



Rapid facial mimicry in Platyrrhini: Play face replication in spider monkeys (*Ateles fusciceps*, *Ateles hybridus*, and *Ateles paniscus*)

Giada Cordoni¹  | Annalisa Ciantia¹ | Jean-Pascal Guéry² | Baptiste Mulo³ | Ivan Norscia¹ 

¹Department of Life Sciences and Systems Biology, University of Torino, Turin, Italy

²La Vallée des Singes, Romagne, France

³ZooParc de Beauval & Beauval Nature, Saint Aignan sur Cher, France

Correspondence

Giada Cordoni and Ivan Norscia, Department of Life Sciences and Systems Biology, University of Torino, Via Accademia Albertina 13, 10123 Turin, Italy.

Email: giada.cordoni@unito.it and ivan.norscia@unito.it

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Abstract

Rapid facial mimicry (RFM), the rapid and automatic replication of facial expression perceived, is considered a basic form of empathy and was investigated mainly during play. RFM occurs in Catarrhini (Old World primates), but it is not still demonstrated in Platyrrhini (New World primates). For this reason, we collected video data on playful interactions ($N_{\text{play_interactions}} = 149$) in three species of spider monkeys (*Ateles fusciceps*— $N = 11$, *Ateles hybridus*— $N = 14$, and *Ateles paniscus*— $N = 6$) housed at La Vallée des Singes and the ZooParc de Beauval (France). For the first time, we demonstrated the occurrence of RFM in Platyrrhini (analyzing 175 events). Players' sex, age, species, relationship quality, and kinship did not modulate RFM probably due to the species' complex fission–fusion dynamics and flexible interindividual social relationships. Compared to the absence of any playful expressions or the presence of only not replicated play face, RFM prolonged the session duration and was sequentially associated with more types of more intense offensive playful patterns (patterns aimed at attacking/pursuing the playmate). We proposed that RFM may favor synchronization and context sharing between players, thus decreasing the risk of behavior misinterpretation while simultaneously fostering a more competitive nature of play. In conclusion, this study stimulates additional research on the evolutionary origins of motor mimicry in primates, possibly dating back to before the divergence of New and Old World monkeys. Furthermore, it also points toward the possibility that RFM may not always lead to cooperation but also to competition, depending on the context and species' social and cognitive features.

KEYWORDS

competition, emotional contagion, Platyrrhini, play face, synchronization

1 | INTRODUCTION

Play behavior—by recruiting and differently recombining motor patterns from various contexts (e.g., aggressive and sexual)—constitutes a distinct and independent behavioral system (Burghardt, 2011; Pellis et al., 2019). While a certain level of cooperation is necessary for play to continue (Kraus et al., 2019), competition can also arise among players based on factors such as sex, age, species, and dominance relationship (Bauer & Smuts, 2007; Cordoni et al., 2021, 2023; Palagi et al., 2016).

According to the Polyvagal Theory, play behavior serves as a form of neural exercise enhancing the efficiency of the neural circuit responsible for regulating the fight-or-flight response (Porges, 2009, 2015). Although play, and especially play fighting, involves many behavioral patterns typical of the fight-or-flight response (Cordoni et al., 2023), it can be distinguished from “serious” aggressive or defensive behaviors by specific structural features, including pattern repetition and longer session duration (Cordoni et al., 2023). Play may also be regulated by social engagement which encompasses facial expressions, gestures, and vocalizations among interacting subjects (Porges, 2009, 2015). In both human and nonhuman primates, distinctive playful facial expressions are observed during play, often involving face-to-face interactions (Annicchiarico et al., 2020; Palagi et al., 2016; Preuschoft & van Hooff, 1997). Face-to-face interaction may serve as effective exercise for improving and enhancing the social engagement system (Porges, 2009, 2015). While not uniformly observed with equal frequency across all nonhuman primate species (Norscia & Palagi, 2016; Palagi et al., 2016; Palagi, Norscia, et al., 2019), the relaxed open mouth that individuals show during play grades from play face (open mouth and exposed lower teeth) to the full play face (wider-open mouth with lower and upper teeth exposed; Cordoni & Palagi, 2012; Davila-Ross et al., 2015; Palagi et al., 2016; Waller et al., 2020). These playful expressions—homologous of human smile and laughter (Davila-Ross & Dezechache, 2021; van Hooff & Preuschoft, 2003)—convey nonaggressive intentions and a positive context thus reducing the risk of aggressive escalation and down regulating the fight-or-flight response (Cordoni & Palagi, 2011, 2012; Demuru et al., 2015; Gervais & Wilson, 2005; Pellis & Pellis, 1996).

During play, subjects may rapidly replicate facial expressions perceived (Iacoboni, 2009). This phenomenon—known as rapid facial mimicry (RFM)—involves the rapid (<1 s), automatic and involuntary replication by one individual of the facial expression displayed by a trigger (i.e., the first individual emitting the facial stimulus). Indeed, RFM finds its roots in the automatic coupling of perception and action within the brain's sensorimotor areas, as foreseen by the perception action model (PAM) possibly involving the mirror neuron system (de Waal & Preston, 2017; Ferrari et al., 2003; Gallese et al., 1996). Facial expressions are more likely to be mimicked during face-to-face interactions (Annicchiarico et al., 2020; Herrando & Constantinides, 2021). Consequently, for RFM to occur, it is essential that the potential receiver perceives the facial stimulus (Bertini et al., 2021; Gallo et al., 2022; Herrando & Constantinides, 2021;

Palagi et al., 2019, 2020). According to the PAM, observing another's facial expression activates shared neural areas that enable replication not only of the expression but also of the emotion it conveys (de Waal & Preston, 2017).

In primates, RFM has been demonstrated primarily in Catharrini including humans (Chartrand & van Baaren, 2009; Olszanowski et al., 2019), bonobos (Bertini et al., 2021), chimpanzees (Palagi et al., 2019), lowland gorillas (Bresciani et al., 2021; Palagi et al., 2019), Bornean orangutans (Davila-Ross et al., 2008), geladas (captive, Mancini et al., 2013; wild, Gallo et al., 2022), Tonkean and Japanese macaques (Scopa & Palagi, 2016).

RFM can be modulated by individual, hormonal, environmental, and social factors (see for review Kraaijenvanger et al., 2017; Palagi et al., 2020). For example, in chimpanzees and juvenile lowland gorillas, RFM can be more prevalent between individuals with close bonds (Palagi et al., 2019). Additionally, in bonobos and chimpanzees, the levels of mimicry can increase in response to a stimulus emitted by dominant individuals (Furuichi, 2012; Gruber & Clay, 2016).

