The Emotional Expressions and Emotion Perception in Nonhuman Primates

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Abstract and Keywords

The expression of emotions and their recognition in conspecifics are pivotal to social life. As Darwin postulated in his pioneering book *The expression of the emotions in man and animals*, many morphological features and functions of emotional expressions characterized in humans are homologous to those of other animals. Intriguingly, despite this early work, scientists have been skeptical about the feasibility of studying emotions in nonhumans and, therefore, the study of their emotional expressions has been limited. However, recent technological advances in neuroscience, genetics, and fine-scale behavioral analyses enable researchers to investigate human emotions in direct comparison with other animals. Throughout this chapter, the authors provide convincing evidence that nonhuman primates produce and recognize conspecific emotional expressions. Some of them, especially the bared-teeth display, are used in multiple contexts, suggesting cognitively sophisticated functions. The flexible use of emotional expressions seems to be tightly linked to species sociality, such as level of tolerance.

Keywords: emotional expression, emotion perception, evolution, primates, sociality

Adaptive Functions of Emotional Expressions and Emotion Perception

FOR decades, the concept of emotion has long been the subject of considerable debate due to differing definitions adopted across disciplines, ranging from functional (Anderson & Adolphs, 2014) to cognitive and socioconstructive (Barrett et al., 2007; Lazarus, 1991) accounts. Although the nature of emotion and to what extent we should attribute animal behavior to an emotion are still debatable (de Waal, 2011); there is a wide consensus that the ability to communicate internal emotional states is critical for social species. In this chapter, we focus on expressions of emotion and how these are perceived by conspecifics. We employ a broad definition of how emotional expressions are operationalized, which

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reads as follows: Any change in the face, body, or voice that is in principle perceivable by conspecifics (via visual, auditory, or olfactory channels) and that results from an altered mental state triggered by biologically relevant stimuli (e.g., a snake, an emotional conspecific) (Kret et al., 2019). Adopting this operational definition has two advantages. First, it allows the inclusion of both explicit expressions resulting from muscle activity and implicit emotion-induced changes such as piloerection and pupil size. Second, it facilitates a direct comparison between human and nonhuman primates and incorporates literature on both primatology and psychology, circumventing terminological discrepancies.

(p. 130) Primates are characterized by their gregariousness and highly developed sociocognitive capacities (Dunbar, 2003; Kappeler & van Schaik, 2002). Properly regulating behaviors in response to internal and external social stimuli is therefore critical for individuals within groups to maintain stable social relationships (Kret & Ploeger, 2015). Preston and de Waal (2002) have proposed an autonomous neural mechanism—the Perception–Action Model (PAS)—as a core mechanism which enables emotional state matching with others (de Waal & Preston, 2017; Preston & de Waal, 2002). The ability to match one's own emotional state with that of another is adaptive from both a kin and nonkin's perspective, since it allows mothers to better accommodate the needs of their offspring and unrelated group members to prepare a fight or flight response in anticipation of potential threats (Preston & de Waal, 2002; Frijda, 2016). This autonomous neural mechanism is presumed to be widespread in all animal taxa, but its complexity and the level of cognitive control presumably varies widely across species. Given the complex nature of primate sociality, primates are expected to have evolved enhanced emotion communication capacities (de Waal & Preston, 2017; Gruber & Sievers, 2019; see Clay et al., this volume).

Socioecological Constraints on Emotion Communication

Emotional expressions have evolved for various reasons. Some expressions, such as pupil dilation, may have evolved due to perceptual benefits (Mathôt, 2018), but without obvious social selective pressure, although in humans and chimpanzees these emotional cues might be picked up by others and influence their emotional state (Kret et al., 2013, 2014; for a review, see Kret, 2015). Other explicit emotional signals, such as facial or vocal expressions, often show key similairities in closely related species due to homology (Andrew, 1963; Preuschoft and van Hooff, 1995). However, specific forms and functions of such expressions are known to vary depending on socioecological conditions to which a species has adapted (for a review, see Waller and Micheletta, 2013).

