snapshot, the behavioural context or the behaviour of the social interaction partners. It is highly likely that there is important information present in

these more dynamic and contextual elements, that could elaborate or even change the meaning of a facial expression. A still photograph might also miss some of the very subtle movements produced as part of a flow of movement. However, the benefit of focussing on the peak intensity snapshots, is that by reducing the complexity of dynamic and contextualised facial expressions (for example, a sequence of mouth opening during play) to a simple discrete form (a playface with specific and typical features of mouth opening), researchers might be able to better compare the fundamental structure of the facial expression across individuals and species. Quantitative comparative analysis is also more more straight-forward than comparison of dynamic sequences^{30,31}. This approach also enables researchers to isolate the key featural elements of these facial expressions to investigate their perception by conspecifics. The development of objective, anatomically based systems (Box 1) that can help trace the homology of specific expressions and better understand species differences and similarities has greatly facilitated research with dynamic facial expressions. In this Review, we assess the state of the art in non-human primate facial expression research. First, we review the literature on production and perception of non-human primate facial expressions, from pivotal empirical findings that defined the traditions in the field to contemporary advances. . Second, we will discuss potential future directions and ideas to drive the field forward, focussing on the need to examine facial expressions as they occur within real-world social interaction. .

Production of facial expressions

As with all animal behaviour, the study of primate facial expressions started with observation, with scientists including facial expressions in their descriptions of species behavioural repertoires. These descriptions often included the social context in which the expression was produced, and the function of the expressions inferred from changes in the behaviour of receivers, or the outcome of the social interactions in which the facial expressions occurred or both. However, accurately describing the appearance of facial expressions is not straightforward. Describing facial expressions

as static displays that form discrete categories is the traditional approach (and by far the most dominant approach), but the true complexity of facial expressions can be oversimplified (perhaps unintentionally) using this method.

Researchers are familiar with the issues inherent in studying discrete categories of static expressions, but they are difficult to overcome because it is extremely time-consuming and labour-intensive to analyse a full dynamic sequence . There is also an historical and dominant theoretical focus on prototypicality in human research³² , which is highly influential and promotes a focus on discrete categories. The past approach to the study of facial expressions has been incredibly important to highlight the importance of this mode of communication, and identify potential evolutionary continuity across species^{2,33}. However, over the last two decades there has been a move towards a bottom-up approach to capture the fine-grained variation and progress a more detailed understanding of facial behaviour. In this section, we first review the traditional research with a focus on static categories of expressions and then focus on contemporary research that uses a more bottom-up approach to analyse facial expressions in non-human primates.

Approaching expressions as discrete units

The assumption that facial expressivity is composed of prototypical, discrete displays has long resulted in more research on the common, static features of displays than the aspects of facial expressions that are harder to capture. Considering static expressions, the facial behavioural repertoire of non-human primate species is often described as a handful of expressions that are given broad labels. These labels usually describe the face holistically and are accompanied with an assumption of the underlying meaning, function, or emotion an animal is thought to be feeling^{34–37}. Some of these expression types occur almost ubiquitously across the primate order, for example in many primates species (including marmosets³⁸, macaques³⁹, chimpanzees and bonobos²⁹, capuchins⁴⁰, baboons²⁹) the lips are retracted to expose the teeth in the bared-teeth display (sometimes referred to as the fear grin or fear grimace^{41,42}, highlighting the assumed emotional

meaning). Other components such as ear flattening, teeth chattering and mouth opening can accompany the bared-teeth display, but this can vary both within and between species. Despite morphological similarities across species, the function of the expression can differ between species, occurring more during positive interactions in more egalitarian species, which are characterised by more open and diverse social relationships, weakly constrained by kinship and dominance relationships. Contrastingly, the bared-teeth display is used more during submission and aggression contexts in more despotic species, where dominance and kinship strongly constrain social interactions^{13,14,39,43}. There is a similar ubiquity in the open-mouth displays that typically occur during play (and consequently, often referred to as the 'play face'), which are documented in a wide range of monkeys and apes^{29,30,40,44–46}, the prosimian primates⁴⁷ and even in non-primate mammals (including rats⁴⁸, wolves⁴⁹, domestic dogs⁵⁰ and sea lions⁵¹). Compared to the bared-teeth, the function of the open-mouth display seems more conserved between species, communicating non-aggressive intent during a potentially risky interaction^{52,53}.

All species appear to have at least one facial expression of threat⁵⁴, which is normally described based on the contextual behaviour of the individual producing the expression (for instance, as 'threat face') as opposed to the visual appearance⁵⁵. Functionally, these displays are thought to be produced to reduce the need for costly physical conflict⁵⁶. There are also species-specific facial expressions that seem to have less continuity between genera, such as the affiliative teeth-chattering and lip-smacking displays seen in some species such as capuchins and macaques^{57–60}. Why some expressions are found across many species, and others are only found in other groups is unknown. For certain facial expressions, separating the visual and vocal components can be difficult. In such cases, the facial expression is often labelled according to the co-occurring vocalisations: for example, the scream face of many primate species⁶¹ and the pant-hoot face in chimpanzees⁶². However, despite the visual and vocal components of the display being studied almost exclusively in isolation^{18,63} there is little data on whether the visual and vocal components convey different, enhancing or redundant information.

In sum, scientists have documented a broad range of facial expressions across non-human primate species, some of which are unique to certain species, and others which are common to many. However, the traditional focus identifying discrete units of expression has the potential to miss meaning and function associated with more dynamic and contextual features.

Towards a more ecologically valid and bottom-up approach

Facial expressions are dynamic by definition, and they often incorporate other behavioural components from the same or different sensory modalities (for instance, body posture and vocalisations often co-occur with facial movements)^{59,64–66}. Primate facial expressions (and other signals) can also be highly blended with each other, morphing from one to another during a social interaction, adding another dimension to the communicative interaction and making it difficult for researchers to decide on the unit of analysis⁶⁷. They are also variable at both the species and individual level⁶⁸. All these sources of variation highlight the limitations of the traditional approach to studying facial expressions as fixed sets of facial movements. The importance of the dynamic properties of communication is well documented in vocalisation^{69,70} and gesture research^{71,72} but for facial expressions, this data remains limited (although see ⁷³ for an example of how sequences of communicative signals can be studied across modalities).

Recent research on the facial expressions often uses the facial action coding system ('FACS'), an observational coding method designed to capture and quantify the movements of the face^{74,75} (Box 1). The facial action coding system uses a numbered notation system of surface facial movements. The system includes 33 action units, which indicate the muscular basis (for instance, 'AU10', known as 'upper lip raiser', resulting from *levator labii superioris* contraction), and 25 action descriptors of more general head and eye movements. Researchers can use this system to identify and record facial movements without any *a priori* assumptions of the meaning of the expression; coding is traditionally done manually but automated methods are emerging⁷⁶. Although the system

was originally developed for human expressions, the same numbered system is now used in a range of non-human primate species and even non-primate species⁷.

This descriptive method has been central to researchers' attempts to probe deeper into the variability and complexity of primate facial expression. Indeed, in addition to providing researchers with a unified framework to describe facial movement, the facial action coding system has allowed researchers to include the onset and offset of each action unit/descriptor, therefore providing them with the basis for detailed analyses that reflect actual facial behaviour rather than arbitrarily defined categories. For instance, the silent bared-teeth display (Figure 2), a facial movement pattern found in many non-human primate species, is considered homologous to the human smile^{14,61}. Extensive research on human facial behaviour has shown marked variability within the human smile, both in appearance and context⁷⁷. These findings were only possible because the authors considered which action units were present in which context, rather than considering smiles as one homogeneous set of facial movement or archetypical facial expression. .

In socially tolerant species, such as the crested macaque (*Macaca nigra*), social interactions are only weakly constrained by kinship and dominance and the silent bared-teeth display is used across a variety of social contexts including play, affiliation, mating, and conflict. Prior to the widespread use of facial action coding systems, only anecdotal and descriptive accounts of this diversity existed³⁹. Using a set of metrics derived from the facial action coding system, researchers revealed the apparent specificity of several facial movements for a given social context (for instance, AD184 'jaw wobble' in mating bared-teeth displays versus AU27 'jaw stretch' in play bared-teeth displays)¹¹. Not only were social contexts predicted by the composition of the facial behaviour, but also by dynamic features such as the intensity of certain action units (such as the intensity of AU12 'lip corner puller'). These findings suggest that there are subtle but meaningful variations within the bared-teeth display category that have previously been lumped together.

Variability in the silent bared-teeth display of geladas (*Theropithecus gelada*) further conveys the complexity of facial communication. A study found that the lip-flip expression, where

the upper lip is pulled up and everted revealing teeth and gums,() always co-occurred with action units that are characteristic of the silent bared-teeth display (AU10: upper lip raiser; AU12: lip corner puller; and AU25: lips part), thereby acting as an optional and additional component to the bared-teeth display⁷⁸. Although the bared-teeth display with and without lip-flip was frequently associated with both nonaggressive and submissive behaviours, bared-teeth displays featuring the lip-flip were more frequently preceded by an approach from another individual than the bared-teeth display alone, particularly in males. Because it is so conspicuous, the lip-flip could therefore function as a additional component enhancing the signal value of the bared-teeth display⁷⁹.