In nonhuman primates, the presence of RFM is often associated with longer durations of playful sessions indicative of higher success of play interactions (e.g., Davila-Ross et al., 2008; Palagi et al., 2019; Weisfeld, 1993). Furthermore, it has been proposed that RFM may be more likely to occur when there is a higher risk of play escalation to communicate the benign intent of the subject (Bresciani et al., 2021). In particular, this can occur when the play session is highly competitive and the exchange of offensive (i.e., behavioral patterns aimed at attacking and pursuing the partner) and defensive (i.e., behavioral patterns aimed at eluding the attack and pursuit by the partner) patterns is markedly unbalanced between players (Cordoni et al., 2021, 2023).

To date, there are no available data on RFM in Platyrrhini (New World monkeys). Investigating RFM in New World monkeys can help to better understand the evolution of motor replication phenomena in primates, linked to interindividual synchronization and possibly emotional contagion, a basic form of empathy (Casetta et al., 2021; de Waal & Preston, 2017; Gallo et al., 2022; Rizzolatti & Caruana, 2017).

In this study, we investigated the presence of RFM in three different species of spider monkeys—one of the largest New World primates—namely *Ateles fusciceps*, *Ateles hybridus*, and *Ateles paniscus*. Spider monkeys live in a fission–fusion society characterized by male philopatry (as it occurs in chimpanzees and bonobos, the species phylogenetically closest to humans; Langergraber et al., 2012). Within this society, community members regularly undergo fission by splitting into smaller sub-groups. These sub-groups undergo multiple changes throughout the course of a single day by fusing to form temporary larger groups and then splitting again with different compositions (Aureli & Schaffner, 2008, 2010).

The literature contains reports of playful activity in spider monkeys, even among adult individuals. Furthermore, communicatory signals such as head-shaking (a behavior-promoting approach and friendly contact during copulation, affiliation, greeting, and play) and play face are performed during play interactions (Chapman &

Chapman, 1987; Pellis & Pellis, 1997, 2011). No studies have explored the possible presence of rapid replication of such playful signals. However, recent research has provided evidence of contagion of yawning and scratching (which, as mimicry, are motor replication phenomena; Palagi et al., 2020) in wild spider monkeys (*Ateles geoffroy*). This research found that individuals were more likely to replicate the yawning or scratching behavior of others when they observed it, compared to when they did not observe it (Valdivieso-Cortadella et al., 2023). These findings make spider monkeys a suitable model species to investigate rapid mimicry, its potential modulating factors, and its function(s). In the current research, we primarily focused on exploring the potential presence of play face rapid mimicry due to the limited data on head-shaking and on adopting a comparative approach by contrasting our findings with those already published on RFM in other primate species.

1.1 | Prediction 1—Occurrence of RFM

Considering that spider monkeys show behavioral contagion (Valdivieso-Cortadella et al., 2023) and engage in playful activities (Aureli & Schaffner, 2010; Chapman & Chapman, 1987; Pellis & Pellis, 1997, 2011), we expected to find the presence of RFM in the three species under investigation.

1.2 | Prediction 2—Individual and social factors modulating RFM

In wild spider monkeys, it was observed that the presence of yawning and scratching contagion (a form of motor replication) remained unaffected by factors such as sex, relationship quality, and kinship among the individuals involved (Valdivieso-Cortadella et al., 2023). Since RFM is considered another form of motor replication (Palagi et al., 2020), we expected that in spider monkeys—as it occurs for behavioral contagion—the presence of RFM would not be influenced by individual or social factors.

1.3 | Prediction 3—RFM, play session length, and sequential relation

Since in several primate species, RFM is associated with longer durations of playful sessions (Davila-Ross et al., 2008; Palagi et al., 2019; Weisfeld, 1993), we expect that also in spider monkeys, the duration of play interactions would be longer when RFM is present, as opposed to when it is absent or only unreplicated PF is present (Prediction 3a). Furthermore, since RFM may foster a clearer communication of nonaggressive intent between playmates when play becomes more competitive (Palagi et al., 2020), we expected that RFM would be more often preceded and followed by more types of offensive playful patterns than just the unreplicated PF (Prediction 3b).

2 | METHODS

2.1 | Ethical statement

The current study was purely observational and did not involve any animal manipulation. For this reason, approval from the authors' institutional animal care committees was not required. The study adhered to all the legal requirements of the country in which the research was conducted.

2.2 | Study groups

We conducted an observational study on three distinct species of spider monkeys.

A. fusciceps (Colombian spider monkey). This group was composed of 11 individuals (Table 1) housed at the *ZooParc de Beauval*. The animal enclosure was composed of an indoor facility (50 m²) comprised of a masonry with two connecting rooms and a central corridor and an outdoor space featuring two connected islands (600 m²). Islands were enriched with ropes, wooden planks, platforms, trees, and bushes. The animals received food three times per day (09:00, 13:00, and 18:00; fruits, vegetables, pellets for vitamin intake and mineral salt supplementation).

A. paniscus (black spider monkey). The colony was composed of six individuals (Table 1) housed at *La Vallée des Singes*. Animals were housed in an indoor facility (100 m²) with two connecting rooms and a central corridor and an island (2000 m²) equipped with trees, ropes, and bridges.

A. hybridus (brown or variegated spider monkey). The group included 14 individuals (Table 1) housed at *La Vallée des Singes*. Animal enclosures were composed of both an indoor (90 m²; three connecting rooms and a central corridor) and outdoor (1400 m²; island with dense vegetation, trees, bushes, bridges, ropes, and platforms) facility.

Both *A. paniscus* and *A. hybridus* received food four times per day (08:00, 12:00, 14:00, and 18:00; vegetables, fruit, and pellets).

Kinship relationships across all colonies were documented through animal studbooks and information provided by park staff. In none of the groups did we record any aberrant or stereotypic behavior (Lutz, 2014; Novak & Suomi, 2008). We followed Shimooka et al. (2008) for age class categorization: adult >8 years, subadult 5–8 years, juvenile 2–5 years, and infant <2 years. We found no difference across individual ages of the three study groups (ANOVA $N_{\text{individuals}} = 30$, $F = 2.262$, $p = 0.123$; see below for explanation on the statistical tests).

2.3 | Data collection

Video data were collected during the following periods: February–April 2022 at *La Vallée des Singes* and May–June 2022 at the *ZooParc de Beauval*. Animals were followed 5 h per day with

TABLE 1 The three groups of spider monkeys observed in this study.