Facial communication, by means of facial muscle movements, is more prominently found in diurnal than nocturnal species and in those living in large rather than in simple social groups, where close proximity or face-to-face communication is more likely to occur (Dobson, 2009a; Smuts et al., 2008). Parr and her colleagues have summarized some of the existing hypotheses describing physical and socioecological conditions that constrain or fa-

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vor a species' communicative repertoire (Parr et al., 2015). For example, body size constrains the length and frequency of vocalization, as well as facial mobility for facial expressions. Larger animals, compared to smaller animals, produce lower-frequency vocalizations as well as longer calls (Ey et al., 2007) and have more variable facial movements (Dobson, 2009a). These physical boundaries of expressions are tightly linked to species' capability of perceiving variable signals (Kiltie, 2000).

(p. 131) Social complexity is not only correlated with a species' general or sociocognitive capacities, but it is also known to predict the complexity of its communicative repertoire (Dunbar, 1993; Freeberg et al., 2012; Schmidt & Cohn, 2001). For example, species living in large groups have more varied communicative repertoires than those living in small groups (McComb & Semple, 2005). Moreover, tolerant species, compared to despotic species, are likely to have more variable and flexible communicative repertoires, since an error in expressing submissive signals can lead to a higher risk in species with a steep hierarchy (Ciani et al., 2012; Dobson, 2012; Maestripieri, 1999; Parr et al., 2005; Preuschoft & van Hooff, 1995; Rebout et al., 2020). For example, one such species, rhesus macaques, compared to Tonkean macaques (a tolerant species), use bared-teeth displays more unidirectionally from lower-ranking to higher-ranking individuals to display submission (Beisner & McCowan, 2014; Thierry et al., 1989). Moreover, the number of facial displays in the genus *Macaca* is found to be larger in tolerant species than despotic species (Preuschoft & van Hooff, 1995).

The aforementioned studies have increased general knowledge about species' communicative repertoires. However, the link between species' sociality and their capacity of emotion communication has been mostly left untouched. Few studies have thus far compared closely related species in terms of emotional expression (Beisner & McCowan, 2014; Flack & de Waal, 2007; Preuschoft, 1995; Preuschoft & van Hooff, 1995). If emotional expression and emotion perception are indeed tightly linked to a species' communicative repertoire, then we may hypothesize that the complexity of, and the sensitivity to, emotions are directly linked to a species' social characteristics. For example, highly tolerant species living in complex social groups may have higher flexibility and variability in expressing emotions, as well as higher sensitivity to detect emotional expressions (Parr et al., 2005; Waller & Micheletta, 2013). However, without testing this possibility in combination with different emotional expressions and by comparing different species directly with each other under the same conditions, the existence of such species' differences remains speculative.

Behavioral Studies of Emotional Expression in Nonhuman Primates

More than a century ago, Darwin proposed the evolutionary continuity of emotional expressions and corresponding functions in human and nonhuman animals (Darwin, 1872). Ekman later experimentally tested the universality of emotional expressions across different cultural populations in humans and suggested that some emotions are basic and have

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discrete evolutionary functions which constitute a set of fundamental human emotional states important to regulate social life (Ekman, 1992). Although the classification of discrete emotions and their scalability are controversial (Anderson & Adolphs, 2014; Barrett, 1998; Devidze et al., 2006; McNaughton & Corr, 2004; Pfaff et al., (p. 132) 2005; Russell, 1980, 2003), the dominant view is that there are at least some emotions including, for instance, disgust, which are expressed similarly across different cultures (e.g., Izard, 1994) and are present in nonhuman primates (e.g., Berridge, 2000). In this section, we discuss several emotional expressions that have been most widely described in the nonhuman primate literature, and discuss their communicative value.

