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Facial display replication behaviors in nonhuman primates

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ABSTRACT

Nonhuman primates exhibit advanced facial display replication behaviors, such as yawn contagion and facial mimicry, which play critical roles for social coordination and communication. These behaviors are increasingly understood through the behavioral ecology view as predictive signals that reduce uncertainty in social interactions. Recent studies highlight interspecific variability: while yawn contagion synchronizes group vigilance and strengthens intergroup cohesion in species like geladas (*Theropithecus gelada*), its absence in lowland gorillas (*Gorilla gorilla*) underscores the role of social structure. Rapid facial mimicry, prevalent in play contexts across great apes and New World monkeys, facilitates real-time behavioral alignment, whereas delayed facial mimicry in chimpanzees (*Pan troglodytes*) reflects complex social negotiation. Neurobiological mechanisms implicate the mirror neuron system alongside distributed networks (e.g., posterior cingulate, insula), though debates persist on their innateness versus associative origins. Emerging technologies, such as deep learning, reveal nuanced facial expressions in species like golden snub-nosed monkeys (*Rhinopithecus roxellana*), linking morphological variations to multifunctional communication. This synthesis integrates cross-species comparisons, contextual influences, and theoretical advances to elucidate how facial display replication enhances social cohesion and adaptive strategies, hoping to provide novel insights into the origins of primate social cognition and its implications for understanding human emotional and communicative evolution.

Keywords: Yawn contagion; Facial mimicry; Imitation; Social structure; Nonhuman primates

INTRODUCTION

In humans, facial imitation can constitute a higher-order cognitive process involving sophisticated social cognition through goal decoding and flexible behavioral reconstruction. This capacity manifests in the context-sensitive reproduction of emotional facial displays such as smiling, frowning, and crying, serving both emotional expression and social response functions (Fischer & Hess, 2017; Hess & Blairy, 2001; Paz et al., 2022). While debates persist regarding the extent to which nonhuman primates possess true imitative abilities (Catmur et al., 2007; Heyes, 2010; Tomasello & Call, 1997; Whiten et al., 2004), there is compelling evidence that they engage in facial display replication—a behavior characterized by the automatic mimicry of observed facial expressions. Current investigations into these replication behaviors across nonhuman primate species have established a critical foundation for comparative analyses of facial display functions. This line of research enables systematic comparisons of expression reproduction patterns between humans and other primates, while also facilitating interspecies evaluations within primate taxa.

As research on facial display replication in nonhuman primates gains increasing attention, this review aims to summarize the relevant findings, introduce the main facial displays of interest in the primate field and their diversity across different species, and discuss the influencing factors and social functions of facial display replication. It is anticipated that this review will foster a deeper understanding of the psychological characteristics of nonhuman primate species and their role in social structures, while also providing insights into the origins and development of human cognition, emotional development, and social skills.

FACIAL DISPLAYS IN NONHUMAN PRIMATES

Facial display, expressed through the movement and variation

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of facial muscles, can convey the state of an individual (Baden, 2017; Cordoni et al., 2024; Davila-Ross & Palagi, 2022; Liu et al., 2023; Palagi et al., 2020; Paz et al., 2022). While traditional frameworks often link facial expressions to emotional states, recent research challenges this view by proposing that primate facial displays may primarily function as predictive signals of future behavior rather than mere reflections of internal emotions (Waller et al., 2017). The behavioral ecology view posits that facial expressions serve to reduce uncertainty in social interactions, enabling receivers to anticipate and adapt to likely outcomes, such as conflict resolution or affiliative exchanges (Fridlund, 1994). For example, crested macaques (*Macaca nigra*) modify their behavior based on conspecifics' facial displays, associating specific expressions like the bared-teeth face with peaceful outcomes (Waller et al., 2016). To avoid anthropocentric assumptions about emotional states, standardized methodologies like the Facial Action Coding System (FACS) have been adapted for nonhuman primates (e.g., ChimpFACS, MaqFACS). These systems objectively quantify facial movements based on muscle activation, revealing intentionality in expression production. For instance, orangutans adjust the intensity and complexity of their play faces depending on the audience's attention (Waller et al., 2015), demonstrating cognitive flexibility previously attributed only to gestures or vocalizations.

Facial displays are essential for nonhuman primates in communication, shaping social dynamics by conveying intentions (Davila-Ross & Palagi, 2022; Palagi et al., 2020; Paz et al., 2022). Experimental evidence shows capuchin monkeys use conspecifics' facial expressions to evaluate environmental stimuli (Morimoto & Fujita, 2012), while macaques predict social outcomes (e.g., grooming vs. conflict) based on facial cues (Waller et al., 2016). Such findings highlight the role of facial expressions in reducing ambiguity during interactions, a critical adaptation in socially complex species. By studying these displays, researchers gain insights into primate social structures, communication hierarchies, and evolutionary trajectories (Waller et al., 2017). This predictive framework also bridges proximate mechanisms (e.g., neurobiological correlates in the amygdala) with ultimate functions, such as avoiding costly conflicts or strengthening cooperative bonds. These advances not only refine our understanding of nonhuman primate behavior but also provide evolutionary context for the origins of human facial communication.

The facial displays of nonhuman primates that have received more scholarly attention mainly include yawning and play faces (Cordoni & Palagi, 2013; Palagi & Cordoni, 2012; Scopa & Palagi, 2016; Vick & Paukner, 2010; Waller & Cherry, 2012). Yawning, a behavior documented across all major primate taxa (Baden, 2017; Campbell & Cox, 2019), contrasts with play faces, which are context-specific displays observed in select species. Play faces have been confirmed in prosimians such as ring-tailed lemurs (*Lemur catta*) (Palagi et al., 2020), Japanese macaques (*Macaca fuscata*) (Scopa & Palagi, 2016), New World monkeys like spider monkeys (*Ateles spp.*) (Cordoni et al., 2024), and great apes such as chimpanzees (*Pan troglodytes*) (Palagi & Cordoni, 2012). These findings highlight the taxonomic diversity of play face occurrence (Palagi et al., 2019b). Yawning, as a natural response, often occurs when an individual is tired, sleepy, or just waking up. Its typical characteristics are a wide opening of the mouth and extension of the jaw, which not only helps to bring fresh air to the brain but also stretches and relaxes tired jaw muscles, allowing the body to recover and relax (Palagi et al., 2020). Beyond its physiological role, yawning exhibits morphological variability across species, particularly in the degree of teeth exposure, which may reflect distinct social or communicative functions. For instance, in geladas (*Theropithecus gelada*), "covered" yawns (with minimal teeth exposure) and "uncovered" yawns (with full teeth display) are associated with different social contexts, such as affiliative interactions versus tension reduction (Leone et al., 2014; Palagi et al., 2009). Similarly, Tonkean macaques (*Macaca tonkeana*) display graded yawning patterns, where the visibility of teeth correlates with arousal levels and social hierarchy dynamics (Deputte, 1994). In mangabeys (*Cercocebus spp.*) and drills (*Mandrillus leucophaeus*), yawns involving pronounced canine exposure often serve as threat displays or dominance signals, whereas reduced teeth exposure may accompany relaxed states (Setchell & Jean Wickings, 2005; Thierry et al., 2000). In chimpanzees (*P. troglodytes*), yawning can be divided into full and modified types, with the latter being accompanied by additional movements and a reduced degree of mouth opening compared to the former (Vick & Paukner, 2010). This modified yawn may indicate that chimpanzees have a certain degree of voluntary control over facial movements, further reflecting that yawning behavior may exhibit diverse functions depending on the context. For example, "tense" yawns with partial teeth exposure in chimpanzees are linked to anxiety or social uncertainty, contrasting with "relaxed" full yawns observed during rest (Zannella et al., 2017). Although the variant forms of yawning may vary due to species differences or different contexts, the basic pattern of yawning shows similarities across nonhuman primate species, making it possible to recognize yawning in different primate species (Palagi et al., 2009; Vick & Paukner, 2010; Zannella et al., 2017). The integration of morphological features, such as jaw movement and teeth visibility, underscores the multifunctional nature of yawning, spanning physiological regulation, emotional expression, and social communication.