Name	Sex	Age (years) ^a	Species	Location	Mother and/or father
Amazona (Am)	F	32	A. f.	BEA	
Medeline (Me)	F	21	A. f.	BEA	
Naya (Na)	F	6	A. f.	BEA	Am + Ri
Cattleya (Cat)	F	4	A. f.	BEA	Am + Ri
Bebè (Bb)	F	0	A. f.	BEA	Am + Ri
Ricardo (Ri)	M	29	A. f.	BEA	
Mocoa (Moc)	M	13	A. f.	BEA	Am + Ri
Quimbayo (Qu)	M	10	A. f.	BEA	Am + Ri
Huilo (Hu)	M	10	A. f.	BEA	Me + Ri
Yopo (Yop)	M	7	A. f.	BEA	Me + Ri
Kilipi (Kil)	M	4	A. f.	BEA	Me + Ri
Lutz (Lu)	M	31	A. p.	VDS	
Gege (Ge)	F	24	A. p.	VDS	
Caline (Can)	F	18	A. p.	VDS	
Cayenne (Cay)	M	8	A. p.	VDS	Can + Lu
Youpla (Yo)	F	19	A. p.	VDS	
Macopi (Mac)	F	11	A. p.	VDS	Yo + Lu
Mia (Mia)	F	29	A. h.	VDS	
Mika (Mik)	F	27	A. h.	VDS	
Cali (Cal)	F	15	A. h.	VDS	Mik
Tio (Tio)	M	13	A. h.	VDS	Mia
Chiapas (Chi)	M	12	A. h.	VDS	Mik
Suely (Sue)	F	10	A. h.	VDS	Mia
Soa (Soa)	F	6	A. h.	VDS	Mik
Raffy (Raf)	M	19	A. h.	VDS	
Manabi (Man)	F	5	A. h.	VDS	Cal
Yasuni (Yas)	M	4	A. h.	VDS	Mik + Raf
Luebe (Lue)	M	2	A. h.	VDS	Mia + Raf
Sama (Sam)	F	2	A. h.	VDS	Sue + Raf
Zulia (Zul)	F	1	A. h.	VDS	Cal + Raf
Olaya (Ol)	F	0	A. h.	VDS	Mik + Raf

Note: F = female, M = male, A. f. = *Ateles fusciceps*, A. p. = *Ateles paniscus*, A. h. = *Ateles hybridus*, BEA = ZooParc de Beauval, VDS = La Vallée des Singes.

^aAt the time of the observations.

alternating morning (08:00–13:00) and afternoon (13:00–18:00) sessions. Each individual within the three groups was observed for a total of 7 h. Videos were recorded with a full HD hand camera (Panasonic HC-V180, zoom 50×, 60 fps) and then analyzed in slow motion and frame-by-frame by using free software Avidemux 2.8.1

and PotPlayer. The data were collected by an observer (A.C.) who underwent training (35 h) supervised by G.C. and I.N. for behavioral pattern recognition and methodological procedure application. Additionally, A.C. received a training of 40 h during fieldwork for animal identification and observational method application. The interobserver reliability—measured by Cohen's *K*—was never below 0.80.

We employed (i) the scan animal sampling for collecting data on solitary (moving, resting, feeding, and foraging), affiliative (proximity, body contact, grooming, and embrace), aggressive, and playful behavioral states of groups at 10-min intervals (this sampling was conducted live by using a voice recorder); and (ii) the all occurrences sampling method for gathering data on playful interactions (Altmann, 1974). In particular, for each play session, we recorded (i) players' identities (i.e., species, age, and sex), (ii) behavioral patterns in their sequential order (Table 2), (iii) play face duration (in cs), and (iv) session duration (in s). Our analysis encompassed a total of 149 play fight sessions in which playmates were always visible. The dyadic play frequencies normalized on the number of individuals presented in each group did not statistically differ (Kruskal–Wallis test—Monte Carlo randomization $H = 3.881$, $df = 2$, $p = 0.149$).

2.4 | Operational definitions

2.4.1 | Play session

According to previous reports, play is characterized by behavioral patterns that are considered play markers (i.e., play faces, head-shaking; Pellis & Pellis, 1997) and does not include any submissive or aggressive behaviors. A play session commenced when one individual initiated any playful pattern with a companion and concluded when either the two players disengaged from each other or an uninvolved third individual interrupted the interaction. Two consecutive sessions were considered as different if the play interruption lasted at least 10 s (Cordoni et al., 2021, 2023). Playful behavioral patterns were distinguished as offensive (i.e., behavioral patterns aimed at attacking and pursuing the partner), defensive (i.e., behavioral patterns aimed at eluding an attack, freeing oneself from a playmate's grab or fleeing from the pursuit by the partner), and neutral (i.e., behavioral patterns neither offensive nor defensive; Cordoni et al., 2021, 2023).

2.4.2 | Play face

As reported in the literature, during a play face, the mouth is opened with lower teeth exposed, while during a full play face the mouth is more widely opened with both lower and upper teeth exposed (Cordoni & Palagi, 2012; Preuschoft & van Hooff, 1997; Figure 1). Due to the limited sample size, we combined play face and full play face into a single category, hereafter referred to as “Play Face” (PF). The duration of each PF was quantified through a frame-by-frame

TABLE 2 Behavioral patterns recorded in this study for spider monkeys.

Behavioral pattern	Definition
Affinitive patterns	
Body-contact	Two or more individuals are lying down, sitting, or standing with a part (or more parts) of their bodies in contact
Embrace	An individual wraps their arm around the shoulder or back of another individual or two individuals approach each other and initiate contact by wrapping their arms around the other's body and placing their heads at the other's shoulder or abdomen
Grooming	An individual manipulates and cleans the fur of a companion with their hands or mouth
Play patterns	
Attempt play bite	An individual unsuccessfully tries to close their mouth on the playmate's body
Pirouetting	An individual spins around while standing or hanging from a branch. This pattern can be performed either in solitary or social manner
Play bite	An individual closes their mouth on the playmate's body in a non-harmful way
Play brusque rush	An individual jumps with their four limbs on the playmate generally in a quadrupedal position and either bounces away or stays for initiating a play session
Play climb or stand on another	An individual moves or sits/stands on the playmate's body regardless of the playmate position (sitting, lying, or standing)
Play drag	An individual hauls the playmate taking them from the fore or hind limbs
Play fight	Two or more individuals play in tight and continuous physical contact by performing many of the behavioral patterns described in this table (e.g., bite, slap, stamp, and run)
Play flee	An individual swiftly moves away on the ground or in a tree while the playmate pursues them
Play head shaking	An individual rapidly and repeatedly moves their head from side to side. It may occur before copulation, grooming, and play.
Play jump	An individual lifts their feet from the ground and descends either onto the ground or the playmate while in temporary bipedal position. Playful jump entails minimal or no forward motion
Play kick	An individual gently uses their feet to hit the playmate
Play object	An individual throws, shakes, bites, flips, and hits an object either solitary or socially
Play pull	An individual quickly moves a playmate toward them by grabbing their legs, arms, hands, or another part of the companion's body
Play push	An individual displaces the playmate far from them with hands or feet
Play retrieve	An individual blocks with their hands the playmate to prevent their flight. It is different from play pull that is generally performed with both feet and hands during play.
Play run	An individual moves rapidly either alone or behind the playmate generally fleeing
Play shelter	An individual protects themselves from slaps, bites, stamps, and so on, by their playmate putting their arms over the head
Play slap	An individual uses their open hands for hitting any part of the playmate's body
Play stamp	An individual hits either on the ground or on the playmate with their feet in a repeated way
Play wriggle	An individual moves rapidly their body to get rid of the grip of the playmate
Somersault	An individual flips over the ground or on vertical supports either solitary or socially
Tickle	An individual uses their hands, feet, or head for gently rubbing a part of the playmate's body

analysis. We defined the start of the expression as the first frame in which the inferior and superior lips were separated, and the end as the first frame in which the lips were closed again. Conversely to play bite, during the performance of PF players never closed their mouth on the partner's body. In total, we recorded 207 PFs performed within the 149 playful sessions that were analyzed.