Detailed methods such as the facial action coding system) have also revealed variability in the facial behaviour of individuals in response to the attentional state of receivers⁸⁰. Such sensitivity to others suggests that the cognitive mechanisms underpinning facial expressions might be more complex than previously thought. According to the emotional approach, non-human and human primate facial expressions are typically seen as automatic responses driven by emotions , in contrast to gestures which are usually considered intentional and goal-directed¹⁸. In part, this belief stems from the observation that gestures change depending on the attentional state of the receiver^{e.g.81}, suggesting an intentional shift to capture the attention of a recipient, whereas facial expressions do not. However, orangutan play faces have been found to be more intense and contain a larger number of individual action units when play partners engage in direct, face to face play than when facing apart ⁸⁰. Similar results were obtained in a large scale study examining the facial behaviour of five hylobatid species (gibbons and siamangs) across multiple contexts and in relation to the attentional state of the interacting individuals⁸². Facial expressions were longer if they were produced in a social context (grooming, agonistic behaviour and play) as opposed to non-social contexts (self-grooming and resting), and when individuals were facing each other. These examples illustrate how detailed analysis of the form and function of facial expressions can form the basis of investigations into the cognitive mechanisms underpinning communication via the face.

The development of a facial action coding system for multiple primate species has also enabled researchers to undertake larger scale comparative studies that examine the physical, social, and ecological correlates of facial behaviour. Pioneering this approach, the original human facial action coding system was applied to the facial behaviour of 12 non-human primate species to measure facial mobility, defined as the total number of action units observed within a species^{83,84}. Inter-species variations in facial mobility were first hypothesized to track differences in body size and resulting allometric constraints (the physical constraint of body size)⁸⁴. Phylogenetically informed regression analysis (where the evolutionary relationships between species are controlled for) revealed that larger species had greater facial mobility than smaller-bodied species, which suggests that allometry has a crucial role in restricting the evolution of facial mobility: smaller species potentially have a reduced range and intricacy of facial behaviour and limited ability to perceive facial movements relative to larger ones⁸⁵. In a subsequent study using the same dataset, researchers examined the socio-ecological correlates of facial mobility while controlling for phylogeny and body size⁸³. Group-size, a potential driver of facial mobility due to the potential requirement for increased communication complexity as group size increases⁸⁶, was a significant predictor of facial mobility, echoing similar findings in the vocal domain^{87–90}. By contrast, arboreality (whether a species lives in trees)) was not a significant predictor of facial mobility. Thus, this study did not support the widespread assumption that facial movements can be more easily perceived on the ground, where visibility is higher compared to the dense foliage of most forest canopies¹⁵.

The use of fine-grained approaches such as the facial coding system also enables quantification of variation in facial expression production between individuals. Human studies are starting to show that facial expressivity varies considerably across individuals. People with different personalities types respond differently to social interaction¹ and more expressive individuals have social advantages such as being more well liked^{27,91}. Non-human primates also show individual variation in how generally facially expressive they are and these trait differences have a direct impact on social outcomes for that individual⁹². For instance, in a study that compared the

expressivity of dominant male rhesus macaques, individual rhesus macaques varied in their quantity of facial movements (the number of action units observed per unit time) and in the diversity of movements (the amount of unique action units incorporated into their typical repertoire)⁹². Individuals that used a higher quantity of facial movements had stronger friendships with others, raising the possibility that these individuals have an advantage in forming and maintaining social bonds. Similarly, individuals with higher diversity of facial movements occupied more advantageous positions in the social network, which has positive consequences for fitness. Taken together, these findings from both human and non-human primates suggest that an individual differences approach can be a powerful tool to test hypotheses about adaptive function, where the advantage of producing facial expression at high frequency can be measured.

One of the difficulties of using the facial action coding system for comparative research is the absence of standardised analytical methods to enable researchers to make the most out of the richness of the data while coping with its complexity (including binomial, categorical or proportional data, with numerous dependencies between participants, videos, or muscles movements). NetFACS is a tool that conceptualises facial behaviour as a network of facial muscles that interact to produce communication: action units constitute nodes in a network that are linked when they co-activate⁹³. NetFACS builds on decades of developments in the field of network theory and provides versatility and broad application potential to facial behaviour as a dynamic and complex communication system. Using this tool, a study found that more socially complex macaque species (species with high social tolerance and therefore more flexible and complex relationships) used a higher diversity of unique action unit combinations, which were also less specific to a given social context and less predictable than those of less socially complex species⁹⁴. These findings illustrate a new framework for the standardised use of facial action coding system data across species⁹³ and support the social complexity hypothesis for communicative complexity⁸⁶, which proposes that the evolution of communication has been driven by living in complex social groups.

Non-human primates produce a wide range of facial expressions across various social contexts, many of which bear similarity to human facial expressions. Traditional approaches tend to categorised these expressions as a limited set of discrete and independent behaviours, often focussing on the static components with limited attention to the more dynamic, variable or contextual elements. A more bottom-up approach has developed which allows researchers to measure facial expressions in much greater detail, by examining the component parts of facial expressions and comparing across species. Through this more detailed approach the adaptive function of facial expressivity is starting to be demonstrated empirically. On the whole, findings suggest that facial expressions have a social bonding function within social interaction.

Perception of facial expressions

On the whole, studies of facial expression perception are less common than those focused on production^{63,63,95}. However, an understanding of how non-human primates process facial expressions is essential to fully understand facial expression as a communicative system, and to understand the meaning of facial expressions to other primates. Therefore, a body of experimental research has been conducted to help understand precisely what expressions might mean to other individuals and what cognitive mechanisms might underpin these processes. As a starting point to help design their experiments, proponents of the traditional emotional framework tend to think that facial expressions contain information about an individual's emotions³³, whereas others tend to think they convey information about motivation and/or potential future actions²⁴. However, all studies of non-human primate facial expression perception are broadly trying to understand and assess the information content (often termed signal value) of facial expressions.

Methodology

Multiple experimental methods have been employed to assess non-human primate facial expression processing skills (Table 1). Discrimination tasks aim to determine whether individuals can distinguish between two or more facial expressions. These include the match-to-sample

paradigm, in which animals are trained to match a sample image with one of two options, and the oddity (or 'odd-one-out') paradigm, in which animals are trained to choose one of several images that does not match the others. The dot-probe task measures a subject's reaction time to a dot overlaying a visual image of a facial expression. If reaction times are influenced differentially by the underlying stimuli, the difference an attentional bias either towards or away from the image. Simpler attentional bias experiments typically measure the time spent looking at one stimulus compared to another, or their latency to first glance at each stimulus, revealing whether one stimulus is more interesting, attention grabbing or unexpected to the animal.

The advantages and disadvantages of each paradigm are key to evaluating which paradigm to choose, and the interpretation of the findings. Some experimental paradigms can be tricky to implement within a study group as they require lengthy periods of habituation and training before subjects are able understand the task, and therefore before meaningful data can be collected. In the match-to-sample and the oddity tasks, subjects are required to first understand that they have to identify either a similar or dissimilar stimulus relative to other stimuli present. This lengthy training, however, is often rewarded with the benefits of being able to answer complex questions about perception and allows us to develop a better understanding of what stimuli or concepts individuals associate together into meaningful groups. Other paradigms require little to no training, such as dot probe or attentional bias (looking tasks) and are therefore easier to implement compared to trained paradigms. Unlike the trained-response tasks, these paradigms rely on spontaneous, natural responses to stimuli, which can be important for maximising ecological validity. However, without training, the complexity of the questions which can be asked is limited to assessing looking biases (how does looking behaviour change), and it becomes difficult to make inference about cognitive mechanisms or understanding.

Signal value of facial expressions

To understand whether and how non-human primate facial expressions are meaningful to conspecifics, and therefore have signal value, the first step was to demonstrate empirically that non-human primates can distinguish between facial expressions. Therefore, studies have been conducted to demonstrate facial expression discrimination across various species of non-human primate, using a range of paradigms. For example, match-to-sample tasks have been used to show facial expression discrimination in some species, such as long tailed macaques⁹⁶, Japanese macaques, chimpanzees^{98–100}, rhesus macaques¹⁰¹ and crested macaques¹⁰². The oddity paradigm has been used to show the same skill in capuchin monkeys¹⁰³. On the whole, the findings suggest that facial expressions are perceived as meaningful, defined stimuli, and therefore have signal value to other animals. Findings from these discrimination tasks also suggest that non-human primate facial expression processing uses both configurational (the relative relationship between features) and featural (the specifics of the features themselves) cues^{96,100,103}, similarly to humans¹⁰⁴. Probing the patterns in non-human primates' discrimination of facial expressions in these experiments can also reveal which information is most salient and being used to categorise facial expressions. For example, crested macaques seem to categorise facial expressions in relation to social function¹⁰², whereas chimpanzees seem to rely more on the physical features of each expression⁹⁸. However, it is hard to determine without more research whether these are true species differences or related to the specifics of each experiment.

Methods that index attention to facial expressions can further probe how, when, and why primates look at facial expression stimuli. For instance, humans show an attention bias towards threat facial expressions relative to other facial expressions¹⁰⁵, interpreted as an adaptive response towards threatening stimuli¹⁰⁶ (although later work shows a more complex interaction with emotion and anxiety¹⁰⁷). Using the dot-probe paradigm in non-human primates, some studies have found an attentional bias towards threat facial expressions relative to neutral faces (rhesus macaques^{108–110}; long tailed macaques¹¹¹) whereas other studies have not (chimpanzees¹¹²; capuchins¹¹³). Simpler attentional bias experiments have also shown an attentional bias towards threat facial expressions

relative to other facial expressions in rhesus macaques^{114,115}, but the mixed results across studies suggests that there could be species differences, or the effect is not robust. Studies have also found attentional biases, not towards threat facial expressions but towards bared-teeth expressions (relative to other facial expressions) in orangutans¹¹⁶ and snub-nosed monkeys¹¹⁷. A bias towards bared-teeth expressions could also be explained through the lens of adaptive vigilance to threat (or conflict avoidance) because bared-teeth expressions are often produced in response to threats. However, it might not just be threat-related expressions that capture attention in non-human primates, as attentional bias towards lip smacking (relative to neutral faces) has also been shown in rhesus macaques using video clips¹¹⁸ but not still images¹¹⁹.