The occurrence of yawning is not strictly limited by the context in which an individual is located, while play faces are often displayed in specific contexts. Play faces are unique facial expressions presented by individuals during play fighting, characterized by an open mouth display that may show either both upper and lower teeth or only the lower teeth. Captive chimpanzees, for instance, display play faces during rough-and-tumble play and can be further subdivided based on whether the upper teeth are exposed (Palagi et al., 2020, 2019b). This expression appears in various primate species, playing a signaling role in social interactions, indicating that the current behavior is friendly and non-aggressive, which helps maintain harmonious social relationships. Therefore, play faces have significant context specificity, are closely linked to play behavior, and frequently appear during play.

Notably, some open-mouth displays in relaxed contexts may represent distinct expressions from canonical play faces. A study on golden snub-nosed monkeys (*Rhinopithecus roxellana*) documented individuals slightly opening their mouths without exposing their canines during relaxed states, accompanied by relaxed postures of the limbs, head, neck, and shoulders (Zhang et al., 2019). While this relaxed open-mouth display shares some morphological features with play

faces, it occurs in non-play contexts, is a unique open-mouth display of golden snub-nosed monkeys, which is different from the existing typical relaxed open mouth (ROM), and may serve different communicative functions. The relationship between these expressions requires further clarification, as existing literature typically uses "relaxed open mouth" and "play face" interchangeably when describing play-related displays in species such as great apes, macaques, and geladas (Palagi & Cordoni, 2012; Waller & Cherry, 2012). These play-associated expressions appear homologous to human laughter in both function and neural processing (Palagi et al., 2020; Parr & Waller, 2006; Tsao et al., 2008), suggesting their evolutionary importance in maintaining positive social interactions through non-threatening communication.

FACIAL DISPLAY REPLICATION BEHAVIORS IN NONHUMAN PRIMATES

Primates possess a complex facial muscle structure, which allows them to produce a greater variety of expressions. The diversity and complexity of facial expressions also reflect their highly social nature and the need for complex emotional expression (Burrows, 2008; Scheider et al., 2016). In humans, facial imitation involves more than just replicating facial muscles and it also includes the accurate perception, interpretation, and responsive interaction to others' facial expressions. Given the scarce evidence of facial imitation akin to that in humans among nonhuman primates, behaviors such as yawn contagion and facial mimicry may represent objective phenomena of facial display replication, potentially underscoring the advanced emotional and cognitive abilities of nonhuman primates. These abilities are vital for their survival, reproduction, and social cohesion within complex social contexts.

The concept of facial display replication behaviors

Facial display replication behaviors manifest as the observation and replication of other individuals' facial movements, which are predominantly spontaneous and unconscious. In the realm of nonhuman primate research, for instance, yawn contagion and facial mimicry are currently the focal points of academic interest. Yawn contagion pertains to the phenomenon wherein an individual yawns in response to observing or perceiving the yawning behavior of another. Without visual or auditory stimulation from the first individual (the initiator), the second individual (the observer) typically does not yawn. The delay in the yawning response of the observer can range from less than 1 second to between 1 and 5 seconds, or even extend to several minutes. For example, yawn contagion is common in captive chimpanzee groups, with response latencies typically ranging from a few seconds to several minutes. Some studies have observed an average delay of approximately 1.5 minutes (Campbell & Cox, 2019). Similarly, individual differences exist in the latency of yawn contagion among bonobos, with some studies recording an average delay of less than 1 minute, though the overall range may still span from a few seconds to 3–4 minutes (Demuru & Palagi, 2012).

Facial mimicry is further categorized into rapid facial mimicry and delayed facial mimicry (Hess & Fischer, 2013; Palagi et al., 2020). Rapid facial mimicry refers to the quick replication of facial expressions within 1 second after the triggering stimulus, and this imitation is generally considered a spontaneous, unconscious reaction (Hess & Fischer, 2013; Palagi et al., 2020). It is likely that rapid facial mimicry is an automatic response mediated by the mirror neuron system (Palagi et al., 2020), but there is a lack of evidence in nonhuman primates for true imitation that implies novel behavioral replication guided by an understanding of the demonstrator's intent, similar to that in humans (Piaget, 1962). Another type of facial mimicry is delayed facial mimicry, which describes the behavior where an individual does not immediately imitate upon observing another's expression but does so within 1 to 5 seconds after the stimulus presentation (Palagi et al., 2020). Although delayed facial mimicry suggests slightly more deliberate processing, it remains unclear whether it involves comprehension of the emotional intentionality behind the expression. It is worth mentioning that some researchers also categorize behaviors with a response delay of less than 1 second in yawn contagion as rapid facial mimicry and those with a 1- to 5-second response delay as delayed facial mimicry based on the definition of facial mimicry. Both yawn contagion, the involuntary replication of yawning after observing others, and facial mimicry underscore the interplay between neurobiology and social ecology. The subsequent sections will first outline the biological basis of facial display replication and then explore these specific behaviors in detail.