2.4.3 | RFM (Prediction 1)

To investigate the presence of RFM during playful interactions, we established two distinct conditions: *yes-perception* and *no-perception*. In the *yes-perception* condition, we recorded the number of PF performed by the subject within 1 s after the trigger

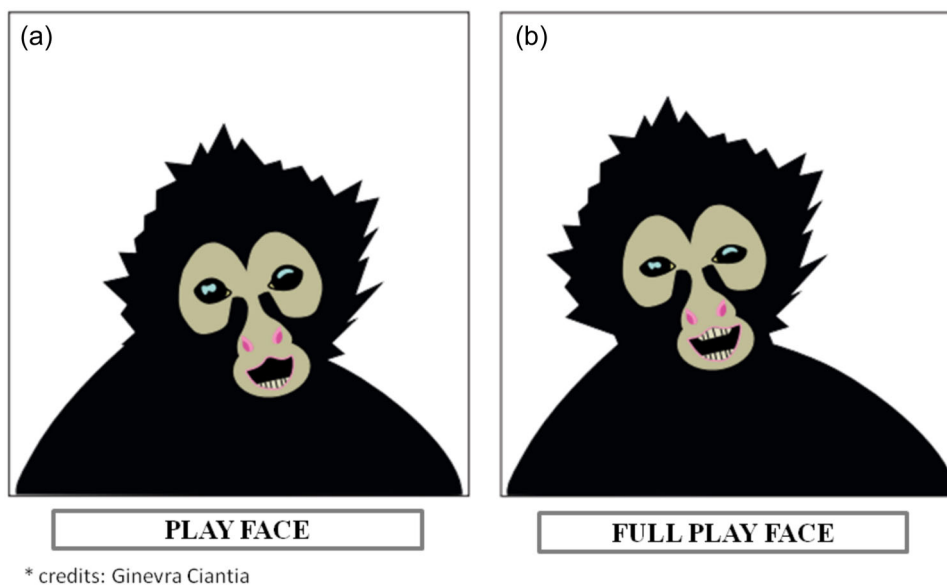


FIGURE 1 Play faces in spider monkeys. Graphical representation of play face (a; opened mouth and lower teeth exposed) and full play face (b; opened mouth and both upper and lower teeth exposed) in spider monkeys (*Ateles* sp.). Image credit Ginevra Ciantia.

(i.e., the first individual emitting the facial stimulus) has emitted the facial stimulus within the visual field of the subject. In the *no-perception* condition, we recorded the number of PF performed by the potential receiver within 1 s after the trigger has emitted the stimulus out of their visual field. If the potential receiver, who was initially looking away, turned their face towards the trigger that was still displaying a PF, this case was categorized as *yes-perception* condition because the potential receiver actually perceived the stimulus. If one of the players had their back to the camera, we were unable to confirm the presence of a playful expression. Consequently, such event was excluded from the analysis.

2.4.4 | Play face conditions (Prediction 3a)

We compared the mean session duration under three different conditions: (i) no expression (*no-exp*)—no PF was performed by the players during the session, (ii) not-mimicked expressions (*not-mim-exp*)—at least one PF was performed but not replicated during the session, and (iii) RFM—at least one event of RFM was observed during the session.

2.4.5 | Sequential analysis (Prediction 3b)

To verify which types of playful patterns occurred immediately before and after either RFM or unreplicated PF, we carried out a sequential analysis by using the software Behatrix (see Section 2.5 for software description).

2.4.6 | Kinship and relationship quality (Prediction 2)

We categorized individuals into kin (including mother-offspring, father-offspring, and sibling dyads) and non-kin (comprising all other dyads). We computed quartiles based on dyadic hourly frequencies of affiliative contacts (grooming, embrace, body contact interactions) within each group. Subsequently, dyads were categorized as “strong-bond” if their affiliation frequency equaled or exceeded the maximum quartile, while remaining dyads were labeled as “weak-bond.”

2.5 | Statistical analyses

We ran four generalized linear mixed models (GLMMs).

The first model (GLMM_{RFM}; $N_{\text{events}} = 175$; Prediction 1) included as target variable the presence/absence of a PF displayed by the potential receiver within 1 s after the emission of facial stimulus by the trigger (binomial variable, presence = 1, absence = 0). Fixed variables included the perception condition (binomial variable, *yes-perception* = 1, *no-perception* = 0) and the species (factorial variable, *A. fusciceps* = 1, *A. paniscus* = 2, and *At. hybridus* = 3).

The second model (GLMM_{ind_factors}; $N_{\text{events}} = 134$; Prediction 2) included as target binomial variable the presence (=1)/absence (=0) of RFM. The fixed factors included in the model were sex combination (factorial variable, male-male = 0, male-female/female-male = 1, female-female = 2), age difference (scale variable) and species (factorial variable, *A. fusciceps* = 1, *A. paniscus* = 2, and *A. hybridus* = 3).

We ran a GLMM as control (GLMM_{control_ind_factors}; $N_{\text{events}} = 42$; Prediction 2) included as target variable the presence (=1)/absence

(=0) of a spontaneous PF and as fixed factors the same variables comprised in the $GLMM_{ind_factors}$.

The third model ($GLMM_{soc_factors}$; $N_{events} = 134$; Prediction 2) included as target binomial variable the presence (=1)/absence (=0) of RFM. The fixed factors were relationship quality (factorial variable, strong bond = 1, weak bond = 0), kinship (binomial variable, kin = 1, non-kin = 0) and species (factorial variable, *A. fusciceps* = 1, *A. paniscus* = 2, and *A. hybridus* = 3).

We ran a GLMM as control ($GLMM_{control_soc_factors}$; $N_{events} = 42$; Prediction 2) included as target variable the presence (=1)/absence (=0) of a spontaneous PF and as fixed factors the same variables comprised in the $GLMM_{soc_factors}$.