Efforts to build on the discrimination experiments described above to understand what *meaning* non-human primates extract from facial expressions (in terms of the specific information content and not just whether they are processed as perceptual units) have taken various approaches. In one of the only attempts to empirically demonstrate the emotional valence of facial expressions, the match-to-sample paradigm was used to test how chimpanzees matched facial expressions with videos of familiar positive (food) or negative (veterinary procedures) scenes¹²⁰. The play face was associated with positive scenes and the scream face with negative scenes, suggesting some generalised emotional meaning of facial expressions that goes beyond social context. Other experiments have focussed directly on the meaning of facial expressions as communicative signals in terms of how they might be used by others. For example, non-human primates are more likely to follow the gaze direction of others who are producing a facial expression compared to a neutral expression (long tailed macaques¹²¹, Barbary macaques¹²², and Rhesus macaques¹²³), which suggests that the facial expression adds salience to a potentially useful gaze cue. Similarly, macaques look longer at agonistic interactions containing threat expressions when the directionality is incongruous (subordinate individuals threatening dominant individuals), which indicates that they understand that facial expressions can refer to the external environment¹²⁴. The meaning of expressions as used by others has also been demonstrated through an innovative paradigm in which subjects were

required to make a choice between two boxes on the basis of the information provided by facial expressions^{125–127}. Based on the facial expressions of a human demonstrator (with great apes as the subject)¹²⁵ or conspecific (with capuchin monkeys as the subject)^{126,127}, subjects more often selected the box that had been responded to with 'happy' human expressions and capuchin forehead raises (an affiliative display) compared to potentially negative expressions .

The two main frameworks in non-human primate facial expression research, the emotional framework¹²⁸ and the predictive framework²⁴ introduced in the first section of this review, also have implications for conceptualising the information content of non-human primate facial expressions, and the underpinning mechanisms. According to the emotional framework, two potential mechanisms for facial expression interpretation are: emotional contagion (the automatic matching of the emotion of the receiver with that of the sender^{129,130}) and the perhaps more cognitively complex cognitive empathy (understanding the meaning or cause of an individual's emotion, without necessarily experiencing the same emotion¹³¹). Evidence to support emotional contagion is drawn from studies of rapid facial mimicry: the rapid production of the same facial expression as the sender by the receiver^{132,133} which is associated with longer play bouts and therefore might enhance social coordination^{44,134}. However, as all the studies have been conducted in the context of play, it is possible that the phenomenon is restricted to play. Indeed, the concept of mimicry has been questioned given that animals might more simply be simultaneously producing play expressions during play²⁴. Mimicking (or 'catching') the facial expressions of another individual is often not in the interest of the receiver as responses to facial expressions might instead be alternative expressions depending on dominance, group membership and other contextual factors²⁴. Flexibility and the ability to respond in a different way to the facial expressions of others is probably integral to non-human primate communication.

According to the predictive framework, also known as the behavioural ecology view^{22,24}, the facial expressions of others are seen as indications of their likely future behaviour, to which individuals can respond based on what is most beneficial to them. Supporting this framework, there

is one study showing that crested macaques can predict the outcome of a social interaction using the facial expressions of the interacting conspecifics⁵⁶. However, there is also a view that as the interests of senders and receivers often conflict and the experience and ‘meaning’ of signals could also differ widely between sender and receiver¹³⁵.

Innateness and the environment

To understand the mechanisms underpinning non-human primate facial expression perception, and what influences their development, researchers have conducted electrophysiological and imaging studies, and examined the influence of environmental factors on development. On the whole, the evidence suggests that the neural processes and brain regions that non-human primates use to process facial expressions—for example the amygdala^{101,136} and inferior temporal sulcus¹³⁷—overlap with those used in humans^{104,138}. This overlap suggests a common evolutionary origin for expression perception across primates. Non-human primate facial expression perception is also usually considered to be somewhat hard-wired. For example, rhesus macaques raised in isolation produced disturbance related behaviors in response to pictures of macaque threat facial expressions (which they had never seen before ok), implying some innate understanding of threat facial expressions¹³⁹.

Early life environment can also impact the development of facial expression processing^{118,140}. Maltreated rhesus macaques showed slower reaction times to social threat than animals who experienced competent maternal care, suggesting that the threatening images captured their attention more and interfered with attentional control and cognitive processes¹⁴⁰. However, in this study, the animals who exhibited higher behavioural reactivity during maltreatment (compared to those who showed dulled behavioural patterns) showed greater attentional bias towards threat, suggesting that those who reacted more to stressful events were consequently more sensitive to threatening facial expressions in later life. Those who experienced higher prenatal cortisol exposure (suggesting that the mother experienced stress) showed bias *away* from threatening facial

expressions. Taken together, these findings show that early life experience in non-human primates does impact facial expression perception, but in a complex way. Similarly, rhesus macaques raised in an adverse early environment did not show the typical attentional bias to positive facial expressions (lip-smacking), whereas those raised in more enriched environments showed attention bias relative to the duration and frequency of their social engagement¹¹⁸. Responses to facial expressions also seem to change with age. For instance, one experiment showed that adult golden snub-nosed monkeys displayed differential looking towards facial expression types, but sub-adults did not¹¹⁷. Facial expression expertise also generally improves with age, plateauing in adulthood, and is enhanced by early social input¹⁴¹.

Challenges

Two major methodological barriers limit progress in non-human primate facial expression perception research. First and foremost, the body of research is based on a narrow range of species, namely macaques and chimpanzees, whereas there are over 500 species of primate in total¹⁴². In contrast to research on facial expression production (which can take place in a range of both wild and captive settings) the perception research is largely experimental and cognitive, and so usually relies on access to those few species available in captive facilities⁶³. Thus, the current understanding of non-human primate facial expression perception might not be representative of the entire primate group.

Second, there is a heavy reliance on paradigms that present stimuli in static, discrete configurations without context, dynamic movement or accompanying behaviours. Researchers tend to use either still images or videos and decide whether to use depictions of real conspecifics or computer-generated avatars, all of which have differing advantages and disadvantages (Table 2). There is, however, inevitably a trade-off between how well the stimulus reflects naturalistic behaviour, and how easily it can be used the test the question as more realistic stimuli are not suited to controlled experimental paradigms. With some exceptions, most experiments show facial

expressions as static, discrete units, which limits the ability to assess how non-human primates process facial expressions in naturalistic settings. However, some studies have begun to use stimuli that are blended, dynamic or multimodal.

Multimodal signals are usually defined as those that contain two or more sensory modalities⁷⁹ (visual, auditory, olfactory or tactile), which is the technically correct definition, but sometimes used to refer to multicomponent signals that contain qualitatively different types of signals from the same modality, such as facial expressions and gestures¹⁵. Regardless of which modalities are combined, simultaneous and combined production of signals is integral to non-human primate communication^{143–145} and context can also modulate the meaning of signals. For instance, context has been shown to have an important role in human facial expression processing^{146–148}. Different components of facial expressions, such as head orientation and face identification, are not always processed in the same way by the non-human primate brain¹⁴⁹, suggesting that there is a complex process of integration across these components. More cross-species work is needed to fully understand the complex visual integration of bodies, brains and contexts¹⁵⁰. However, the implication of the current understanding of this complexity is that presenting facial expressions outside of the context in which they naturally occur simplifies a complex communication system and could potentially render the stimuli devoid of relevance. Indeed, signals that accompany the target signal (of same or different modality) might even provide key context. Complementary observational studies on non-human primate perception during social interaction^{e.g. 122} could also help inform us as to whether the skills demonstrated in experiments are reflective of the animals' spontaneous behaviour. Wild studies are particularly important, but rare⁶⁰ and make up only 8% research on facial expression¹⁸ (Slocombe, Waller, Liebal 2011).

Summary and future directions

Non-human primate facial expressions are well documented and form part of the behavioural repertoire of almost all primate species, most of which are highly social. These facial expressions occur across a broad range of social contexts and can be used more or less flexibly depending on the primate species, with species exhibiting greater social complexity also exhibiting greater complexity of facial expressions⁹⁴. Studies of non-human primate facial expression have been crucial to develop a more nuanced understanding of the meaning of mammalian facial expression generally, conceptualising these behaviours not just (or at all) as emotional signals, but instead as predictors of potential action^{22,24,25} and tools for social influence²⁶. Emotion could function in a predictive system as a mechanism, of course, but we argue that the adaptive value still lies in the behavioural response. As such, a focus on the behavioural response as social function (instead of emotion per se) has led to empirical demonstration of the social bonding function of facial expression across primate species^{27,92,94}. These findings are helping to build a better understanding of the evolution of facial expression systems, and how this has formed part of the evolution of communicative complexity.