Among the different expressions of emotion, fear-induced responses have received most attention in both human and nonhuman primate emotion research (Cook & Mineka, 1989, 1990; LoBue & DeLoache, 2008; Weiss et al., 2015). Interestingly, most behavioral research on how primates respond to fear-inducing external stimuli, such as predators, has focused on vocalizations, in terms of linguistic properties, such as referential signaling (Seyfarth et al., 1980). However, the detection of a fear-inducing stimulus often provokes facial expressions (Parr et al., 2005). These facial expressions fundamentally share universal morphological and physiological characteristics which function to increase sensory vigilance, such as increased eye aperture and flared nostrils (Susskind et al., 2008). A growing number of studies on fear in primates, ranging from a phylogenetic analysis of facial movements to several cognitive and neuroimaging experiments (Cook & Mineka, 1989, 1990; Kalin et al., 2001, 2004; LoBue & DeLoache, 2008; Preuschoft & van Hooff, 1995; Weiss et al., 2015), have indeed supported the view that the expression and perception of fear have evolutionary origins in a predatory defense mechanism which later served a social function, such as tension reduction or conflict avoidance (Öhman, 1986, 2009). For example, naïve primates, when exposed to snake-related objects, exhibit avoiding behaviors (Weiss et al., 2015). These seemingly innate behavioral responses associated with snakes also become informative to other conspecific members (Cook & Mineka, 1990). The responses to social threat in primates show similar behavioral patterns to those observed in response to snakes, and the amygdala is known to mediate both predator-related and social threat-related fear responses (for a review, see Öhman, 2009). Therefore, the expression of fear is expected to be highly conserved across species and to have a conspicuous communicative signal. Given the space available for this chapter, we confine our discussion to the visual domain.

The bared-teeth display is one of the most frequently observed facial expressions in nonhuman primates, regardless of social structure or complexity, and most often in response to fear or aggression (marmosets: Stevenson & Poole, 1976; several species of macaques: de Waal & Luttrell, 1985; Thierry et al, 1989; mandrills: Bout & Thierry, 2005; orangutans: Liebal et al., 2006; chimpanzees: Waller & Dunbar, 2005; bonobos: de Waal, 1988). Although there are morphological similarities in the bared-teeth display across species, the frequency and function of its usage, as well as the contexts in which it is expressed, are known to vary. In some species, this expression has been ritualized to express subordinance (Flack & de Waal, 2007; Maestripieri & Wallen, 1997), benign intentions (Waller & Dunbar, 2005), and even affiliation and friendship (Bout & Thierry, 2005), which seem

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to be linked to sociocognitive characteristics, such as tolerance (Dobson, 2012; Thierry et al., 2000). In humans, it has been ritualized into the social smile (Van Hooff, 1972), with multiple social purposes (Martin et al., 2017). Although the involved facial muscles can vary slightly across contexts, using a similar expression (p. 133) in multiple contexts suggests behavioral flexibility and perhaps even the existence of a cognitive capacity for top–down control of emotional expressions (Kret et al., 2019).

Unlike the emotional expressions that have evolved in life-threatening situations, the expression of positive emotions is presumed to be less likely to have a specific pattern of behavioral reactions, since it is less critical to an individual's survival and therefore more susceptible to variation over the course of evolution (Fredrickson, 1998; Tooby & Cosmides, 1990). Nonetheless, one of the positive emotional expressions—the relaxed open-mouth display or play face—considered to be homologous to human laughter, has been widely reported across many nonhuman primate species (Davila–Ross et al., 2008, 2015; Palagi, 2006; Pellis & Pellis, 1996; Van Hooff, 1972; Van Hooff & Preuschoft, 2003; Waller & Dunbar, 2005). The relaxed open-mouth display is mostly observed in a play context, such as tickle play (Bard et al., 2014; Palagi, 2008), wrestling (Maestripieri & Ross, 2004; Petit et al., 2008), or ritualized play fighting (Palagi et al., 2007; Palagi & Mancini, 2011). Although it is unclear whether the relaxed open-mouth display is highly conserved across species due to some physical or physiological functions, it is generally acknowledged that it originates from the ritualized play bite, signaling nonaggressive intent (Parr et al., 2015; Poole, 1978; Van Hooff, 1972), and has been reported across mammalian species (Henry & Herrero, 1974; Pal, 2010; Poole, 1978).