The biological basis of facial display replication behaviors

The neural mechanisms underlying facial display replication involve several key brain regions, each playing a distinct role depending on the specific type of facial behavior being replicated. In the case of yawn contagion, strong associations have been identified with the posterior cingulate and precuneus (Palagi et al., 2020; Platek et al., 2003; Rana et al., 2022). Additionally, the ventromedial prefrontal cortex, superior temporal sulcus, and amygdala are involved in processing the social and emotional information related to yawning (Cooper et al., 2012; Franzen et al., 2018). For facial mimicry, the insula, premotor areas, and inferior frontal gyrus are more closely related (Palagi et al., 2020; Rana et al., 2022). The mirror neuron system has been proposed as a potential biological basis for behavioral imitation phenomena, particularly in primates (Pellegrino et al., 1992). This system was initially discovered in the premotor and parietal cortices of macaque monkeys, where neurons are activated during cognitive tasks, imitation, or repeated observations of the same behavior (Gallese et al., 1996; Rana et al., 2022; Rizzolatti et al., 1996). Research has also explored the sensory modalities that trigger facial mimicry in both humans and nonhuman primates. In humans, both visual and auditory modalities can elicit facial mimicry, such as yawning (De Weck et al., 2022). In nonhuman primates, especially geladas, auditory stimuli have been shown to induce yawn contagion (Pedruzzi et al., 2024).

Studies using indirect measurement methods like neurophysiology and imaging have provided further insights. When humans perform imitation tasks, the premotor cortex, parietal cortex, and higher visual areas are activated (Buccino et al., 2004; Cooper et al., 2008, 2012; Koski et al., 2002; Palagi et al., 2020; Rana et al., 2022). Moreover, when imitating facial expressions, the medial frontal cortices and medial temporal cortices of humans are also activated (Mukamel et al., 2010; Rana et al., 2022). The mirror neuron system is believed to be widely distributed across multiple brain regions, with each region containing only a few neurons

with mirror mechanisms (Haker et al., 2013; Keysers & Gazzola, 2010; Moore et al., 2012; Rana et al., 2022; van der Gaag et al., 2007). This system is not only involved in imitation but also in understanding the actions and intentions of others (Ferrari et al., 2023). However, the mirror neuron system framework has faced criticism. Although it is often invoked to explain imitation, evidence suggests that mirror neuron activity may result from associative learning rather than being an innate adaptation for imitation (Heyes, 2010). Additionally, neuroimaging studies in humans reveal that imitation involves distributed networks beyond the classically defined mirror regions, including prefrontal and hippocampal areas (Catmur et al., 2007). These findings caution against over-reliance on mirror neurons as the sole explanation for primate facial display replication.

YAWN CONTAGION

Yawn contagion in nonhuman primates

The phenomenon of yawn contagion has been widely documented and studied in humans (Chan & Tseng, 2017; Cooper et al., 2012; Franzen et al., 2018; Giganti & Ziello, 2009; Giganti & Zilli, 2011; Norscia & Palagi, 2011; Platek et al., 2003; Provine, 1986, 1989; Senju et al., 2007). Similarly, yawn contagion is prevalent among nonhuman primates. Researchers have observed this phenomenon in various nonhuman primate species, including chimpanzees, bonobos (*Pan paniscus*), Bornean orangutans (*Pongo pygmaeus*), geladas (*T. gelada*), Tonkean macaques (*M. tonkeana*), red-capped mangabeys (*Cercocebus torquatus*), indri lemurs (*Indri indri*), black-and-white ruffed lemurs (*Varecia variegata*), drills (*M. leucophaeus*) (Amici et al., 2014; Anderson et al., 2004; Campbell & Cox, 2019; Campbell & de Waal, 2011; Davila Ross et al., 2008; Demuru & Palagi, 2012; Galotti et al., 2024; Lemes & Amici, 2024; Palagi & Norscia, 2019; Pedruzzi et al., 2022; Tan et al., 2017; Valente et al., 2023; van Berlo et al., 2020).

It is important to note that studying yawn contagion in primates by having them watch yawning videos in a laboratory setting may be influenced by anxiety behaviors, leading to results that differ from the true responses under natural conditions. Therefore, the phenomenon of yawn contagion in primate species needs to be verified by observing their behaviors in both captive natural environments and wild group settings. For example, under experimental conditions, the frequency of yawning in stump-tailed macaques (*Macaca arctoides*) when watching yawning videos is significantly higher than when watching control videos. Nevertheless, these yawning videos also triggered self-directed scratching responses in stump-tailed macaques, which may indicate that the occurrence of yawn contagion is due to the tension caused by watching the videos. Therefore, whether true yawn contagion exists in stump-tailed macaques requires further research under natural and wild conditions to verify (Paukner & Anderson, 2006). Similarly, although early methods of playing yawning videos to ring-tailed lemurs *(L. catta*) and red ruffed lemurs (*Varecia rubra*) did not reveal yawn contagion (Reddy et al., 2016); recent reports show that in captive settings, red ruffed lemurs and black-and-white ruffed lemurs do indeed exhibit yawn contagion under natural conditions (Lemes & Amici, 2024). In certain species, the results of yawn contagion observed under laboratory video playback and in captive natural conditions are consistent. These findings suggest that the occurrence of yawn contagion in primates may vary across laboratory settings, captive conditions, and wild groups due to species differences (Gallo et al., 2021). For instance, a study on adult female chimpanzees watching videos of yawning or non-yawning open-mouth displays found that yawning videos triggered a higher frequency of yawns in chimpanzees, thus confirming the presence of yawn contagion in adult chimpanzees (Anderson et al., 2004). Research on captive chimpanzees further supports the findings of yawn contagion in the laboratory, indicating that yawn contagion naturally occurs in the daily behavior of chimpanzees (Campbell & Cox, 2019).

However, not all nonhuman primate species exhibit yawn contagion behavior. For example, yawn contagion has not been observed in lowland gorillas (*Gorilla gorilla*) (Amici et al., 2014). Whether in natural settings or in response to yawning stimuli presented in laboratory videos, yawning behavior of gorillas does not increase due to observing yawns of other individuals (Palagi et al., 2019a). Similarly, contagious yawning has not been found in Japanese macaques (*M. fuscata*) (Palagi & Norscia, 2019), which may be related to their low tolerance in social relationships and characteristics of social interaction (Palagi et al., 2020).