Many of non-human primate facial expressions show very clear physical and contextual similarity across primate species, including humans, analysis of which has greatly informed our understanding of the function of facial expression in social interaction. For example, human smiles and laughter share an evolutionary history with the non-human primate bared-teeth display and play face respectively, which helps clarify the benign intent function of the human smile, and the similar (yet distinct) playful function of human laughter^{8,11,13,14,52}. Comparative research on other human facial expressions are less well documented, possibly because smiling and laughter are more frequently produced and potentially more relevant than other expressions during spontaneous human social interaction²⁷.

Overall, the field is trying to move towards studying facial expressions as part of a dynamic communicative interaction. However, empirical research still largely focuses on static, prototypical expressions as discrete behaviours. Humans produce a busy stream of facial movement during social

interaction²⁷ which is not reflected in traditional accounts of basic facial expressions³². The extent to which this pattern is similar to or different from other primates is unknown. In many cases it is the observational data on *human* facial expression that is needed to make these comparisons, because observational approaches are more common in non-human primate research.

Very little is known about the everyday facial movement produced by humans during social interaction and there is a need for a comprehensive ethogram of human facial behaviour to make comprehensive comparisons across species. For instance, observational studies of human facial expression show that most of the universal, basic facial expressions (anger, disgust, fear, sadness and surprise) are produced very rarely during everyday conversational social interaction (with the notable exception of smiling), despite a huge amount of facial movement activity overall^{1,27}. Ideally, evolutionary comparisons should focus on what species (including humans) actually do with their faces during real-world interactions, as opposed to studies of perception of posed expressions. Non-human primates might produce a similarly busy stream of facial movement during social interaction or might instead produce more clearly defined discrete displays. Analysis of individual differences is one way to capture how facial behaviour manifests in real-world, naturalistic contexts, and enables testing of the advantages and disadvantages of being more or less expressive^{27,92}. Finally, typically, non-human primate facial expression stimuli are directed at the participant, which is only one way in which individuals experience facial expressions during their everyday life. There are some innovative studies depicting facial expressions directed towards objects^{125–127} and as part of third party social interactions^{56,123,124} but more innovative, ecologically relevant paradigms that reflect real-world, naturalistic social interactions are needed.

To truly understand the nature of facial expression during social interaction, researchers need to combine understanding of production and perception, which are almost always studied independently. Facial expression is a sequence of back and forth between sender and receiver, and yet understanding of this overall system is poor. Wearable devices, such as wearable eye-trackers¹⁵¹ could provide information about how individuals view and respond to facial expressions in

naturalistic settings. A more complete picture of the way non-human primates use and understand facial expressions as part of their social interaction, can lead to better investigation of the extent to which human facial expression is built on ancient foundations or has evolved novel and potentially unique characteristics.

Box 1: Facial action coding systems

Originally developed for humans, the facial action coding system ('FACs') was based on work that detailed the surface movements produced by specific underlying muscle contractions¹⁵². The relationship between muscle contraction and facial appearance changes is largely informed by the pioneering 19th century photographs of surface electrical stimulation of facial muscles¹⁵³ and 20th and 21st century surface and intramuscular electrical stimulation studies^{154–156}.

The facial action coding system identifies 58 component movements in the human face: 33 action units that indicate the muscular basis and 25 action descriptors that describe a more general movement (such as head movements and eye movements). The intensity of each component is recorded using a 5-point grading system (from A: subtle, low-intensity movements, to E: movements with maximal muscle contraction). The same numbered system has been modified for use in a range of non-human primate species, including chimpanzees¹⁵⁷, rhesus macaques¹⁵⁸, barbary macaques¹⁵⁹, crested macaques¹¹, Japanese macaques¹⁶⁰, gibbons and siamangs¹⁶¹, orangutans¹⁶², and common marmosets¹⁶³. Beyond primates, it has been adapted for domesticated species including dogs¹⁶⁴, horses¹⁶⁵, and cats¹⁶⁶. For most species, the first step in adapting the system was facial dissections to understand whether and how facial muscles differ from the reference species (humans)^{4,167–171}; intramuscular electrical stimulation was conducted in some cases to verify the correspondence between facial muscle contraction and surface movement^{155,172}. Many of the same movements have been identified across species⁷, but on the whole there are fewer actions units and action descriptors in other species than in humans. There are also additional movements identified in some species, such as ear movements in macaques¹⁵⁸.

The basic premise of the facial action coding system is that although some appearance changes associated with facial muscle movements might vary across individuals and species, minimal criteria for identifying and coding the action units do not vary. Thus, facial action coding can be used to describe facial movements across individuals whose faces might vary in relation to bony structures, fat deposits, hair covering, and other characteristics. Manual coders train from a detailed manual and take a certification test to ensure coding reliability, and several computerised automated human facial analysis systems based on the facial coding system^{76,173–175} enable more efficient data collection. Unfortunately, automated systems to track non-human primate facial behaviour are at a much earlier stage of development¹⁷⁶.

Table 1

Match-to-sample	Can be adapted to various stimuli and complexities Enables precise control over experimental conditions	Partially relies on memory Training can be time consuming and reduce sample size if not all individuals pass training. Might not reflect naturalistic behaviour	Trained
Oddity (odd-one-out)	Can be adapted to various stimuli and complexities Enables precise control over experimental conditions	Training can be time consuming and reduce sample size if not all individuals pass training. Might not reflect naturalistic behaviour Potential for side bias	Trained
Dot probe	Limited training needed	Potential for side bias Preference might be based on factors other than those desired, therefore an	Trained and Spontaneous

	Can be used with subjects of varying ages and cognitive abilities No reliance on memory	assumption about the cause of any attentional changes needs to be made	
Attentional bias	Reveals naturalistic response Non-invasive Simple No reliance on memory No training needed	Potential for side bias Preference might be based on factors other than those desired, therefore an assumption about the cause of any attentional changes needs to be made	Spontaneous

Table 2

Still images	Widely used and well understand Easy standardisation across stimuli	Low contextual and temporal information Low ecological validity Cannot capture dynamic expressions
Videos	High contextual and temporal information High ecological validity	Background noise present which may detract attention Difficult to achieve standardisation across stimuli Difficult to know if full video sequence has been seen by subject
Avatars	Easy standardization across stimuli Precise control and manipulation of features, allowing for stimuli typically hard to capture in real animals	Lacks ecological validity Potential for uncanny valley effects

Figure captions

Figure 1. Examples of bared-teeth facial expressions across primate species. Bornean orangutan (*Pongo pygmeas*), Gelada (*Theropithecus gelada*), Human (*Homo sapiens*), Bonobo (*Pan paniscus*), crested macaque (*Macaca nigra*). Orangutan – Credit: Bo Tornvig/Photodisc/Getty Images; Crested

macaque, Gelada, Bonobo: Credit Anup Shah/Getty Images; Humans: Credit: Flashpop/DigitalVision/Getty Images

Figure 2. Demonstration of facial action coding system (ChimpFACS)¹⁵⁷. The blending of four movements forms three of the more commonly described stereotypical expressions in chimpanzees (the bared-teeth display, the play face (or open-mouth face), and the scream face⁹⁸. Arrows depict the directional movement of the action unit compared to neutral. Images were generated from a chimpanzee 3D avatar, using blender (<https://www.blender.org>)

Figure 3. Illustration of methods used in perception experiments. Four examples of experimental paradigms used in the study of facial processing and perception. A. In the match-to-sample paradigm, subjects learn to match two same-type stimuli together, which can then be used to see if animals can successfully categorise different facial expression types. First, the sample expression appears (here: playface). Then the ‘matched’ expression appears (left, playface) along with a foil (right, bared teeth). Finally, the subject selects the expression that matches the sample. B. In the oddity task, subjects are presented with multiple stimuli on the screen (of which all but one are the same stimuli type) and are required to identify which stimulus is the odd-one-out. Multiple same-type expressions are presented simultaneously, alongside a different-type expression. Subjects are then required to select the different expression. C. In the dot probe task, individuals are trained to press a cue which can appear on the screen in one of two locations. Pairs of stimuli (one which appears in the position of the cue, and one which does not) are presented moments before, which allows researchers to measure selective attention towards one of the stimuli (by looking at the impact on latency to press the following cue). After a fixation screen, two stimuli are briefly presented side by side: an expression (typically a threat) and a neutral face. This is then replaced with a congruent cue to be touched (behind the expression) or an incongruent cue to be touched (not behind the expression). Latency to touch the cue is measured. D. In the attentional bias task, images of stimuli (often pairs) are presented and looking behaviour towards the stimuli is measured to assess naturalistic and spontaneous responses to stimuli.

Highlighted references

13. Van Hooff, J. A comparative approach to the phylogeny of laughter and smiling. *Non-Verbal Commun.* 209–41 (1972).

- This work compared human smiling and laughing to primate bared-teeth display and play face, setting a framework for the comparative approach to the evolution of human facial expressions.

98. Parr, L. A., Hopkins, W. D. & Waal, F. B. M. de. The Perception of Facial Expressions By Chimpanzees, Pan Troglodytes. *Evol. Commun.* , 1–23 (1998).

- This experimental study showed that chimpanzees can identify and discriminate between different static, discrete facial expressions.

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65. Partan, S. R. Single and multichannel signal composition: facial expressions and vocalizations of rhesus macaques (*Macaca mulatta*). *Behaviour* , 993–1027 (2002).

- This comprehensive description of rhesus macaque communication emphasises the multimodal elements and the importance of multimodal communication for communicative complexity.

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67. Parr, L. A., Cohen, M. & Waal, F. de. Influence of Social Context on the Use of Blended and Graded Facial Displays in Chimpanzees. *Int. J. Primatol.* , 73–103 (2005).

- This observational study shows the extent to which chimpanzee facial expressions do not always fit discrete categories.