Infant chimpanzees as young as 4 weeks of age engage in tickle play which often accompanies this expression (Bard et al., 2014). Due to the reciprocal nature of play interactions, developing immatures learn how to signal and read play intentions from facial and bodily expressions (Burghardt, 2005; Fagen, 1993; Pellis & Pellis, 1996). Through practice, youngsters become competent in decoding cooperative or competitive signals from interaction partners, a critical skill in social living (Pellis & Pellis, 2017). In humans, positive emotions such as joy, interest, contentment, and love, are suggested to build an individual's physical and cognitive capacities by broadening the momentary thought–action repertoire (Broaden-and-Build Model of Positive Emotions: Fredrickson, 1998). Similarly, a study in nonhuman primates has shown that species' involvement in social play correlates with the relative volume of the amygdala and hypothalamus (Lewis & Barton, 2006). This indicates that producing and processing emotional signals during play are adaptive for the development of sociocognitive skills (see Zaharia et al., this volume; Veiga et al., this volume). Humans laugh not only during social play, but also in daily conversations and even without a social partner (e.g., reading comics, watching a comedy, thinking about something funny). Laughing without a social partner may reflect their genuine emotional state (see Mireault, this volume). Interestingly, similar to the social smile, laughter in humans also serves more cognitively sophisticated functions, such as signaling friendly intentions to a stranger (for a review, see Gervais & Wilson, 2005). It would be interesting to investigate whether the relaxed open-mouth display in nonhuman pri-

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mates similarly occurs exclusively during solo play or also outside of the play context, and whether this relates to sociality.

Similar to fear-induced facial expressions, the expression of disgust also has an adaptive function to inhibit sensory exposure, and therefore is commonly considered to be conserved across species (Susskind et al., 2008). Interestingly, humans make (p. 134) disgusted facial expressions even in socially immoral contexts which are similar to expressions following, for instance, the smell of rotten food. It has therefore been suggested that the expression of moral disgust originates from the same behavioral mechanism to avoid biological contaminants (Chapman et al., 2009). However, only a couple of studies thus far have investigated the expression of disgust, and its communicative value in nonhuman primates has rarely been explored (Berridge, 2000; Steiner & Glaser, 1984), In one study by Berridge (2000), researchers gave infants of humans, rats, and multiple species of nonhuman primates different tastes. One of these substances had a bitter taste, and the resulting facial expression was strikingly similar across species. Sarabian and her colleagues explored the disgust response in multiple species of nonhuman primates (Sarabian et al., 2017, 2018; Sarabian & MacIntosh, 2015). In their studies, the primates not only sensed potential biological contaminants through visual cues, but also through olfactory and tactile cues. Furthermore, certain nonhuman primates were able to discriminate parasite-infected individuals from olfactory cues and adjust their grooming behavior accordingly (Poirotte et al., 2017). However, how primates express aversion, and whether these putative expressions are perceived by others, should be further examined.

The specific characteristics of the facial expression of anger in nonhuman primates are not well documented, except in a few great ape species (e.g., bulging lips in chimpanzees and lip press in bonobos: van Hooff, 1971; de Waal, 1988), perhaps due to the lack of conspicuity in the expression of these emotions, or the large variability within or across species. Anger-related emotional expressions are often termed as agonistic or aggressive displays without descriptions of emotional states. Aggressive displays have been generally described in terms of an individual’s exaggerated bodily expressions, rather than the facial expressions (Nishida et al., 1999). Since body size often correlates with physical strength, nonhuman primates often show exaggerated body movements with hair erection or use of objects, such as branches, to appear more threatening (Fessler & Gervais, 2010; Nishida et al., 1999). Furthermore, sexually isomorphic species living in small groups with lower levels of agonistic interactions, such as gibbons, may rely more on other behavioral signals, such as vocalizations, to signal aggressive intent (Raemaekers et al., 1984). Therefore, it is likely that the communicative signal of anger takes many different behavioral forms across and within species (Andersson, 1980).

There have been many anecdotal reports of nonhuman primates showing grief or sadness about the death of conspecifics, especially of their offspring. The most frequently reported behavior is the prolonged carrying of a dead infant which is often accompanied by inspection and grooming, and sometimes cannibalism (Anderson, 2016; Gonçalves & Biro, 2018; Watson & Matsuzawa, 2018). It is too early to draw conclusions on whether there are highly conserved facial or other behavioral features within or across primate species

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in expressing grief or sadness. However, it is noteworthy that responding to other's distress or grief is considered to be closely linked to empathy (Preston & de Waal, 2002; see Clay et al., this volume). Therefore, further comparative studies on these putative emotional expressions and perception of them should (p. 135) follow, with a view to enriching our understanding of the origins of human hyper cooperativeness and prosociality.