Factors influencing yawn contagion

In the phenomenon of yawn contagion, an individual's response is not just influenced by their own tendency to spontaneously yawn, but also by the triggering yawner's features. This has been confirmed in studies on bonobos (Demuru & Palagi, 2012). In wild primate groups, the occurrence of yawn contagion is also not affected by the specific form of yawning (such as variant forms), duration, distance, or whether a sound is produced (Gallo et al., 2021; Pedruzzi et al., 2025). However, when primates watch videos of conspecifics yawning, the yawn contagion phenomenon suggests that it has selectivity based on species category and kinship. For example, a study on red-capped mangabeys found that individuals have a stronger reaction to the yawns of familiar individuals, indicating that kinship and familiarity between species are important factors influencing yawn contagion (Pedruzzi et al., 2022). Observational studies on chimpanzees also support this view (Amici et al., 2014). In primate groups, the level of familiarity between individuals is indeed a key factor affecting yawn contagion. Bonobos exhibit a higher frequency of yawn contagion in their close social relationships, particularly when the yawn is initiated by a female (Demuru & Palagi, 2012). Furthermore, chimpanzees yawn more frequently when watching videos of familiar individuals yawning than when watching unfamiliar individuals or familiar individuals resting, while there is no significant difference in yawning frequency between yawning videos of unfamiliar individuals and resting videos. This further indicates that the response of chimpanzees to yawn contagion is influenced by the level of familiarity between individuals (Campbell & de Waal, 2011). In geladas, studies have shown that yawn contagion is more pronounced among individuals with high levels of closeness (Palagi et al., 2009). Nevertheless, a recent investigation into these primates found no association between the strength of social bonds, as gauged by grooming behavior, and yawn contagion (Pedruzzi et al., 2025). Similarly, in another study on chimpanzees, it was found that susceptibility to contagious yawning increases with age but remains unaffected by emotional closeness to the

yawning model (Madsen et al., 2013), indicating that other factors may contribute to this phenomenon. Figure 1 and Table 1 present an overview of yawn contagion in representative nonhuman primates mentioned above, describing the occurrence of yawn contagion, response delays, and key influencing factors across different species.

Yawn contagion enhances social cohesion

The occurrence of yawn contagion is closely related to the familiarity between individuals, species category, and kinship. While some researchers have hypothesized that yawn contagion in primates might potentially facilitate the transmission of prosocial behaviors and contribute to social group cohesion, current evidence remains inconclusive. For instance, experimental observations show that bonobos exhibit yawn contagion even when exposed to videos of yawning by unfamiliar conspecifics. This phenomenon has been interpreted as potentially conveying unconscious prosocial signals that could theoretically assist in forming connections with new group members. Such interpretations have led to speculation that this mechanism might have played a role in bonobos' evolutionary development of social grouping strategies, possibly as an adaptive response to external threats. Therefore, prosocial behaviors in human societies may have some convergent evolution with those of bonobos (Tan et al., 2017). Additionally, yawn contagion can stabilize social groups by regulating social connections. For instance, the high degree of synchronization and coordination in indri lemurs, as well as communication within and between groups, may be related to their yawn contagion phenomenon (Valente et al., 2023). In primate groups with weaker social connections, yawn contagion almost never occurs. This phenomenon supports the social relationship hypothesis, which posits that some primate species invest less in establishing long-term social relationships, aligning with the finding that they rarely exhibit yawn contagion. In contrast,

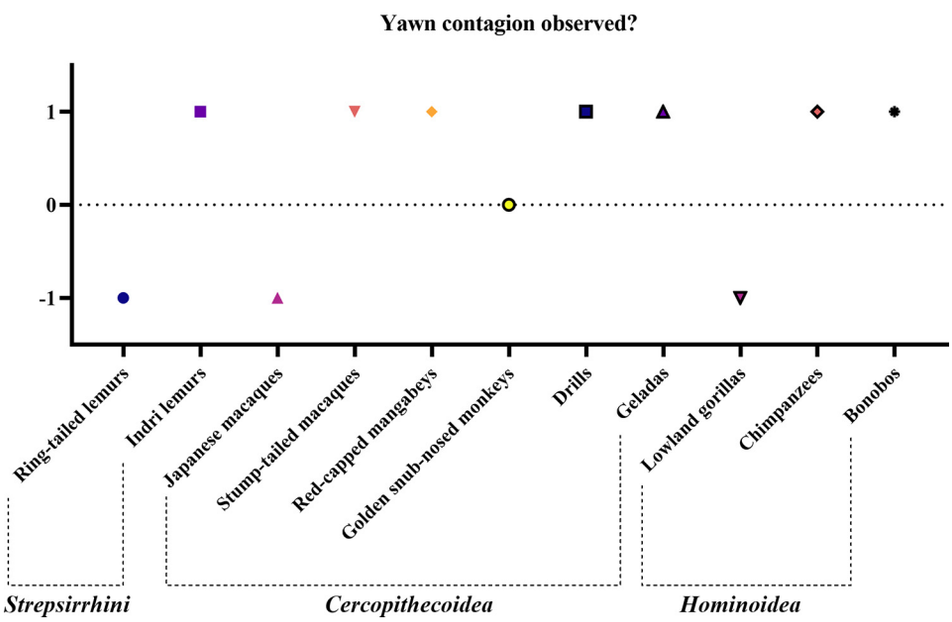

Figure 1 Yawn contagion in several representative nonhuman primates

The y-axis of the graph is labeled to indicate the status of yawn contagion in various nonhuman primates: a value of "1" signifies that yawn contagion has been observed in the species; a value of "-1" indicates that yawn contagion has not yet been observed in the reported species; and a value of "0" denotes that yawn contagion has not yet been studied in this species. Note: The figure illustrates yawn contagion in selected primate species. Future research may include a broader range of species to better represent the diversity of yawn contagion.

Table 1 Yawn contagion in representative nonhuman primates

Species	Yawn contagion observed?	Contextual dependency	Social modulation	Key studies
Chimpanzees (*Pan troglodytes*)	Yes	Bonding, stress	Kin/familiarity bias	Anderson et al., 2004; Campbell & Cox, 2019; Madsen et al., 2013
Bonobos (*Pan paniscus*)	Yes	Affiliative interactions	Female-initiated yawns are more contagious	Demuru & Palagi, 2012; Tan et al., 2017
Lowland gorillas (*Gorilla gorilla*)	No	N/A	N/A	Amici et al., 2014; Palagi et al., 2019a
Geladas (*Theropithecus gelada*)	Yes	Intergroup coordination	Social bond strength	Gallo et al., 2021; Palagi et al., 2009
Japanese macaques (*Macaca fuscata*)	No	N/A	N/A	Palagi & Norscia, 2019
Stump-tailed macaques (*Macaca arctoides*)	Yes	Captivity vs. wild disparities	N/A	Paukner & Anderson, 2006
Red-capped mangabeys (*Cercocebus torquatus*)	Yes	Affiliative grooming	Familiarity-driven	Pedruzzi et al., 2022
Indri lemurs (*Indri indri*)	Yes	Group coordination	Vocalization-linked	Valente et al., 2023
Drills (*Mandrillus leucophaeus*)	Yes	N/A	N/A	Galotti et al., 2024
Golden snub-nosed monkeys (*Rhinopithecus roxellana*)	Not studied (typical yawns)	Relaxed open-mouth displays	N/A	Zhang et al., 2019
Ring-tailed lemurs (*Lemur catta*)	No	N/A	N/A	Reddy et al., 2016

lowland gorillas, which have weaker social connections compared to other species with strong social bonds, do not show yawn contagion in studies (Palagi et al., 2019a). However, a study on wild gelada groups with multilevel social structures found that yawn contagion was more frequent between groups than within groups. This result supports the view that yawn contagion between groups helps coordinate activities among gelada groups, increasing their tolerance and spatial cohesion. In coordinating activities between groups, male geladas are more likely to respond to the yawns of other individuals (Gallo et al., 2021). While the prior study on wild geladas with multilevel social structures found that yawn contagion was more frequent between groups than within groups (Gallo et al., 2021), the other study reveals that in a zoo environment, female geladas show stronger yawn contagion and modality matching with other females (Pedruzzi et al., 2025). This discrepancy might stem from differences in social dynamics between wild and captive settings. Future research needs to delve deeper into the factors causing these differences in yawning patterns and social responses among geladas in various environments.