In the fourth model ($GLMM_{duration}$; $N_{events} = 129$; Prediction 3a), the binomial target variable indicated over (=1) or under (=0) the mean play session duration value (mean value of session duration was calculated separately for each group). The fixed factors were play face conditions (factorial variable, *no expression* = 0, *not-mimicked expression* = 1, RFM = 2) and species (factorial variable, *A. fusciceps* = 1, *A. paniscus* = 2, and *A. hybridus* = 3).

In all models, the dyad identity was entered as random factor.

We analyzed the distribution of play session duration (nonnormal distribution, Shapiro-Wilk test $p < 0.05$) under the three play face conditions (*no-exp*, *not-mim-exp*, RFM). We employed the Kruskal–Wallis test for k-independent samples and Monte-Carlo randomization (10,000 permutations) for the nonindependence of data due to the same individuals being present in different dyads. Then, we applied a post-hoc test for pairwise comparison with Bonferroni correction. Finally, for sequential analysis (see Section 2.4), we created a string for each RFM event by reporting the behavioral patterns separated by a break symbol (i.e., |). The resulting string represented the ordered concatenation of RFM event and behavioral patterns before and after it. By employing the free open-source software Behatrix 0.9.11 (<http://www.boris.unito.it/pages/behatrix>; Friard & Gamba, 2020), we analyzed the sets of behavioral sequences and organized data into contingency tables. The program generates the code for a flow diagram (Graphviz script) of behavior-RFM-behavior transitions. We carried out the same sequential analysis also with PF as control condition.

3 | RESULTS

3.1 | Prediction 1—Occurrence of RFM

The $GLMM_{RFM}$ was carried out to verify the presence of RFM. The full model (including the fixed factors) and the null model (only including the random factor) significantly differed (likelihood ratio test: $\chi^2 = 9.8196$, $df = 3$, $p = 0.020$; Table 3 and Figure 2; see Table S1 for effect size measure non-accounting for the random factors). Because the predictor had a significant effect on the target variable, we applied the drop1 procedure. We found that the perception condition had a significant effect on the probability of observing the presence/absence of playful expressions performed by one player

within 1 s after the emission of the first expression by the trigger (Table 3). In particular, the probability of a response within 1 s was higher when the facial expression of the trigger was seen by the observer (*yes-perception*) than when it was not (*no-perception*).

3.2 | Prediction 2—Individual and social factors modulating RFM

The $GLMM_{ind_factors}$ was run to verify possible modulation of RFM occurrence (presence/absence) by individual factors (i.e., sex-class combination, age difference, and species). We did not obtain any significant difference between the full and the null model (likelihood ratio test: $\chi^2 = 6.022$, $df = 5$, $p = 0.304$; Table 3; see Table S1 for effect size measure non-accounting for the random factors). Hence, none of the considered individual factors affected the occurrence of RFM.

The $GLMM_{control_ind_factors}$ was run as control. The full model did not differ from the null model (likelihood ratio test: $\chi^2 = 3.970$, $df = 5$, $p = 0.554$; Table 3; see Table S1 for effect size measure non-accounting for the random factors).

The $GLMM_{soc_factors}$ was carried out to test for possible modulation of RFM occurrence (presence/absence) by social factors (i.e., relationship quality, kinship, and species). We did not obtain any significant difference between the full and the null model (likelihood ratio test: $\chi^2 = 2.574$, $df = 4$, $p = 0.431$; Table 3; see Table S1 for effect size measure non-accounting for the random factors). Hence, none of the tested social factors affected the occurrence of RFM.

The $GLMM_{control_soc_factors}$ was run as control. The full model did not differ from the null model (likelihood ratio test: $\chi^2 = 3.562$, $df = 4$, $p = 0.469$; Table 3; see Table S1 for effect size measure non-accounting for the random factors).

3.3 | Prediction 3—RFM, play session length, and sequential relation

3.3.1 | Prediction 3a

We ran the $GLMM_{duration}$ to evaluate the possible influence of play face conditions on the session duration (over/under mean session duration value; binomial distribution). The full model significantly differed from the null model (likelihood ratio test: $\chi^2 = 51.976$, $df = 4$, $p < 0.001$; Table 3). We found that the expression condition influenced the session duration (Table 3). In particular, the session was longer in the presence of RFM rather than in the absence of expressions or in the presence of not-mimicked expressions (Figure 3).

We also carried out a comparison of session durations (in s; scale distribution) across the three play face conditions and we obtained significant differences (Kruskal–Wallis test Monte-Carlo randomization $N_{no-exp} = 77$, $N_{no-mim-exp} = 30$, $N_{RFM} = 22$, $\chi^2 = 24.203$, $df = 2$, $p < 0.001$). Post hoc test revealed the following results: *no-exp* versus *not-mim-exp* ($Q = -18.081$, $p = 0.074$), *no-exp* versus RFM

TABLE 3 Results of the generalized linear mixed models (GLMMs).

GLMM_{RFM} target variable: presence/absence of a PF within 1 s after the stimulus random factors: dyads (N = 175) full model vs null model: $\chi^2 = 9.8196$, $df = 3$, $p = 0.020$				
	Estimate	SE	z Value	p
Intercept	-4.513	1.223	-3.690	<0.001
Perception condition (yes-perception)	2.448	1.078	2.271	0.023
Species (<i>Ateles paniscus</i>)	0.676	1.107	0.611	0.541
Species (<i>Ateles hybridus</i>)	0.344	0.694	0.496	0.620
Effect size				
Perception condition (no-perception)	0.014			
Perception condition (yes-perception)	0.142			
Species (<i>Ateles fusciceps</i>)	0.067			
Species (<i>Ateles paniscus</i>)	0.123			
Species (<i>Ateles hybridus</i>)	0.092			
GLMM_{ind_factors} target variable: presence/absence of an RFM event random factors: dyads (N = 134) full model vs null model: $\chi^2 = 6.0224$, $df = 5$, $p = 0.304$				
Effect size				
Age difference (in years; 0)	0.165			
Age difference (8)	0.160			
Age difference (16)	0.155			
Age difference (24)	0.150			
Age difference (32)	0.144			
Species (<i>Ateles fusciceps</i>)	0.167			
Species (<i>Ateles paniscus</i>)	0.145			
Species (<i>Ateles hybridus</i>)	0.158			
Sex combination (male-male)	0.296			
Sex combination (female-male/male-female)	0.174			
Sex combination (female-female)	0.034			
GLMM_{control_ind_factors} target variable: presence/absence of a spontaneous PF random factors: dyads (N = 42) full model versus null model: $\chi^2 = 3.970$, $df = 5$, $p = 0.554$				
Effect size				
Age difference (in years; 0)	2.43×10^{-6}			
Age difference (8)	7.44×10^{-6}			
Age difference (16)	2.28×10^{-5}			
Age difference (24)	6.96×10^{-5}			
Age difference (32)	2.13×10^{-4}			
Species (<i>Ateles fusciceps</i>)	4.22×10^{-11}			
Species (<i>Ateles paniscus</i>)	3.10×10^{-2}			
Species (<i>Ateles hybridus</i>)	1.48×10^{-2}			
Sex combination (male-male)	1.91×10^{-5}			
Sex combination (female-male/male-female)	7.40×10^{-5}			
Sex combination (female-female)	5.13×10^{-12}			