Experimental Studies of Emotion Perception in Nonhuman Primates

There are far fewer studies concerning the perception of emotional expressions in nonhuman primates than there are concerning how those emotions are expressed. Although it is possible to infer how nonhuman primates perceive emotional expressions by analyzing subsequent behaviors of the recipient, only controlled experiments can address the specific nature of the mechanisms underlying emotion perception (e.g., the capacity to categorize emotional expressions, the sensitivity to graded or variable signals of emotions, the role of expression modality on emotion perception). There have been a number of experimental approaches to investigating emotion perception in nonhuman primates, ranging from touchscreen-based tasks, such as matching-to-sample and dot-probe tasks, to eye-tracking studies (Kano & Tomonaga, 2010b; Kret et al., 2016; Parr & Heintz, 2009; van Berlo et al., 2020). Whereas the matching-to-sample task is widely used to test nonhuman primates' ability to categorize emotional expressions, dot-probe and eye-tracking tasks have been used to test attentional biases toward emotional expressions.

Studies using the matching-to-sample and similar paradigms have found that nonhuman primates can reliably discriminate and categorize images of conspecific emotional expressions (chimpanzees: Kano et al., 2008; Parr, 2001, 2003, 2004; Parr et al., 1998, 2008, 2009; crested macaques: Micheletta et al., 2015; tufted capuchin monkeys: Calcutt et al., 2017; for a review, see Nieuwburg et al., 2021). It is noteworthy that whereas tolerant species, such as crested macaques, showed error patterns influenced by functional similarities of facial expressions, chimpanzees, a despotic species, showed error patterns influenced by facial feature similarities (Micheletta et al., 2015; Parr et al., 1998). These results indicate that a species' tolerance may predict their capacity to decode facial expressions, but this assertion warrants further investigation.

The dot-probe task, a reliable paradigm to test implicit attentional biases (van Rooijen et al., 2017), has also produced concordant results in rhesus macaques, showing that bared-teeth displays (a negative expression in this species) captured attention faster than neutral expressions. In contrast, positive facial expressions did not capture macaques' attention (Lacreuse et al., 2013; Parr et al., 2013). Studies on great apes using the dot-probe paradigm have produced mixed results. Whereas bonobos showed an attentional bias toward emotional scenes compared to neutral scenes (Kret et al., 2016; van Berlo et al., 2020), chimpanzees did not (Kret et al., 2018; Wilson & Tomonaga, 2018). It is unclear whether this discrepancy can be explained by the species' different sociality or methodological differences (e.g., the use of color versus monotone pictures, or face (p. 136) and

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isolated body pictures versus rich emotional scenes) between these four studies. To test whether a species' sociality accounts for the difference in the attentional bias toward emotions, it would be necessary to measure this in closely related but socially different species, such as chimpanzees, bonobos, and humans, with either a set of systematically well-controlled stimuli or a very large stimulus set where low-level differences between unique stimuli are averaged out within the different emotional conditions they constitute (e.g., Kret et al., 2016).

Similar to the dot-probe task, eye-tracking methodology can further elucidate whether the animal is drawn toward, or avoids looking at, certain emotional expressions. For example, rhesus macaques preferred to look at neutral faces over aggressive faces when they were in a stressful condition, but displayed an opposite tendency when they were in an enriched condition (Bethell et al., 2012). Studies on chimpanzees and orangutans have shown the apes' sustained attention toward negative emotional expressions compared to positive and neutral expressions (Kano & Tomonaga, 2010a; Pritsch et al., 2017). Although further work is necessary, the likely explanation of the difference between them would be related to the steepness of hierarchy, as attending to negative expressions in rhesus macaques may elicit substantial stress compared to chimpanzees and orangutans.

There have been a number of experimental studies investigating neural and physiological mechanisms underlying emotion processing in nonhuman primates. Similar to the findings in humans, studies in chimpanzees have shown brain lateralization when processing emotional expressions (Parr & Hopkins, 2000) and specific event-related potential (ERP) waveforms elicited by affective pictures (Hirata et al., 2013). Moreover, peripheral temperature changes, such as nasal temperature drop, were also found in nonhuman primates when processing negative emotional expressions (Dezecache et al., 2017; Kano et al., 2016; Nakayama et al., 2005). In nonhuman primates, the neuropeptide hormone oxytocin also seems to modulate the sensitivity to emotional expressions and regulate emotional behaviors (Chang & Platt, 2014; Crockford et al., 2013; Dal Monte et al., 2014; Parr et al., 2013, 2018). Genetic variation of oxytocin and vasopressin receptor genes found in chimpanzees and bonobos further suggests that behavioral and perceptual differences in these species are closely linked to their genetic and physiological differences (Staes et al., 2014). Therefore, it is most parsimonious to assume that there is evolutionary continuity in both emotional behaviors and their processing in humans and nonhuman primates.