Yawn contagion promotes emotional expression and communication

The phenomenon of yawn contagion in nonhuman primates may reveal their emotional connections, particularly involving complex empathetic abilities, which may be the evolutionary basis of human empathy (Amici et al., 2014). In geladas, female individuals exhibit heightened sensitivity and emotional coordination with their companions, as evidenced by their precise matching of distinct yawning types (covered teeth, uncovered teeth) and stronger contagion effects among socially affiliated pairs (Palagi et al., 2009). This phenomenon aligns with human empathy theories proposing that emotional contagion relies on shared representations and mirroring mechanisms (Preston & de Waal, 2002; Rizzolatti et al., 2001). In red-capped mangabeys, yawn contagion has been observed to correlate with social bonding behaviors, potentially facilitating group cohesion through behavioral synchrony. While this phenomenon may reflect underlying social sensitivity, its interpretation as an empathic response requires further investigation (Pedruzzi et al., 2022). The observed similarities in yawn contagion patterns between chimpanzees and humans may reflect shared mechanisms underlying social communication across species. While young chimpanzees show reduced susceptibility to yawn contagion - mirroring developmental patterns seen in humans, this phenomenon should be interpreted cautiously regarding cognitive implications (Campbell & de Waal, 2011). Evidence from mirror self-recognition studies suggests certain cognitive capacities in chimpanzees that may relate to basic forms of social awareness (Anderson et al., 2004). The contagious yawning phenomenon has been proposed as a potential mechanism for emotional synchronization in group-living species, highlighting potential parallels in the evolutionary development of social communication systems. In bonobos, the social context of yawn contagion shows demographic patterns resembling human social dynamics, particularly regarding female-initiated events correlating with their central social role. While some researchers have drawn tentative connections between yawn contagion and empathic processes in both bonobos and humans (Demuru & Palagi, 2012). These observations primarily demonstrate behavioral convergences rather than confirming equivalent psychological states.

Furthermore, during the occurrence of yawn contagion, primate individuals exhibit behavioral variations in yawning morphology and context-specific social correlates. Studies on geladas have documented distinct yawn types categorized by mouth opening degree (e.g., Y1, Y2, Y3) and the presence of vocalizations, with these differences potentially reflecting context-specific signaling rather than direct emotional states (Leone et al., 2014; Pedruzzi et al., 2025). For instance, high-intensity yawns (e.g., Y3, with exposed gums) are more frequently performed by male geladas in tense social interactions, often accompanied by self-directed behaviors like scratching, which may signal arousal or social tension. Conversely, low-intensity yawns (e.g., Y1, with covered teeth) are predominantly observed in affiliative contexts among females and are sometimes paired with lip smacking, a gesture linked to social cohesion (Leone et al., 2014). While the adaptive significance of these morphological differences remains under investigation, recent work highlights their role in modulating yawn contagion dynamics across sensory modalities (Pedruzzi et al., 2025). This behavioral complexity contrasts with facial mimicry, which often occurs in contexts requiring rapid behavioral coordination, such as play. The following section examines the nuances of facial mimicry and its role in strengthening social bonds.

FACIAL MIMICRY

Rapid facial mimicry

Facial mimicry refers to the involuntary, spontaneous replication of another individual's facial expressions (Hess & Fischer, 2013; Palagi et al., 2020). Specifically, rapid facial mimicry occurs within the first second following exposure to a facial stimulus, representing an instinctive response linked to nonconscious processing mechanisms (Hess & Fischer, 2013; Palagi et al., 2020). Rapid facial mimicry is not unique to humans; this phenomenon has also been observed in some great ape species, such as chimpanzees and gorillas (Davila Ross et al., 2008; Davila-Ross & Palagi, 2022; Dimberg & Thunberg, 1998; Palagi et al., 2019b). As research has progressed, rapid facial mimicry has been found in some Old World monkey species, such as geladas (Mancini et al., 2013), rhesus macaques (Facondini et al., 2024) and Tonkean macaques (Scopa & Palagi, 2016), challenging the traditional view that rapid facial mimicry is limited to humans and great apes. Recently, rapid facial mimicry has been confirmed for the first time in New World monkeys (such as brown-headed spider monkeys, brown spider monkeys, and red-faced spider monkeys) (Cordoni et al., 2024), further indicating that rapid facial mimicry has evolutionary homology between humans and other primates (Mancini et al., 2013). However, rapid facial mimicry has not been observed in some species, such as Japanese macaques (Scopa & Palagi, 2016), and the reasons for this still require further investigation. Several nonhuman primate species that have been investigated on rapid facial mimicry are summarized (Figure 2).

Bornean orangutans can rapidly imitate open-mouth behavior of their playmates, usually completing the process within 1 s, providing strong evidence for the existence of rapid facial mimicry in nonhuman primates. Notably, the rapid facial mimicry behavior of Bornean orangutans shows different characteristics in two categories: different age groups and

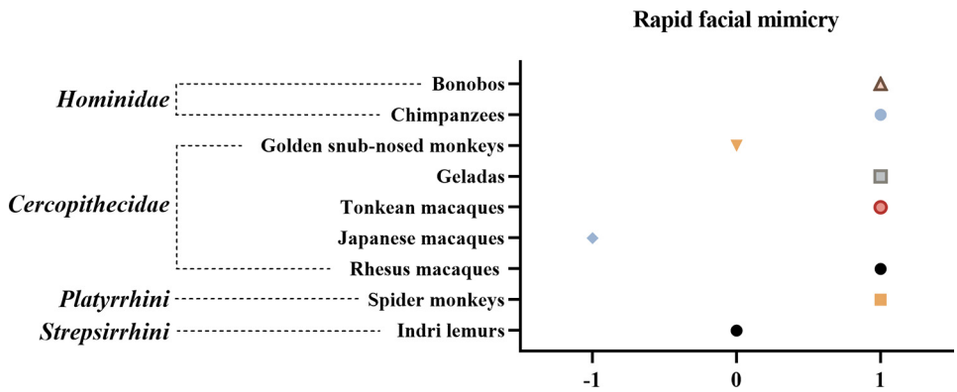

Figure 2 Rapid facial mimicry in several representative nonhuman primates

The x-axis of the graph is labeled to indicate the status of rapid facial mimicry (RFM) in various nonhuman primates: a value of "1" signifies that RFM has been observed in the species; a value of "-1" indicates that RFM has not yet been observed in the reported species; and a value of "0" denotes that RFM has not yet been studied in this species. Note: The figure focuses on selected primate species. Future research may encompass a broader range of species to better capture the diversity of RFM.