157. Vick, S.-J., Waller, B. M., Parr, L. A., Smith Pasqualini, M. C. & Bard, K. A. A Cross-species Comparison of Facial Morphology and Movement in Humans and Chimpanzees Using the Facial Action Coding System (FACS). *J. Nonverbal Behav.* , 1–20 (2007).

- This study modified the facial action coding system for use with a non-human primate species.

83. Dobson, S. D. Socioecological correlates of facial mobility in nonhuman anthropoids. *Am. J. Phys. Anthropol.* , 413–420 (2009).

- This study tested the social complexity hypothesis by showing that facial mobility is positively related to social group size across primate species.

122. Teufel, C., Gutmann, A., Pirow, R. & Fischer, J. Facial expressions modulate the ontogenetic trajectory of gaze-following among monkeys. *Dev. Sci.* , 913–922 (2010).

- This study is a rare example of an observational study that documented responses to facial expressions (and gaze following) during real-world social interaction.

126. Morimoto, Y. & Fujita, K. Capuchin monkeys (*Cebus apella*) use conspecifics' emotional expressions to evaluate emotional valence of objects. *Anim. Cogn.* , 341–347 (2012).

- This innovative experimental study showed that capuchin monkeys preferentially selected boxes based on conspecific reactions (including facial expressions), which suggests that they can interpret the meaning of the expressions and use this information to modify their behaviour.

21. Barrett, L. F., Adolphs, R., Marsella, S., Martinez, A. M. & Pollak, S. D. Emotional Expressions Reconsidered: Challenges to Inferring Emotion From Human Facial Movements. *Psychol. Sci. Public Interest* , 1–68 (2019).

- This meta-analysis of human facial expression research showed that there is no strong link between felt emotion and produced or perceived facial expressions.

11. Clark, P. R. *et al.* Morphological variants of silent bared-teeth displays have different social interaction outcomes in crested macaques (*Macaca nigra*). *Am. J. Phys. Anthropol.* , 411–422 (2020).

- This study used the facial action coding system to show that there are subtle variations within the primate bared-teeth expression, thought to be a homologue of the human smile.

94. Rincon, A. V. *et al.* Higher Social Tolerance Is Associated with More Complex Facial Behavior in Macaques. <https://elifesciences.org/reviewed-preprints/87008v2> (2023) doi:10.7554/eLife.87008.2.

- This paper describes a tool that combines the facial action coding system with social network analysis) to quantify complexity of facial expression systems across species.

92. Whitehouse, J. *et al.* Facial expressivity in dominant macaques is linked to group cohesion. *Proc. R. Soc. B Biol. Sci.* , (2024).

- This paper is an empirical demonstration of the social bonding function of facial expression in rhesus macaques.

References

1. Rollings, J., Kavanagh, E., Balabanova, A., Keane, O. & Waller, B. M. Facial behaviour and first impressions in computer mediated communication. *Comput. Hum. Behav.* , 108391 (2024).
2. Kavanagh, E., Kimock, C., Whitehouse, J., Micheletta, J. & Waller, B. M. Revisiting Darwin's comparisons between human and non-human primate facial signals. *Evol. Hum. Sci.* , (2022).
3. Darwin, C. *The Expression of the Emotions in Man and Animals*. (John Murrar, London, 1872).
4. Burrows, A. M. The facial expression musculature in primates and its evolutionary significance. *BioEssays* , 212–225 (2008).
5. Burrows, A. M., Parr, L. A., Durham, E. L., Matthews, L. C. & Smith, T. D. Human faces are slower than chimpanzee faces. *PloS One* , e110523 (2014).
6. Burrows, A. M., Rogers-Vizena, C. R., Li, L. & Mendelson, B. The Mobility of the Human Face: More than Just the Musculature. *Anat. Rec.* , 1779–1788 (2016).
7. Waller, B. M., Julle-Daniere, E. & Micheletta, J. Measuring the evolution of facial 'expression' using multi-species FACS. *Neurosci. Biobehav. Rev.* , 1–11 (2020).
8. Mehu, M. & Dunbar, R. I. M. Relationship between Smiling and Laughter in Humans (*Homo sapiens*): Testing the Power Asymmetry Hypothesis. *Folia Primatol. (Basel)* , 269–280 (2008).
9. Mehu, M., Grammer, K. & Dunbar, R. I. M. Smiles when sharing. *Evol. Hum. Behav.* , 415–422 (2007).

10. Samson, A. V. M. & Waller, B. M. Not Growling but Smiling: New Interpretations of the Bared-Teeth Motif in the Pre-Columbian Caribbean. *Curr. Anthropol.* , 425–433 (2010).
11. Clark, P. R. *et al.* Morphological variants of silent bared-teeth displays have different social interaction outcomes in crested macaques (*Macaca nigra*). *Am. J. Phys. Anthropol.* , 411–422 (2020).
12. Waller, B. M. & Dunbar, R. I. M. Differential Behavioural Effects of Silent Bared Teeth Display and Relaxed Open Mouth Display in Chimpanzees (*Pan troglodytes*). *Ethology* , 129–142 (2005).
13. Van Hooff, J. A comparative approach to the phylogeny of laughter and smiling. *Non-Verbal Commun.* 209–41 (1972).
14. Preuschoft, S. “Laughter” and “Smile” in Barbary Macaques (*Macaca sylvanus*). *Ethology* , 220–236 (1992).
15. Liebal, K., Waller, B. M., Slocombe, K. E. & Burrows, A. M. *Primate Communication: A Multimodal Approach*. (Cambridge University Press, 2014).
16. Graham, K. E. & Hobaiter, C. Towards a great ape dictionary: Inexperienced humans understand common nonhuman ape gestures. *PLOS Biol.* , e3001939 (2023).
17. Kamiloglu, R. G., Çalışkan, C., Slocombe, K. E. & Sauter, D. A. Threat vocalisations are acoustically similar between humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *Bioacoustics* , 679–692 (2023).
18. Slocombe, K. E., Waller, B. M. & Liebal, K. The language void: the need for multimodality in primate communication research. *Anim. Behav.* , 919–924 (2011).
19. Tomasello, M. *Origins of Human Communication*. (MIT press, 2010).
20. Waller, B. M. & Micheletta, J. Facial expression in nonhuman animals. *Emot. Rev.* , 54–59 (2013).

21. Barrett, L. F., Adolphs, R., Marsella, S., Martinez, A. M. & Pollak, S. D. Emotional Expressions Reconsidered: Challenges to Inferring Emotion From Human Facial Movements. *Psychol. Sci. Public Interest* , 1–68 (2019).
22. Fridlund, A. J. *Human Facial Expression: An Evolutionary View*. (Academic Press, 1994).
23. Hinde, R. A. & Rowell, T. E. COMMUNICATION BY POSTURES AND FACIAL EXPRESSIONS IN THE RHESUS MONKEY (*MACACA MULATTA*). *Proc. Zool. Soc. Lond.* , 1–21 (1962).
24. Waller, B. M., Whitehouse, J. & Micheletta, J. Rethinking primate facial expression: A predictive framework. *Neurosci. Biobehav. Rev.* , 13–21 (2017).
25. Fridlund, A. J. The behavioral ecology view of facial displays, 25 years later. *Sci. Facial Expr.* 77–92 (2017).
26. Crivelli, C. & Fridlund, A. J. Facial Displays Are Tools for Social Influence. *Trends Cogn. Sci.* , 388–399 (2018).
27. Kavanagh, E., Whitehouse, J. & Waller, B. M. Being facially expressive is socially advantageous. *Sci. Rep.* , 12798 (2024).
28. Nishida, T., Kano, T., Goodall, J., McGrew, W. C. & Nakamura, M. Ethogram and Ethnography of Mahale Chimpanzees. *Anthropol. Sci.* , 141–188 (1999).
29. van Hooff, J. A. R. A. M. The facial displays of the catarrhine monkeys and apes. in *Primate Ethology* 1–37 (Routledge, New York, 1967).
30. Chevalier-Skolnikoff, S. The Primate Play Face: A Possible Key to the Determinants and Evolution of Play. *Rice Inst. Pam. - Rice Univ. Stud.* (1974).
31. Preuschoft, S. Primate Faces and Facial Expressions. *Soc. Res.* , 245–271 (2000).
32. Ekman, P., Sorenson, E. R. & Friesen, W. V. Pan-cultural elements in facial displays of emotion. *Science* , 86–88 (1969).
33. Kret, M. E., Prochazkova, E., Sterck, E. H. M. & Clay, Z. Emotional expressions in human and non-human great apes. *Neurosci. Biobehav. Rev.* , 378–395 (2020).