TABLE 3 (Continued)

GLMM_{soc_factors} target variable: presence/absence of an RFM event random factors: dyads (N = 134) full model versus null model: $\chi^2 = 2.574$, $df = 4$, $p = 0.632$				
	Effect size			
Kinship (non kin)	0.108			
Kinship (kin)	0.276			
Relationship quality (weak bond)	0.150			
Relationship quality (strong bond)	0.123			
Species (<i>Ateles fusciceps</i>)	0.108			
Species (<i>Ateles paniscus</i>)	0.106			
Species (<i>Ateles hybridus</i>)	0.166			
GLMM_{control_soc_factors} target variable: presence/absence of a spontaneous PF random factors: dyads (N = 42) full model versus null model: $\chi^2 = 3.562$, $df = 4$, $p = 0.469$				
	Effect size			
Kinship (non kin)	2.20×10^{-4}			
Kinship (kin)	5.56×10^{-12}			
Relationship quality (weak bond)	3.72×10^{-6}			
Relationship quality (strong bond)	2.93×10^{-6}			
Species (<i>Ateles fusciceps</i>)	3.94×10^{-12}			
Species (<i>Ateles paniscus</i>)	10.00×10^{-1}			
Species (<i>Ateles hybridus</i>)	7.67×10^{-4}			
GLMM_{duration} target variable: over/under the mean play session duration value random factors: dyads (N = 129) full model versus null model: $\chi^2 = 51.976$, $df = 4$, $p < 0.001$				
Intercept	-3.917	0.802	-4.887	<0.001
Play face condition (not-mimicked expression)	1.722	0.538	3.201	0.001
Play face condition (RFM)	3.694	0.696	5.307	<0.001
Species (<i>Ateles paniscus</i>)	1.618	1.146	1.413	0.158
Species (<i>Ateles hybridus</i>)	1.221	0.687	1.778	0.075
Tukey test for pairwise comparisons				
no expression versus not-mimicked expression	1.722	0.5378	3.201	0.004
no expression versus RFM	3.694	0.6961	5.307	<0.001
not-mimicked expression versus RFM	1.972	0.600	3.287	0.003

Abbreviations: PF, play face; RFM, rapid facial mimicry; SE, standard error.

($Q = -43.347$, $p < 0.001$), and *not-mim-exp* versus RFM ($Q = -25.267$, $p = 0.048$). Hence, the presence of RFM was associated with a higher session duration values compared to the two other conditions. The mean duration values (\pm SE) for each condition were: *no-exp* 41.0 ± 2.72 , *not-mim-exp* 52.0 ± 4.10 , and RFM 120.72 ± 24.4 .

3.3.2 | Prediction 3b

A total of 251 and 78 transitions occurred between a PF or an RFM event, respectively, and the behavioral patterns before and after it. We found that PF was more likely preceded and followed only by

two offensive behavioral patterns: play biting and play slapping (Figure 4). On the other hand, an RFM event was most likely preceded by play slapping and play biting and followed by play pulling, play biting, and play pushing (Figure 4).

4 | DISCUSSION

In the current study, we showed for the first time the occurrence of RFM during play in three species of spider monkeys (*A. fusciceps*, *A. hybridus*, and *A. paniscus*) housed in comparable captive enclosures under similar management conditions (*Prediction 1* confirmed;

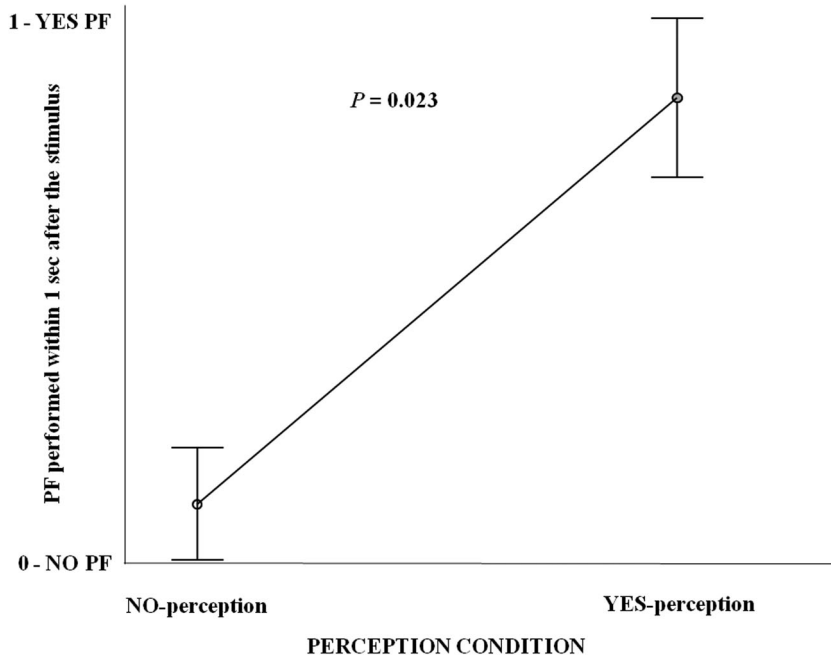


FIGURE 2 Occurrence of the rapid facial mimicry. Graph representing on the Y-axis the presence (=1) and absence (=0) of a play face (PF) performed within 1 s after the stimulus by the potential receiver and in the X-axis *yes-perception* (1) and *no-perception* (0) conditions (see Section 2 for the definition of conditions). Vertical bars: 95% confidence interval; dots: mean values; whiskers: minimum and maximum values.