playmates with age differences of more than 2 years. Specifically, adolescent or adult Bornean orangutans exhibit more frequent rapid facial mimicry between playmates with age differences of more than 2 years, while infant Bornean orangutans tend to engage in rapid facial mimicry with playmates with age differences of less than 2 years (Davila Ross et al., 2008). Studies on chimpanzees and gorillas have found that individuals display rapid facial mimicry during rough-and-tumble play. Their play faces can be further divided into play faces and full play faces based on whether the upper teeth are exposed. A play face is characterized by an open mouth showing only the lower teeth, while a full play face refers to an open mouth showing both the upper and lower teeth, which is more intense than a play face. Notably, gorillas prefer to use full play faces, and the duration of this expression is longer than that of play faces. In contrast, there is no significant difference in the duration of full play faces and play faces in chimpanzees (Palagi et al., 2019b). Geladas also exhibit rapid facial mimicry during play. This behavior is not only present in adults but also in juveniles, especially during mother-offspring play, where the frequency of rapid facial mimicry is the highest and the response speed is the fastest. Geladas mimic play faces and full play faces when they observe these expressions in their companions, but they do not show a significant rapid facial mimicry response to lip smacked expressions. This may be because lip smacked has other meanings in different contexts (Mancini et al., 2013).

Delayed facial mimicry

Delayed facial mimicry, compared to rapid facial mimicry, occurs with a longer time delay, typically between 1 to 5 s. This type of delayed facial mimicry may be less spontaneous than rapid facial mimicry (Davila-Ross et al., 2011), and there are relatively fewer reports of delayed facial mimicry in nonhuman primate species. To date, delayed facial mimicry behavior has been observed in chimpanzees, while it has not been observed in lowland gorillas (Palagi et al., 2019b). Therefore, some researchers propose that delayed facial mimicry may represent an emotional expression behavior in the later stages of individual interactions, which to some extent reflects the complexity and dynamics of social interactions (Mancini et al., 2013; Palagi et al., 2019b; Schmidt & Cohn, 2001). These studies enhance our grasp of the diversity in primate facial expression mimicry within the academic sphere and offer a comparative perspective to better comprehend the evolutionary roots of human facial mimicry.

Factors influencing facial mimicry

Unlike the factors influencing yawn contagion, the occurrence of facial mimicry is limited to play contexts, where the play process provides an important social context for its occurrence. Additionally, individual age is an important factor affecting the emergence of rapid facial mimicry. When individuals are of similar age, play tends to be more competitive due to similar physical size and abilities, thus requiring more rapid facial mimicry as an effective communication strategy (Cordoni et al., 2024; Davila-Ross et al., 2011; Facondini et al., 2024; Pellis & Iwaniuk, 2000). Typically, the frequency of rapid facial mimicry is relatively high among younger primate individuals within a group. Moreover, individual rank is also closely related to the occurrence of facial mimicry. When the individual initiating the facial display is of a higher rank than the responding individual, the likelihood of rapid facial mimicry occurring is greater. For example, in the facial mimicry process of subadult rhesus macaques (*Macaca mulatta*), the individual initiating the facial mimicry often has a higher rank than the responding individual (Facondini et al., 2024). It is noteworthy that no significant influence of individual gender, age, species, and kinship on the occurrence of rapid facial mimicry has been observed to date. Studies on gorillas, chimpanzees, and spider monkeys further confirm that the emergence of rapid facial mimicry is closely related to prolonged playful interactions, a finding that helps to deepen the understanding of the motives and mechanisms behind facial mimicry (Cordoni et al., 2024; Palagi et al., 2019b).

Facial mimicry strengthens social cohesion

As a social behavior, facial mimicry facilitates emotional sharing and behavioral synchrony in primate groups, which may enhance social cohesion through interpersonal attunement mechanisms (Ferrari et al., 2009). While this phenomenon contributes to cooperative interactions through reciprocal alignment processes, its potential fitness benefits remain indirect and context-dependent (Li et al., 2022). Current evidence suggests social coordination mechanisms might ultimately influence adaptive outcomes through improved group stability (Burgoon et al., 2017). Moreover, facial mimicry serves as a mode of transmitting social signals

that support group harmony and stability in primate societies. Comparative studies demonstrate how chimpanzees and gorillas adjust their use of facial mimicry in response to varying social demands, thereby promoting emotional convergence and coordinated behaviors across different interaction types (Palagi et al., 2019b; van Baaren et al., 2004). When performing delayed facial mimicry, chimpanzees aim to demonstrate their play intentions again in the later stages of interaction, prolong positive social contact, and further promote the enhancement of social cohesion (Palagi et al., 2019b). A comparison between rapid and delayed facial mimicry is presented in Table 2. Considering that chimpanzees have higher social cohesion than gorillas, another interpretation of delayed facial mimicry may be a response to the audience effect triggered by reactions, meaning that chimpanzee individuals may observe or expect reactions from other individuals in the group and adjust their behavioral strategies accordingly (Cordoni et al., 2018). Based on recent comparative studies, the emergence of rapid facial mimicry in primates appears closely tied to social dynamics rather than individual personality traits. In tolerant species like Tonkean macaques, the presence of rapid facial mimicry may be facilitated by their socially flexible societies where frequent ambiguous interactions necessitate enhanced communicative coordination (Scopa & Palagi, 2016). Notably, this phenomenon extends beyond tolerant species–recent findings in despotic rhesus macaques demonstrate that rapid facial mimicry frequently occurs during hierarchical interactions, particularly when subordinates interact with dominant group members (Facondini et al., 2024). This suggests facial mimicry serves adaptive functions across social systems, potentially functioning as a predictive mechanism to reduce uncertainty during risky interactions (Diana & Kret, 2025). The persistence of this behavior in despotic species aligns with the hypothesis that mimicry enhances behavioral coordination by minimizing prediction errors in social exchanges, regardless of a species' social tolerance level (Diana & Kret, 2025; Facondini et al., 2024). These findings collectively indicate that facial mimicry constitutes a fundamental adaptive mechanism in primate social cognition rather than being personality-dependent. Rapid facial mimicry not only improves communication efficiency but may also help build stronger social bonds. Spider monkeys, through face-to-face interactions and rapid facial mimicry, may develop closer social connections between individuals, which is crucial for the establishment and maintenance of social relationships (Cordoni et al., 2024). Unlike the species-typical relaxed open mouth (ROM) expression commonly observed in playful interactions among most primate species, the specialized ROM display of golden snub-nosed monkeys (*Rhinopithecus roxellana*) exhibits distinctive morphological characteristics and serves diverse social functions. This unique facial display operates as a multimodal communication system, serving not only as a submissive signal during socially tense encounters but also facilitating post-conflict reconciliation and reinforcing affiliative bonds through habitual affiliative interactions. The functional versatility of this display mechanism extends beyond momentary communication, playing an integrative role in hierarchical negotiation and social cohesion maintenance (Zhang et al., 2019).