34. Nickelson, S. A. & Lockard, J. S. Ethogram of Celebes monkeys (*Macaca nigra*) in two captive habitats. *Primates* , 437–447 (1978).
35. Stevenson, M. F. & Poole, T. B. An ethogram of the common marmoset (*Calithrix jacchus jacchus*): General behavioural repertoire. *Anim. Behav.* , 428–451 (1976).
36. Oswald, M. & Lockard, J. S. Ethogram of the De Brazza's Guenon (*Cercopithecus neglectus*) in captivity. *Appl. Anim. Ethol.* , 285–296 (1980).
37. Skinner, S. & Lockard, JS. An ethogram of the liontail macaque (*Macaca silenus*) in captivity - ScienceDirect. *Appl. Anim. Ethol.* , (1979).
38. Kemp, C. & Kaplan, G. Facial expressions in common marmosets (*Callithrix jacchus*) and their use by conspecifics. *Anim. Cogn.* , 773–788 (2013).
39. Thierry, B., Demaria, C., Preuschoft, S. & Desportes, C. Structural convergence between silent bared-teeth display and relaxed open-mouth display in the Tonkean macaque (*Macaca tonkeana*). *Folia Primatol. (Basel)* , 178–184 (1989).
40. Visalberghi, E., Valenzano, D. R. & Preuschoft, S. Facial Displays in *Cebus apella*. *Int. J. Primatol.* , 1689–1707 (2006).
41. Kirkevold, B. C., Lockard, J. S. & Heestand, J. E. Development comparisons of grimace and play mouth in infant pigtail macaques (*Macaca nemestrina*). *Am. J. Primatol.* , 277–283 (1982).
42. Maestripiéri, D. Gestural Communication in Macaques: Usage and Meaning of Nonvocal Signals. *Evol. Commun.* , 193–222 (1997).
43. Maestripiéri, D. & Wallen, K. Affiliative and submissive communication in rhesus macaques. *Primates* , 127–138 (1997).
44. Cordoni, G., Ciantia, A., Guéry, J.-P., Mulot, B. & Norscia, I. Rapid facial mimicry in Platyrrhini: Play face replication in spider monkeys (*Ateles fusciceps*, *Ateles hybridus*, and *Ateles paniscus*). *Am. J. Primatol.* , e23607 (2024).
45. Pellis, S. M. & Pellis, V. C. Targets, tactics, and the open mouth face during play fighting in three species of primates. *Aggress. Behav.* , 41–57 (1997).

46. Waller, B. M. & Cherry, L. Facilitating Play Through Communication: Significance of Teeth Exposure in the Gorilla Play Face. *Am. J. Primatol.* , 157–164 (2012).
47. Palagi, E., Norscia, I. & Spada, G. Relaxed open mouth as a playful signal in wild ring-tailed lemurs. *Am. J. Primatol.* , 1074–1083 (2014).
48. Panksepp, J. & Burgdorf, J. “Laughing” rats and the evolutionary antecedents of human joy? *Physiol. Behav.* , (2003).
49. Maglieri, V. *et al.* Tell-tale signals: faces reveal playful and aggressive mood in wolves. *Anim. Behav.* , 1–9 (2024).
50. Maglieri, V., Zanolli, A., Mastrandrea, F. & Palagi, E. The relaxed open mouth is a true signal in dogs: demonstrating Tinbergen’s ritualization process. *Anim. Behav.* , 65–74 (2022).
51. Llamazares-Martín, C., Scopa, C., Guillén-Salazar, F. & Palagi, E. Relaxed Open Mouth reciprocity favours playful contacts in South American sea lions (*Otaria flavescens*). *Behav. Processes* , 87–95 (2017).
52. Davila-Ross, M. & Dezechache, G. The Complexity and Phylogenetic Continuity of Laughter and Smiles in Hominids. *Front. Psychol.* , 648497 (2021).
53. Pellis, S. M. & Pellis, W. C. On knowing it’s only play: The role of play signals in play fighting. *Aggress. Violent Behav.* , 249–268 (1996).
54. Bliss-moreu, E. & Moadab, G. The Faces Monkeys Make. in *The Science of Facial Expression* (Oxford University Press, 2017).
55. Petersen, R. M., Dubuc, C. & Higham, J. P. Facial Displays of Dominance in Non-human Primates. in *The Facial Displays of Leaders* (ed. Senior, C.) 123–143 (Springer International Publishing, Cham, 2018). doi:10.1007/978-3-319-94535-4_6.
56. Waller, B. M., Whitehouse, J. & Micheletta, J. Macaques can predict social outcomes from facial expressions. *Anim. Cogn.* , 1031–1036 (2016).
57. Thierry, B., Singh, M. & Kaumanns, W. *Macaque Societies: A Model for the Study of Social Organization*. (Cambridge University Press, 2004).

58. Wiper, S. M. & Semple, S. The function of teeth chattering in male Barbary macaques (*Macaca sylvanus*). *Am. J. Primatol.* , 1179–1188 (2007).
59. Micheletta, J., Engelhardt, A., Matthews, L., Agil, M. & Waller, B. M. Multicomponent and Multimodal Lipsmacking in Crested Macaques (*Macaca nigra*): Lipsmacking Behavior in Crested Macaques. *Am. J. Primatol.* , 763–773 (2013).
60. Albuquerque, N. *et al.* The shape of lipsmacking: socio-emotional regulation in bearded capuchin monkeys (*Sapajus libidinosus*). *Evol. Hum. Sci.* , e16 (2023).
61. Andrew, R. J. Evolution of facial expression. *Science* , 1034–1041 (1963).
62. Parr, L. A. The Discrimination of Faces and Their Emotional Content by Chimpanzees (*Pan troglodytes*). *Ann. N. Y. Acad. Sci.* , 56–78 (2003).
63. Liebal, K., Slocombe, K. E. & Waller, B. M. The language void 10 years on: multimodal primate communication research is still uncommon. *Ethol. Ecol. Evol.* , 1–14 (2022).
64. Genty, E., Clay, Z. & Hobaiter, C. Multi-Modal Use of a Socially Directed Call in Bonobos. *PLOS ONE* , 12 (2014).
65. Partan, S. R. Single and multichannel signal composition: facial expressions and vocalizations of rhesus macaques (*Macaca mulatta*). *Behaviour* , 993–1027 (2002).
66. Taglialatela, J. P. *et al.* Multimodal communication in chimpanzees. *Am. J. Primatol.* , 1143–1148 (2015).
67. Parr, L. A., Cohen, M. & Waal, F. de. Influence of Social Context on the Use of Blended and Graded Facial Displays in Chimpanzees. *Int. J. Primatol.* , 73–103 (2005).
68. Marler, P. Social organization, communication and graded signals: The chimpanzee and the gorilla. in *Growing points in ethology* (Cambridge U Press, Oxford, England, 1976).
69. Fedurek, P., Zuberbühler, K. & Dahl, C. D. Sequential information in a great ape utterance. *Sci. Rep.* , 38226 (2016).
70. Leroux, M. *et al.* Chimpanzees combine pant hoots with food calls into larger structures. *Anim. Behav.* , 41–50 (2021).

71. Hobaiter, C. & Byrne, R. W. Serial gesturing by wild chimpanzees: its nature and function for communication. *Anim. Cogn.* , 827–838 (2011).
72. Liebal, K., Call, J. & Tomasello, M. Use of gesture sequences in chimpanzees. *Am. J. Primatol.* , 377–396 (2004).
73. Aychet, J., Blois-Heulin, C. & Lemasson, A. Sequential and network analyses to describe multiple signal use in captive mangabeys. *Anim. Behav.* , 203–226 (2021).
74. Ekman, P., Friesen, W. V. & Hager, J. C. *Facial Action Coding System*. (Research Nexus, Salt lake City, 2002).
75. Ekman, P. & Friesen, W. V. Facial action coding system: a technique for the measurement of facial movement. *Palo Alto* , 5 (1978).
76. Baltrušaitis, T., Robinson, P. & Morency, L.-P. OpenFace: An open source facial behavior analysis toolkit. in *2016 IEEE Winter Conference on Applications of Computer Vision (WACV)* 1–10 (2016). doi:10.1109/WACV.2016.7477553.
77. Martin, J., Rychlowska, M., Wood, A. & Niedenthal, P. Smiles as Multipurpose Social Signals. *Trends Cogn. Sci.* , 864–877 (2017).
78. Lazow, S. P. & Bergman, T. J. The structural and motivational role of the unique lip-flip movement in the gelada (*Theropithecus gelada*) facial display repertoire. *Am. J. Phys. Anthropol.* , 280–290 (2020).
79. Partan, S. R. & Marler, P. Communication Goes Multimodal. *Science* , 1272–1273 (1999).
80. Waller, B. M., Caeiro, C. C. & Davila-Ross, M. Orangutans modify facial displays depending on recipient attention. 20 (2015).
81. Liebal, K., Pika, S. & Tomasello, M. Gestural communication of orangutans (*Pongo pygmaeus*). *Gesture* , 1–38 (2006).
82. Scheider, L., Waller, B. M., Oña, L., Burrows, A. M. & Liebal, K. Social Use of Facial Expressions in Hylobatids. *PLOS ONE* , e0151733 (2016).

83. Dobson, S. D. Socioecological correlates of facial mobility in nonhuman anthropoids. *Am. J. Phys. Anthropol.* , 413–420 (2009).
84. Dobson, S. D. Allometry of facial mobility in anthropoid primates: Implications for the evolution of facial expression. *Am. J. Phys. Anthropol.* , 70–81 (2009).
85. Kiltie, R. A. Scaling of Visual Acuity with Body Size in Mammals and Birds. *Funct. Ecol.* , 226–234 (2000).
86. Freeberg, T. M., Dunbar, R. I. M. & Ord, T. J. Social complexity as a proximate and ultimate factor in communicative complexity. *Philos. Trans. R. Soc. B Biol. Sci.* , 1785–1801 (2012).
87. Blumstein, D. T. & Armitage, K. B. Does Sociality Drive the Evolution of Communicative Complexity? A Comparative Test with Ground-Dwelling Sciurid Alarm Calls. *Am. Nat.* , 179–200 (1997).
88. Freeberg, T. M. Social Complexity Can Drive Vocal Complexity: Group Size Influences Vocal Information in Carolina Chickadees. *Psychol. Sci. Wiley-Blackwell* , 557–561 (2006).
89. McComb, K. & Semple, S. Coevolution of vocal communication and sociality in primates. *Biol. Lett.* , 381–385 (2005).
90. Wilkinson, G. S. Social and vocal complexity in bats. in *Animal social complexity: intelligence, culture and individualized societies* (eds. De Waal, F. B. M. & Tyack, P. L.) 322–341 (Harvard University Press, Cambridge, Massachusetts, 2003).
91. Birg, J. A. & English, T. Effects of regulating emotional expression on authenticity and likeability in stranger dyads. *J. Soc. Pers. Relatsh.* , 2868–2888 (2024).
92. Whitehouse, J. *et al.* Facial expressivity in dominant macaques is linked to group cohesion. *Proc. R. Soc. B Biol. Sci.* , 20240984 (2024).
93. Mielke, A. *et al.* NetFACS: Using network science to understand facial communication systems. *Behav. Res. Methods* , 1912–1927 (2021).