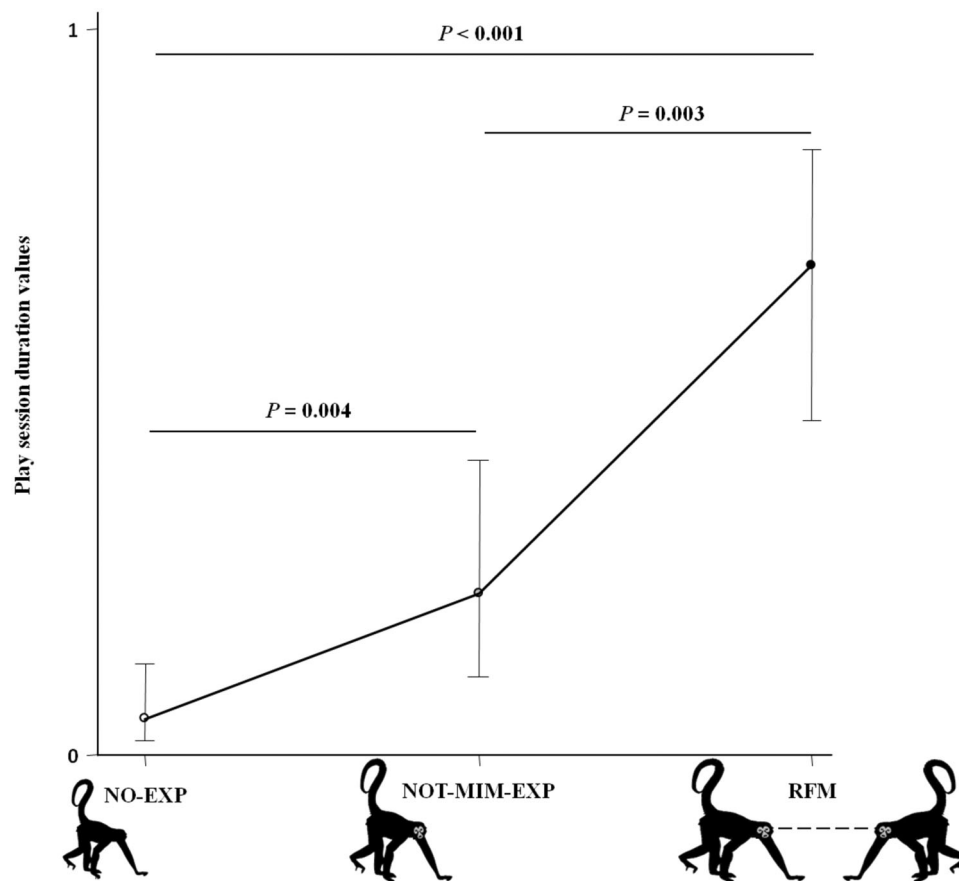


FIGURE 3 Rapid facial mimicry (RFM) and mean play session duration. Graph representing on the Y-axis the play session duration values over (1) and under (0) the mean duration values calculating for each group and on the X-axis the three play face conditions: (i) no expression performed by the players during the session (*no-exp*), (ii) at least one expression performed but not replicated during the session (*not-mim-exp*), and (iii) at least one event of RFM observed during the session (RFM). Vertical bars: 95% confidence interval; dots: mean values; whiskers: minimum and maximum values. Image credit Ginevra Ciantia.

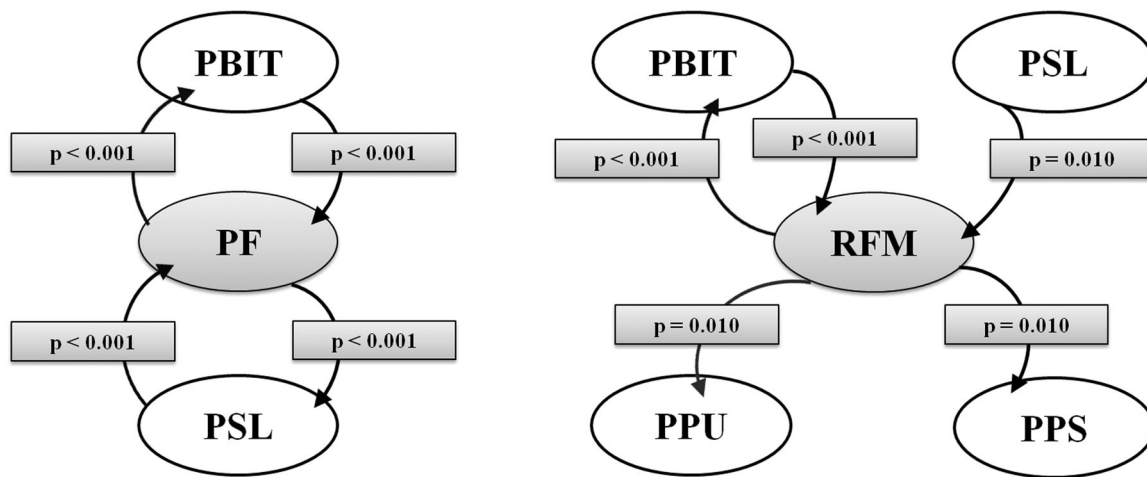


FIGURE 4 Sequential analysis on rapid facial mimicry (RFM) and unreplicated play face (PF). Flow diagram representing transitions between either the mere play face (on the left side) or an RFM event (on the right side) and playful patterns before and after it. The numbers (in percent) beside each transition represent the probability of transitions between behaviors. We set the probability of transitions between behaviors at the percentage value $\geq 5\%$. PBIT, play biting; PSL, play slapping; PPU, play pulling; PPS, play pushing.

Figure 2). We did not identify any individual or social factors influencing the occurrence of RFM in spider monkeys (*Prediction 2* confirmed; Table 3). Furthermore, we found that the presence of RFM was linked to longer durations of playful interactions (*Prediction 3a* confirmed; Figure 3), with RFM events significantly preceded and followed by more types of offensive playful patterns compared to the mere play face (*Prediction 3b* confirmed, Figure 4).

A form of motor replication (i.e., yawn and scratching contagion) was demonstrated in the wild in another species of spider monkey (*A. Geoffroyi*; Valdivieso-Cortadella et al., 2023). Taken together, this and our findings support the possibility that within the Primate order, the evolutionary origins of motor mimicry and contagion may pre-date the separation between Platyrrhini and Catharrhini parvorders. Indeed, yawn contagion has been recently demonstrated in wild Strepsirhine (*Indri indri*; Valente et al., 2023), which further bolsters this scenario. Expanding our perspective, given that RFM has been demonstrated in some Carnivora species such as meerkats (Palagi, Marchi, et al., 2019), sun bears (Taylor et al., 2019), and domestic dogs (Palagi et al., 2015), it is likely that the evolutionary roots of this form of motor replication and (potentially) emotional contagion might extend beyond the split between Primates and other mammalian orders.

Spider monkeys are known for their fission–fusion dynamics, where individuals within a group frequently split and rejoin in groups of varying composition. This necessitates the development of a complex communication system (Dell'Anna et al., 2022; Pellis & Pellis, 1997, 2011). Interindividual relationships among group members can be relatively unstable and change opportunistically. Among females, relationships are typically weak and centered on infants. On the other hand, while males tend to form alliances and develop strong bonds compared to females, young males may face the risk of attacks by adult males when attempting to engage in social interaction with them, as young males can be perceived as potential competitors (Aureli & Schaffner, 2010; Saldaña-Sánchez et al., 2022).