However, a study in lowland gorillas challenges the widely accepted positive association between rapid facial mimicry (RFM) and social cohesion, originally proposed in primate studies (Palagi et al., 2019b; van Baaren et al., 2004). Contrary to observations in chimpanzees and bonobos, where RFM frequency increases with social bond strength, gorillas with stronger social ties displayed less RFM during play interactions than those with weaker bonds (Bresciani et al., 2022; Palagi et al., 2019b). This reversal may relate to species-specific behavioral ecology: lowland gorillas exhibit infrequent social bonding behaviors (e.g., grooming) compared to other great apes (Bresciani et al., 2022). Therefore, facial mimicry in primates plays an indispensable role in stabilizing community structures and is a vital bond in maintaining harmony and stability within social groups. At the same time, the function of facial mimicry within primate social groups is diverse and complex, requiring in-depth exploration based on different species and social contexts.

Facial mimicry as a key element of emotional communication

In primate social interactions, facial mimicry facilitates emotional expression and coordination during play. Studies demonstrate its role in reducing behavioral ambiguity while enabling individuals to evaluate physical and cognitive capabilities within safe contexts. For instance, Bornean orangutans exhibit facial mimicry patterns resembling human interactions with familiar partners, underscoring its cross-species significance in emotional communication (Davila Ross et al., 2008). Among lowland gorillas, rapid facial mimicry coordinates play interactions among same-sex peers, fostering behavioral alignment (Bresciani et al., 2022). This phenomenon transcends great apes; geladas demonstrate intensified rapid facial mimicry in mother-offspring dyads, underscoring its role in bonding (Mancini et al., 2013). In hierarchical macaque groups, such mechanisms extend play duration and reduce risks by enhancing communication efficiency (Facondini et al., 2024). Similarly, Tonkean macaques employ rapid facial mimicry to bolster emotional synchrony and cooperation during playful interactions (Scopa & Palagi, 2016). These findings collectively suggest rapid

Table 2 Contrasting rapid vs. delayed facial mimicry

Dimension	Rapid facial mimicry	Delayed facial mimicry
Time window	≤1 second	1–5 seconds
Behavioral trigger	Conspecific's play face during play interactions	Complex social negotiation in later stages of interaction
Core function	Real-time behavioral alignment; Reducing play ambiguity	Complex social negotiation; Behavioral strategy adjustment
Modulatory factors	Play intensity; Age; Social rank	N/A
Species-specificity	Present in: Spider monkeys, Chimpanzees Absent in: Despotic Japanese macaques	Confirmed in: Chimpanzees
Controversies	Emerges through associative learning; Not strictly empathy-related	Possible response inhibition
Key references	Cordoni et al., 2024; Davila Ross et al., 2008; Heyes, 2010; Mancini et al., 2013; Massen & Gallup, 2017; Scopa & Palagi, 2016	Davila-Ross et al., 2011; Diana & Kret, 2025; Palagi et al., 2019b; Tan et al., 2017

facial mimicry supports adaptive social strategies, allowing individuals to gauge partners' abilities and navigate group dynamics, which may indirectly influence competitive outcomes during play (Cordoni et al., 2024).

SOCIAL FUNCTIONS OF FACIAL DISPLAY REPLICATION BEHAVIORS

Yawn contagion and facial mimicry represent distinct pathways for social coordination in primates. Comparative analyses across species reveal fundamental mechanistic differences between these phenomena (Table 3). Yawn contagion primarily facilitates behavioral synchronization, particularly among unfamiliar individuals, through physiological state alignment rather than direct emotional exchange (Massen & Gallup, 2017). This form of coordination creates baseline social cohesion that may enable subsequent empathetic processes. Conversely, facial mimicry operates through real-time affective matching, serving as a mechanism for emotional state attunement during direct interactions (Scopa & Palagi, 2016). Recent theoretical advances caution against equating facial movements with specific emotional experiences, emphasizing the need for multimodal verification of emotional states (Diana & Kret, 2025). The two phenomena also diverge in communicative specificity: yawn contagion functions as a broad social regulator, while facial mimicry enables precise emotional coordination. Crucially, facial mimicry's capacity to promote mutual understanding depends on contextual integration of expressive signals with other social cues.

The occurrence of yawn contagion does not strictly depend on specific contexts, while facial mimicry usually occurs in playful interactions (Palagi et al., 2020). The triggering mechanism of yawn contagion may be more complex, involving the coordinated action of multiple brain regions,

Table 3 Facial display replication behaviors across representative primate species

Species	Yawn contagion (YC)	Rapid facial mimicry (RFM)	Social structure	Key influencing factors	Contradictory evidence	Behavioral ecology interpretation	Key references
Chimpanzees (*Pan troglodytes*)	Yes	Yes	Fission-fusion	Familiarity bias, play context modulation	Age-dependent susceptibility unrelated to emotional closeness	YC serves intergroup coordination, RFM maintains play reciprocity in fluid social systems	Anderson et al., 2004; Campbell & de Waal, 2011; Madsen et al., 2013; Palagi et al., 2020
Bonobos (*Pan paniscus*)	Yes	Yes	Matriarchal society	Female dominance in YC initiation, prosocial signaling	YC occurs with unfamiliar conspecifics (contradicting kinship hypotheses)	RFM frequencies are lower in tolerant societies and may reflect functional differentiation	Demuru & Palagi, 2012; Tan et al., 2017
Lowland gorillas (*Gorilla gorilla*)	Not yet observed	Limited (rare in play)	Solitary units/ loose groups	Weak social bonds, low interaction rates	Stronger social pairs show less RFM during play	Absence of YC aligns with solitary/less cohesive ecology	Bresciani et al., 2022; Palagi et al., 2019a; Palagi et al., 2019b
Japanese macaques (*Macaca fuscata*)	Not yet observed	Not yet observed	Female dominance	Competitive dynamics, low social tolerance	N/A	Strict dominance hierarchies inhibit risky emotional alignment through facial displays	Palagi & Norscia, 2019; Paukner & Anderson, 2006
Geladas (*Theropithecus gelada*)	Yes	Yes	Multilevel societies	Male-mediated intergroup YC, vocal-yawn coupling	No association between grooming (social bond) and YC in captivity	YC acts as intergroup "behavioral synchronizer" for coordinated movement; RFM strengthens mother-offspring and affiliative bonds in unstable herds	Leone et al., 2014; Pedruzzi et al., 2025
Spider monkeys (*Ateles* spp.)	Yes	Yes	Fission-fusion	Play-driven RFM, age/size-matched play partners	RFM absent in non-play contexts despite social tolerance	Facial alignment replaces physical contact to maintain bonds in arboreal locomotion constraints	Cordoni et al., 2024
Tonkean macaques (*Macaca tonkeana*)	Yes	Yes	Multi-male, multi-female groups	Social tolerance, play coordination	YC latency varies widely depending on audience size	Social tolerance allows risky facial alignment as a hierarchy negotiation tool; RFM reduces play ambiguity in flexible societies	Palagi & Norscia, 2019; Scopa & Palagi, 2016
Golden snub-nosed monkeys (*Rhinopithecus roxellana*)	Not studied	Not studied	Multilevel societies	Context-specific non-imitative expressions distinct from typical ROM	Phylogenetic debate on whether their "unique ROM" display is homologous to play faces	Unique ROM display serves dual function: submission signal & kinship reassurance	Zhang et al., 2019
Rhesus macaques (*Macaca mulatta*)	Yes	Yes	Social hierarchy	Dominant-subordinate RFM asymmetry	YC correlates with self-directed scratching	RFM facilitates submissive signaling and reduces conflict risk in rigid hierarchies	Facondini et al., 2024
Indri lemurs (*Indri indri*)	Yes	Not studied	Pair-bonded/ territorial	Vocal-Yawn coordination	Small wild sample sizes limit generalizability	YC synchronizes duetting pairs in dense forests - acoustic-visual integration	Valente et al., 2023