Discussion and Future Directions

In this chapter, we aimed to shed light on the socioecological selective pressures that have shaped emotion communication by reviewing the literature on emotional expression and emotion perception in nonhuman primates. Indeed, a handful of studies suggest that the way species produce and use emotional expressions is largely influenced (p. 137) by these pressures. In particular, social complexity and tolerance seem to be positively correlated with the variability and complexity of species' emotion communication (Dobson,

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2009b, 2012; Rebout et al., 2020; Thierry et al., 1989; Preuschoft & van Hooff, 1995). However, throughout the review, we have encountered more limitations than concrete empirical findings to link emotions and species' socioecological characteristics in the nonhuman primate emotion literature. In this section, we discuss the preliminary results from which we draw our conclusions, and further outline the limitations and, most importantly, possible future directions of research.

First, some of the facial expressions of emotions, such as bared-teeth and open-mouth displays, are conserved across primate species in terms of morphological characteristics. However, the frequency, flexibility, and function of expressions vary in relation to species' social characteristics. With the exception of a few studies (Dobson, 2012; Thierry et al., 2000), there is a lack of systematic investigation of emotional expressions across closely related species. Moreover, comparative studies on the contexts in which these are expressed in relation to species sociality are virtually absent. It is of critical importance that this gap is addressed, since the expression of emotions in multiple contexts with various functions will likely reveal species' capacities to use and decode emotional signals, as well as the evolutionary trajectory that shaped species' sociality.

Second, observational studies have shown that nonhuman primates are, in general, able to express and recognize emotions. However, unlike observational studies, experimental studies on emotion perception in nonhuman primates are scarce. In particular, we do not know whether certain species are more sensitive than others to particular modalities, a particular valence or intensity of emotional cues, and whether this can be explained by their specific sociality. Since different methodologies often lead to different results, even in the same species, it has to be noted that experimental stimuli should be prepared and presented under ecologically valid, yet controlled conditions.

Third, studies of emotional expressions and perception in nonhuman primates mostly concern facial expressions. Studies in humans, however, have shown that people can be as good at recognizing bodily expressions of emotion as they are at recognizing facial expressions (De Gelder, 2009; Kret et al., 2013). In this regard, studying the expression and perception of emotions through different modalities with regard to species' sociality and their environment (e.g., dense forest or open savannah) could help construct a comprehensive evolutionary framework of emotion.

Finally, studies on the perception of subtle emotional cues have almost never been explored in nonhuman primates. For example, only one study has tested the perception of pupil size in humans and chimpanzees (Kret et al., 2014). A growing body of research in humans suggests that these subtle emotional cues (e.g., pupil size, blushing, tears during sadness or laughter, signs of sweating or goosebumps) play a significant role in cooperative decision making and social bonding (Behrens & Kret, 2019; Prochazkova et al., 2019, 2021; for a review, see Prochazkova & Kret, 2017). Therefore, studying the expression and perception of these subtle emotional cues would provide a promising avenue for future emotion research.

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(p. 138) Conclusion

In broad terms, species' sociality is tightly interconnected with perception, cognition, communication, and behavior (Dobson, 2009b; Dunbar, 1993; Freeberg et al., 2012; Kano et al., 2018). We therefore presume a link with emotional capacities, too. Here, we suggest that species' social complexity and level of tolerance determine the flexibility and complexity in expressing and perceiving emotions. Specifically, we predict that species living in complex and tolerant social environments have higher flexibility and variability in expressing emotions, as well as higher sensitivity to detect emotional expressions in their group mates. We encourage future studies to test this hypothesis in closely related but socially distinct species, such as chimpanzees and bonobos. Studying their expression and perception of emotional expressions would fill the gap between species' sociality and emotional capacities, and thereby help to construct a full evolutionary picture of emotions.

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