Hence, during play (especially play fighting), individuals have to effectively communicate the nature of their actions by using clear and unambiguous signals such as the play face (Cordoni & Palagi, 2012; Palagi & Cordoni, 2012; Palagi et al., 2016). From this perspective, RFM in spider monkeys may communicate more effectively during play, facilitating motor synchronization and fostering a shared understanding of the context (i.e., play) among participants. Face-to-face interaction (i.e., perception condition) can amplify the mimic response by effectively conveying the message “I am like you” to the play partner (Bavelas & Gerwing, 2007; Bavelas et al., 1986; Iki & Hasegawa, 2020). Behavioral synchronization and face-to-face interactions may foster the development of social bonds between individuals (Annicchiarico et al., 2020). In humans, it has been demonstrated that when one subject synchronizes her/his movements with another or mimics another's movements, this last person affiliates more with the synchronizer (Chartrand & van Baaren, 2009; Hove & Risen, 2009). Moreover, children engaging in synchronous play exhibited more shared smiles, increased eye contact, and showed significantly more helping behavior compared to children who did not play in synchrony (Tunçgenç & Cohen, 2018). Mimicking the same facial expression performed by a partner activates a shared neural substrate underlying sensorimotor simulation that supports the corresponding emotion in a same face-same emotion process (Clay et al., 2018; Palagi et al., 2020; Prochazkova & Kret, 2017).

Our study did not reveal any evidence of RFM modulation based on either individual factors—such as sex, age, and species—or social factors, such as relationship quality and kinship. This lack of RFM modulation could be associated with the flexible nature of social relationships in spider monkeys, as indicated by previous studies (Aureli & Schaffner, 2008; Aureli et al., 2013; Saldaña-Sánchez et al., 2022). In spider monkeys, male-male relationships may not be consistently strong as generally described and can be marked by a

dynamic interplay of cooperation and competition (Aureli et al., 2013; Saldaña-Sánchez et al., 2022). On the other hand, females may exhibit a high level of affiliation under specific conditions, such as experiencing stress (Rodrigues, 2013) or facing ecological constraints (Abondano & Link, 2012). In terms of age, juvenile spider monkeys occupy similar positions to adult individuals in grooming and aggression networks, indicating similar connectivity within the group (Boeving et al., 2020). Considering these social dynamics, the reduction of the likelihood of partner misunderstanding during play is crucial for both male and female, immature and adult, as well as weak and close-related individuals. This is essential to limit the risk of attacks, and RFM may enhance the sharing of intents between players. Similarly, the partner's sex, maternal kinship and relationship quality did not influence either yawn or scratching contagion (Valdivieso-Cortadella et al., 2023). The authors discussed this finding by suggesting that in spider monkeys, yawn and scratching contagion might synchronize the emotional states of all group members rather than promote an emotional contagion between strong-related dyads. RFM has been regarded as a bottom-up process on the basis of the evolutionary building blocks for emotional contagion fostering the sharing of emotional experiences between individuals (Hatfield et al., 1994; Kret, 2015; Prochazkova & Kret, 2017; Smith & Rose, 2020). However, mimicking others' facial expressions does not necessarily imply that the subject experiences the same emotional states as others, as the affective component may not always transition from shared motor activation to a complete emotional experience (Prochazkova & Kret, 2017). Hence, in spider monkeys, RFM might not necessarily imply an emotional contagion based on a gradient of social closeness as observed in other primate species (Mancini et al., 2013; Palagi et al., 2019). RFM might induce shared motor activation and synchronize the emotional states of all individuals within the group independently of the quality of interindividual relationships. Of course, we cannot exclude that a larger sample size or a replication of this study in the wild—where there is not a limited degree of fission–fusion dynamics, unlike captive conditions—may reveal the influence of individual and/or social factors on RFM.

We found that RFM may contribute to the continuation of play (Figure 3) as seen in other primate species (e.g., gorillas, Palagi et al., 2019; chimpanzees, Palagi et al., 2019; geladas, Gallo et al., 2022). As mentioned earlier, if RFM may promote motor and emotional synchronization between players, individuals are motivated to prolong the interaction. Additionally, it is noteworthy that—compared to the mere play face—a wider array of different types of more intense offensive playful patterns—such as biting, pushing, slapping, and pulling—are sequentially associated with RFM (Figure 4). We propose that RFM may function to decrease the risk of misinterpreting behavioral patterns while simultaneously fostering a more competitive nature of playful interactions, all within the framework of maintaining a safe context. A proposed function of mimicry is the “decreasing prediction error” (Hutchinson & Barrett, 2019). Through RFM, becoming more like the partner, an individual can predict easier and more accurately the partner's

actions and emotions (Kret & Akyüz, 2022). This alignment might benefit the mimicker, allowing them to better interpret their partner's signals (Kret & Akyüz, 2022). During a prolonged and competitive playful interaction, the mimicker can correctly interpret the partner's signals and actively continue or—if needed—terminate the interaction. Continuing competitive play sessions can enhance the social assessment process among players (Fagen, 1981; Paquette, 1994; Thompson, 1998). Through play, individuals can gather valuable information about the nature of their relationships (cooperative or competitive) as well as assess each other's physical and cognitive capacities (Cordoni et al., 2021, 2023).

In conclusion, while acknowledging the need for more data to generalize our findings, this study lays the groundwork for additional research on the evolutionary origins of motor mimicry. Taking a broader perspective, RFM could represent either an ancestral trait (plesiomorphic character) present in many mammalian orders or a derived trait (apomorphic character) independently evolved in several lineages of mammals, albeit involving similar mechanisms. Considering RFM as a plesiomorphic trait, the focal issue is that the absence of RFM in some lineages of mammals might suggest a loss rather than a gain. On the other hand, considering RFM as an apomorphic trait, the issue is discerning the factors that might have driven the evolution of RFM multiple times across distinct lineages.

This study also points toward the possibility that motor mimicry of expressions supposedly conveying a positive mood, may not always lead to cooperation but also to competition, depending on the context and species' social and cognitive features.

AUTHOR CONTRIBUTIONS

Giada Cordoni: Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); supervision (lead); writing—original draft (lead); writing—review and editing (lead). **Annalisa Ciantia:** Data curation (supporting); formal analysis (supporting). **Jean-Pascal Guéry:** Resources (equal); writing—review and editing (supporting). **Baptiste Mulot:** Resources (equal); writing—review and editing (supporting). **Ivan Norscia:** Conceptualization (lead); funding acquisition (lead); investigation (lead); methodology (lead); supervision (lead); writing—original draft (lead); writing—review and editing (lead).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data sets supporting this article have been uploaded as part of the Supporting Information.

ORCID

Giada Cordoni  <http://orcid.org/0000-0001-7093-0025>

Ivan Norscia  <http://orcid.org/0000-0002-1618-7717>

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