while facial mimicry more relies on the accurate perception, understanding, and response to facial expressions (Palagi et al., 2020; Rana et al., 2022). Although both can enhance community cohesion and promote emotional communication, yawn contagion may focus more on the establishment of new relationships and the harmony and stability within the community. Facial mimicry, on the other hand, focuses more on strengthening emotional resonance and empathy within existing relationships, as well as coordinating play behaviors and social interactions between individuals through imitation. Yawn contagion may reflect a more relaxed state, while facial mimicry can express a richer range of emotional content, including happiness, surprise, sadness, etc. (Rana et al., 2022).

In addition to the aforementioned functions, facial display replication may have other functions and play different roles at different stages of individual development (Anderson & Kinnally, 2021; Bard, 2007). For newborn macaques, facial display replication aids in the development of social cognition by establishing close connections with caregivers (such as the mother or other female individuals), imitating their expressions, learning adult characteristics, and establishing associations to attract the attention of adult females, thus obtaining more care and interaction opportunities (Anderson et al., 2004; Ferrari et al., 2006). The evolutionary conservation of facial display replication emphasizes its central role in individual learning and communication among primates (Rana et al., 2022). This may be an adaptive behavior that has evolved through natural selection, allowing newborns to observe and imitate the expressions of adults, promoting the development of imitative learning abilities, learning the transmission of emotions and the understanding of emotions, thus surviving and reproducing in the environment (Bard, 2007; Davila Ross et al., 2008; Dettmer et al., 2016; Myowa-Yamakoshi et al., 2004; Palagi et al., 2020). In summary, facial display replication behaviors show different forms and its various social functions (Table 4). The similarities and unique characteristics in yawn contagion and facial mimicry, which are particularly prominent in primates, provide insights into the complex mechanisms of emotional communication and social structures of primates, and also inspire the understanding of the origins and evolution of human social behavior.

OUTLOOK

The application of new technologies, such as artificial intelligence, in primate behavioral ecology has begun to transform our understanding of facial display replication in nonhuman primates. For instance, deep learning models are being employed to detect subtle facial expressions in golden snub-nosed monkeys, which may be closely linked to their complex social behaviors (Fang et al., 2024). This technological advancement promises to deepen our comprehension of the role of facial display replication in emotional communication, empathy, and social cohesion among primates. The academic community's interest in these functions is likely to grow, prompting further research. Facial display replication is crucial for early learning and social relationship formation in nonhuman primates. It is a common phenomenon in great apes and is increasingly observed in Old World and New World monkeys. These findings enhance our understanding of facial display replication in nonhuman primates and provide new perspectives for studying cognitive abilities, social learning, and individual relationships within primate social groups. Despite the established importance of the mirror neuron system in imitative behavior, its neurobiological mechanisms warrant further investigation. Future research integrating neurobiology, physiology, cell and molecular biology, neuroimaging, genetics, and artificial intelligence could elucidate the mechanisms of facial display replication and its variations across primate species. Furthermore, cross-species studies are vital for understanding the universality and uniqueness of facial display replication in primates. By examining the similarities and differences in facial display replication among individuals in different primate social groups and contexts, we can better understand the impact of these behaviors on community dynamics and individual relationships, uncover the evolutionary history of facial display replication, and gain insights into the origins and evolution of human emotional and cognitive development and social structures.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

Q.W.W., G.F. and B.G.L. wrote and edited the manuscript. Q.W.W., W.J.X.,

Table 4 Comparative social functions of facial display replication

Feature	Yawn contagion	Facial mimicry
Primary context	General contexts Intergroup coordination in geladas	Play-specific (e.g., RFM) Hierarchy negotiation in macaques
Social function	May convey unconscious prosocial signals that help form bonds with new group members Communication within and between groups Controversy: Absence in gorillas contradicts social complexity predictions	Reinforces existing hierarchies Facilitates risky play escalation Controversy: Despotic species show RFM without enhanced cohesion
Emotional focus	Physiological synchrony	Play intentions Social prediction and affiliation
Neurobiological basis	Posterior cingulate, precuneus	Insula, premotor cortex, mirror neurons
Species-specific patterns	Chimpanzees: Kin bias Geladas: Male-mediated intergroup YC	Orangutans: Age-graded reciprocity Macaques: Despotic macaques use RFM in hierarchical interactions
Contradictory evidence	No empathy-YC link in controlled experiments	Some despotic species show RFM without cohesion
Key references	Anderson et al., 2004; Bresciani et al., 2022; Cooper et al., 2012; Campbell & de Waal, 2011; Gallo et al., 2021; Massen & Gallup, 2017; Palagi et al., 2009, 2019a; Pedruzzi et al., 2024, 2025; Tan et al., 2017; Valente et al., 2023	Bresciani et al., 2022; Cordoni et al., 2024; Davila Ross et al., 2008; Diana & Kret, 2025; Facondini et al., 2024; Lemes & Amici, 2024; Palagi et al., 2020

Y.N.T., G.F. and B.G.L. contributed to the discussion of the study and presented suggestions for manuscript revision. All authors read and approved the final version of the manuscript.

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