94. Rincon, A. V. *et al.* *Higher Social Tolerance Is Associated with More Complex Facial Behavior in Macaques*. <https://elifesciences.org/reviewed-preprints/87008v2> (2023)
doi:10.7554/eLife.87008.2.
95. Kim, Y. & Kret, M. The emotional expressions and emotion perception in nonhuman primates. in *The Oxford handbook of emotional development* 129–145 (Oxford University Press, New York, NY, US, 2022). doi:10.1093/oxfordhb/9780198855903.001.0001.
96. Dittrich, W. Representation of Faces in Longtailed Macaques (*Macaca fascicularis*). *Ethology* , 265–278 (1990).
97. Kanazawa, S. Recognition of facial expressions in a Japanese monkey (*Macaca fuscata*) and humans (*Homo sapiens*). *Primates* , 25–38 (1996).
98. Parr, L. A., Hopkins, W. D. & Waal, F. B. M. de. The Perception of Facial Expressions By Chimpanzees, *Pan Troglodytes*. *Evol. Commun.* , 1–23 (1998).
99. Parr, L. A. Perceptual biases for multimodal cues in chimpanzee (*Pan troglodytes*) affect recognition. *Anim. Cogn.* , 171–178 (2004).
100. Parr, L. A., Waller, B. M. & Heintz, M. Facial expression categorization by chimpanzees using standardized stimuli. *Emotion* , 216–231 (2008).
101. Parr, L. A. & Heintz, M. Facial expression recognition in rhesus monkeys, *Macaca mulatta*. *Anim. Behav.* , 1507–1513 (2009).
102. Micheletta, J. *et al.* Familiar and unfamiliar face recognition in crested macaques (*Macaca nigra*). *R. Soc. Open Sci.* , 150109 (2015).
103. Calcutt, S. E., Rubin, T. L., Pokorny, J. J. & de Waal, F. B. M. Discrimination of emotional facial expressions by tufted capuchin monkeys (*Sapajus apella*). *J. Comp. Psychol.* , 40–49 (2017).
104. Parr, L. A. & Hecht, E. E. Face Perception in Non-Human Primates. in *Oxford Handbook of Face Perception* (eds. Calder, A. J., Rhodes, G., Johnson, M. H. & Haxby, J. V.) 0 (Oxford University Press, 2011). doi:10.1093/oxfordhb/9780199559053.013.0035.

105. Öhman, A., Lundqvist, D. & Esteves, F. The face in the crowd revisited: A threat advantage with schematic stimuli. *J. Pers. Soc. Psychol.* , 381–396 (2001).
106. Ohman, A. & Mineka, S. Fears, phobias, and preparedness: toward an evolved module of fear and fear learning. *Psychol. Rev.* , 483–522 (2001).
107. Bachmann, H. P., Japee, S., Merriam, E. P. & Liu, T. T. Emotion and Anxiety Interact to Bias Spatial Attention.
108. King, H. M., Kurdziel, L. B., Meyer, J. S. & Lacreuse, A. Effects of testosterone on attention and memory for emotional stimuli in male rhesus monkeys. *Psychoneuroendocrinology* , 396–409 (2012).
109. Lacreuse, A., Schatz, K., Strazzullo, S., King, H. M. & Ready, R. Attentional biases and memory for emotional stimuli in men and male rhesus monkeys. *Anim. Cogn.* , 861–871 (2013).
110. Parr, L. A., Modi, M., Siebert, E. & Young, L. J. Intranasal oxytocin selectively attenuates rhesus monkeys' attention to negative facial expressions. *Psychoneuroendocrinology* , 1748–1756 (2013).
111. Cassidy, L. C. *et al.* The Dot-Probe Attention Bias Task as a Method to Assess Psychological Well-Being after Anesthesia: A Study with Adult Female Long-Tailed Macaques (*Macaca fascicularis*). *Eur. Surg. Res.* , 37–53 (2023).
112. Wilson, D. A. & Tomonaga, M. Exploring attentional bias towards threatening faces in chimpanzees using the dot probe task. *PLOS ONE* , e0207378 (2018).
113. Reilly, O. T., Benítez, M. E., Beran, M. J., Barber, S. J. & Brosnan, S. F. No evidence of attentional bias toward threatening conspecific and allospecific faces in capuchin monkeys (*Sapajus [Cebus] apella*) using a dot-probe task. *J. Comp. Psychol. Wash. DC* (2024) doi:10.1037/com0000381.
114. Bethell, E. J., Holmes, A., MacLarnon, A. & Semple, S. Evidence That Emotion Mediates Social Attention in Rhesus Macaques. *PLOS ONE* , e44387 (2012).

115. Howarth, E. R. I. *et al.* Developing and validating attention bias tools for assessing trait and state affect in animals: A worked example with *Macaca mulatta*. *Appl. Anim. Behav. Sci.* , 105198 (2021).
116. Pritsch, C., Telkemeyer, S., Mühlenbeck, C. & Liebal, K. Perception of facial expressions reveals selective affect-biased attention in humans and orangutans. *Sci. Rep.* , 7782 (2017).
117. Zhao, H. *et al.* Facial expression recognition in golden snub-nosed monkeys. *Curr. Zool.* , 695–697 (2020).
118. Rayson, H., Massera, A., Belluardo, M., Ben Hamed, S. & Ferrari, P. F. Early social adversity modulates the relation between attention biases and socioemotional behaviour in juvenile macaques. *Sci. Rep.* , 21704 (2021).
119. Rosati, A. G., Arre, A. M., Platt, M. L. & Santos, L. R. Developmental shifts in social cognition: socio-emotional biases across the lifespan in rhesus monkeys. *Behav. Ecol. Sociobiol.* , 163 (2018).
120. Parr, L. A. Cognitive and physiological markers of emotional awareness in chimpanzees (*Pan troglodytes*). *Anim. Cogn.* , 223–229 (2001).
121. Goossens, B. M. A., Dekleva, M., Reader, S. M., Sterck, E. H. M. & Bolhuis, J. J. Gaze following in monkeys is modulated by observed facial expressions. *Anim. Behav.* , 1673–1681 (2008).
122. Teufel, C., Gutmann, A., Pirow, R. & Fischer, J. Facial expressions modulate the ontogenetic trajectory of gaze-following among monkeys. *Dev. Sci.* , 913–922 (2010).
123. Champ, T. M. *et al.* Social engagement revealed by gaze following in third-party observers of simulated social conflict. *Front. Psychol.* , (2022).
124. Overduin-de Vries, A. M., Bakker, F. A. A., Spruijt, B. M. & Sterck, E. H. M. Male long-tailed macaques (*Macaca fascicularis*) understand the target of facial threat. *Am. J. Primatol.* , 720–730 (2016).
125. Buttelmann, D., Call, J. & Tomasello, M. Do great apes use emotional expressions to infer desires? *Dev. Sci.* , 688–698 (2009).

126. Morimoto, Y. & Fujita, K. Capuchin monkeys (*Cebus apella*) use conspecifics' emotional expressions to evaluate emotional valence of objects. *Anim. Cogn.* , 341–347 (2012).
127. Morimoto, Y. & Fujita, K. Capuchin monkeys (*Cebus apella*) modify their own behaviors according to a conspecific's emotional expressions. *Primates* , 279–286 (2011).
128. Nieuwburg, E. G. I., Ploeger, A. & Kret, M. E. Emotion recognition in nonhuman primates: How experimental research can contribute to a better understanding of underlying mechanisms. *Neurosci. Biobehav. Rev.* , 24–47 (2021).
129. Hatfield, E., Cacioppo, J. T. & Rapson, R. L. Emotional Contagion. *Curr. Dir. Psychol. Sci.* , 96–100 (1993).
130. Prochazkova, E. & Kret, M. E. Connecting minds and sharing emotions through mimicry: A neurocognitive model of emotional contagion. *Neurosci. Biobehav. Rev.* , 99–114 (2017).
131. Preston, S. D. & Waal, F. B. M. de. Empathy: Its ultimate and proximate bases. *Behav. Brain Sci.* , 1–20 (2002).
132. Dimberg, U., Thunberg, M. & Elmehed, K. Unconscious Facial Reactions to Emotional Facial Expressions. *Psychol. Sci.* , 86–89 (2000).
133. Davila Ross, M., Menzler, S. & Zimmermann, E. Rapid facial mimicry in orangutan play. *Biol. Lett.* , 27–30 (2008).
134. Mancini, G., Ferrari, P. F. & Palagi, E. In Play We Trust. Rapid Facial Mimicry Predicts the Duration of Playful Interactions in Geladas. *PLOS ONE* , e66481 (2013).
135. Rendall, D., Owren, M. J. & Ryan, M. J. What do animal signals mean? *Anim. Behav.* , 233–240 (2009).
136. Gothard, K. M., Battaglia, F. P., Erickson, C. A., Spitler, K. M. & Amaral, D. G. Neural Responses to Facial Expression and Face Identity in the Monkey Amygdala. *J. Neurophysiol.* , 1671–1683 (2007).
137. Taubert, J. & Japee, S. Real Face Value: The Processing of Naturalistic Facial Expressions in the Macaque Inferior Temporal Cortex. *J. Cogn. Neurosci.* 1–17 (2024) doi:10.1162/jocn_a_02108.

138. Rutishauser, U., Mamelak, A. N. & Adolphs, R. The primate amygdala in social perception – insights from electrophysiological recordings and stimulation. *Trends Neurosci.* , 295–306 (2015).
139. Sackett, G. P. Monkeys Reared in Isolation with Pictures as Visual Input: Evidence for an Innate Releasing Mechanism. *Science* , 1468–1473 (1966).
140. Morin, E. L., Howell, B. R., Meyer, J. S. & Sanchez, M. M. Effects of early maternal care on adolescent attention bias to threat in nonhuman primates. *Dev. Cogn. Neurosci.* , 100643 (2019).
141. O’Callaghan, O., Whitehouse, J., Paukner, A., Witham, C. L. & Waller, B. M. Maternal care predicts facial expression processing in macaques. *iScience* , 112179 (2025).
142. Fleagle, J. G. & Seiffert, E. R. The Phylogeny of Primates. in *Evolutionary Neuroscience* 483–518 (Elsevier, 2020). doi:10.1016/B978-0-12-820584-6.00020-9.
143. Waller, B. M., Liebal, K., Burrows, A. M. & Slocombe, Katie. E. How Can a Multimodal Approach to Primate Communication Help Us Understand the Evolution of Communication? *Evol. Psychol.* , 147470491301100 (2013).
144. Fröhlich, M. & van Schaik, C. P. The function of primate multimodal communication. *Anim. Cogn.* , 619–629 (2018).
145. Waller, B. M., Kavanagh, E., Micheletta, J., Clark, P. R. & Whitehouse, J. The face is central to primate multicomponent signals. *Int. J. Primatol.* (2022) doi:10.1007/s10764-021-00260-0.
146. Wieser, M. & Brosch, T. Faces in Context: A Review and Systematization of Contextual Influences on Affective Face Processing. *Front. Psychol.* , (2012).
147. Righart, R. & de Gelder, B. Rapid influence of emotional scenes on encoding of facial expressions: an ERP study. *Soc. Cogn. Affect. Neurosci.* , 270–278 (2008).
148. Barrett, L. F., Mesquita, B. & Gendron, M. Context in emotion perception. *Curr. Dir. Psychol. Sci.* , 286–290 (2011).

149. Taubert, J. *et al.* Parallel Processing of Facial Expression and Head Orientation in the Macaque Brain. *J. Neurosci.* , 8119–8131 (2020).
150. Abassi, E. *et al.* Neural Encoding of Bodies for Primate Social Perception. *J. Neurosci.* , e1221242024 (2024).
151. Shepherd, S. V. & Platt, M. L. Noninvasive telemetric gaze tracking in freely moving socially housed prosimian primates. *Methods* , 185–194 (2006).
152. Hjortsjo, C. H. *Man's Face and Mimic Language*. (Nordens Boktryckeri, Sweden, 1970).
153. Duchenne, G.-B. *The Mechanism of Human Facial Expression*. (Cambridge University Press, 1862).
154. Efthimiou, T. N., Hernandez, M. P., Elsenaar, A., Mehu, M. & Korb, S. Application of facial neuromuscular electrical stimulation (fNMES) in psychophysiological research: Practical recommendations based on a systematic review of the literature. *Behav. Res. Methods* (2023) doi:10.3758/s13428-023-02262-7.
155. Waller, B. M. *et al.* Intramuscular electrical stimulation of facial muscles in humans and chimpanzees: Duchenne revisited and extended. *Emotion* , 367–382 (2006).
156. De Bonnacaze, G. *et al.* Variability in facial-muscle innervation: A comparative study based on electrostimulation and anatomical dissection. *Clin. Anat.* , 169–175 (2019).
157. Vick, S.-J., Waller, B. M., Parr, L. A., Smith Pasqualini, M. C. & Bard, K. A. A Cross-species Comparison of Facial Morphology and Movement in Humans and Chimpanzees Using the Facial Action Coding System (FACS). *J. Nonverbal Behav.* , 1–20 (2007).
158. Parr, L. A., Waller, B. M., Burrows, A. M., Gothard, K. M. & Vick, S. J. Brief communication: MaqFACS: A muscle-based facial movement coding system for the rhesus macaque. *Am. J. Phys. Anthropol.* , 625–630 (2010).
159. Julle-Danière, É. *et al.* MaqFACS (Macaque Facial Action Coding System) can be used to document facial movements in Barbary macaques (*Macaca sylvanus*). *PeerJ* , e1248 (2015).

160. Correia-Caeiro, C., Holmes, K. & Miyabe-Nishiwaki, T. Extending the MaqFACS to measure facial movement in Japanese macaques (*Macaca fuscata*) reveals a wide repertoire potential. *PLOS ONE* , e0245117 (2021).
161. Waller, B. M., Lembeck, M., Kuchenbuch, P., Burrows, A. M. & Liebal, K. GibbonFACS: A Muscle-Based Facial Movement Coding System for Hylobatids. *Int. J. Primatol.* , 809–821 (2012).
162. Caeiro, C. C., Waller, B. M., Zimmermann, E., Burrows, A. M. & Davila-Ross, M. OrangFACS: A Muscle-Based Facial Movement Coding System for Orangutans (*Pongo* spp.). *Int. J. Primatol.* , 115–129 (2013).
163. Correia-Caeiro, C., Burrows, A., Wilson, D. A., Abdelrahman, A. & Miyabe-Nishiwaki, T. CalliFACS: The common marmoset Facial Action Coding System. *PLOS ONE* , e0266442 (2022).
164. Waller, B. M. *et al.* Paedomorphic Facial Expressions Give Dogs a Selective Advantage. *PLoS ONE* , e82686 (2013).
165. Wathan, J., Burrows, A. M., Waller, B. M. & McComb, K. EquiFACS: The Equine Facial Action Coding System. *PLOS ONE* , 1–35 (2015).
166. Caeiro, C. C., Burrows, A. M. & Waller, B. M. Development and application of CatFACS: Are human cat adopters influenced by cat facial expressions? *Appl. Anim. Behav. Sci.* , 66–78 (2017).
167. Burrows, A. M., Waller, B. M. & Parr, L. A. Facial musculature in the rhesus macaque (*Macaca mulatta*): evolutionary and functional contexts with comparisons to chimpanzees and humans. *J. Anat.* , 320–334 (2009).
168. Burrows, A. M., Waller, B. M. & Micheletta, J. Mimetic Muscles in a Despotic Macaque (*Macaca mulatta*) Differ from Those in a Closely Related Tolerant Macaque (*M. nigra*). *Anat. Rec.* , 1317–1324 (2016).
169. Burrows, A. M., Waller, B. M., Parr, L. A. & Bonar, C. J. Muscles BlackwellPublishingLtd of facial expression in the chimpanzee (*Pan troglodytes*): descriptive, comparative and phylogenetic contexts. 15 (2006).

- 1083 170. Burrows, A. M., Diogo, R., Waller, B. M., Bonar, C. J. & Liebal, K. Evolution of the Muscles of
1084 Facial Expression in a Monogamous Ape: Evaluating the Relative Influences of Ecological and
1085 Phylogenetic Factors in Hylobatids. *Anat. Rec. Adv. Integr. Anat. Evol. Biol.* , 645–663 (2011).
- 1086 171. Kaminski, J., Waller, B. M., Diogo, R., Hartstone-Rose, A. & Burrows, A. M. Evolution of facial
1087 muscle anatomy in dogs. *Proc. Natl. Acad. Sci.* , 14677–14681 (2019).
- 1088 172. Waller, B. M., Parr, L. A., Gothard, K. M., Burrows, A. M. & Fuglevand, A. J. Mapping the
1089 contribution of single muscles to facial movements in the rhesus macaque. *Physiol. Behav.* ,
1090 93–100 (2008).
- 1091 173. Bishay, M. *et al.* AFFDEX 2.0: A Real-Time Facial Expression Analysis Toolkit. in *2023 IEEE 17th*
1092 *International Conference on Automatic Face and Gesture Recognition (FG)* 1–8 (IEEE, 2023).
- 1093 174. Stöckli, S., Schulte-Mecklenbeck, M., Borer, S. & Samson, A. C. Facial expression analysis with
1094 AFFDEX and FACET: A validation study. *Behav. Res. Methods* , 1446–1460 (2018).
- 1095 175. Lewinski, P., Den Uyl, T. M. & Butler, C. Automated facial coding: Validation of basic emotions
1096 and FACS AUs in FaceReader. *J. Neurosci. Psychol. Econ.* , 227–236 (2014).
- 1097 176. Morozov, A., Parr, L. A., Gothard, K., Paz, R. & Pryluk, R. Automatic Recognition of Macaque
1098 Facial Expressions for Detection of Affective States. *eneuro* , ENEURO.0117-21.2021 (2021).
- 1099