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Rapid facial mimicry as a regulator of play in a despotic macaque species

Giulia Facondini¹ · Luca Pedruzzi^{1,2} · Simone Aere¹ · Martin Böye³ · Alban Lemasson^{2,4} · Elisabetta Palagi^{1,5}

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Abstract

During risky interactions like social play, motor resonance phenomena such as facial mimicry can be highly adaptive. Here, we studied Rapid Facial Mimicry (RFM, the automatic mimicking of a playmate's facial expression, play faces) during play fighting between young rhesus macaques (*Macaca mulatta*) living in a large zoo-housed group. For the first time and in contrast to previous data on highly despotic-intolerant macaques, we found RFM to be present at high frequency in young rhesus macaques, especially when the trigger was dominant over the responder and when both players were subadults. The hierarchical modulation of RFM may be associated with the increased uncertainty and riskiness of play involving a higher-ranking playmate. This highlights the importance of mimicry in improving communication and coordination during such interactions. Interestingly, RFM prolonged playful sessions, possibly indicating a more effective fine-tuning of motor patterns. Moreover, the occurrence of RFM had an effect on shortening the latency to restart playing after a break, possibly acting as an engine to potentially maintain playmates' arousal. When investigating if bystanders could replicate play faces emitted by the playing subjects, we failed to find RFM, thus highlighting that being directly involved in the interaction might be crucial for RFM activation in monkeys. Even though further comparative studies should investigate the role of RFM across tolerant and despotic-intolerant species, our findings offer valuable insights into the communicative and adaptive value of motor resonance phenomena in regulating social play in despotic societies.

Significance statement

In risky interactions involving competition and vigorous physical contact, such as play fighting, replicating partners' facial expressions can serve as a strategy to convey positive mood and intentions. Here we investigated the presence and possible roles of Rapid Facial Mimicry (RFM) in rhesus macaques (*Macaca mulatta*). For the first time, our study demonstrates that communicative strategies, including Rapid Facial Mimicry (RFM), can be both present and frequent in despotic-intolerant macaque species. We demonstrate that the role of mimicry not only prolongs playful interactions but can also be linked to the reinforcement and/or transmission of playful arousal. Our study shows how the adaptive value of motor resonance phenomena may have driven their evolution to cope with challenges during social interactions also for despotic-intolerant species.

Keywords Social play fighting · Contagious behaviours · Emotional arousal · Monkeys · *Macaca mulatta*

Introduction

In human and non-human animals, behavioural synchronization occurs when two or more subjects perform the same action, at the same moment, and within the same spatial context (Duranton and Gaunet 2016). Among its adaptive values, synchronization can act as a defence mechanism (e.g., contagion of vigilance, Iki and Kutsukake 2021) and increase affiliation during shared actions (Duranton and Gaunet 2016). The involuntary synchronization of movements, postures, and facial expressions promotes smoother

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interactions among partners, leading to prosocial behaviours and affiliative bonding (Lakin et al. 2003; Paukner et al. 2009; Roth et al. 2021; Poole and Henderson 2023). Behavioural synchronization can involve the automatic reproduction of motor patterns (motor mimicry) or physiological states (autonomic mimicry) of another individual (i.e., spontaneous mimicry, Palagi et al. 2020).

In humans, where facial mimicry has a precocious emergence (Isomura and Nakano 2016), the phenomenon is one of the portals for the transmission of emotional states from one individual to another (Hess and Fischer 2014; Kavanagh and Winkielman 2016; Prochazkova and Kret 2017). However, the role of motor resonance in emotional contagion is a matter of debate for human and non-human primates (Dezecache et al. 2015). If interpersonal closeness, collaborative contexts, and affiliative intentions heighten the likelihood of mimicking (Hess and Fischer 2014), at the same time, mimicry creates a sense of similarity and a favourable assessment of the counterpart, thus generating a sort of positive feedback resulting in psychological connection between the agents (Guéguen 2009; Roth et al. 2021). Spontaneous facial mimicry is not unique to humans and occurs in other species as well (Palagi et al. 2020).

In particular, social play is a good domain to explore the role of rapid facial communication and the underlying affective states in non-human animals since it involves the extensive use of facial displays, close proximity between subjects, and emotional involvement (Palagi et al. 2016; Davila-Ross and Palagi 2022). Play is widespread in mammals (Palagi and Pellis 2023), and involves patterns borrowed from different domains such as courtship, reproduction, and aggression (Burghardt 2005). When involving motor patterns typical of real fighting, we generally talk about play fighting (Palagi et al. 2016), which still occurs under a relatively safe context (Palagi et al. 2016; Palagi and Pellis 2023) and ranges from highly cooperative (e.g., promoting social bonds) to highly competitive (e.g., training for real combat) (Mills 1990). The play face (PF) is a facial expression observed in many primate and non-primate species during play fighting (Davila-Ross and Palagi 2022). The primate PF has been described as a relaxed, open-mouth expression with lower teeth, and occasionally upper teeth, exposed (van Hooff 1967, 1972; Symons 1974). Because of its morphological and functional similarity (Tsao et al. 2008; Palagi et al. 2019), researchers consider this playful expression homologous to the visual component of human laughter (Davila-Ross and Palagi 2022; Palagi et al. 2022). Two non-mutually exclusive hypotheses have been proposed around the communicative-affective role of the PF.

According to some researchers, the PF is a spontaneous signal transmitting a positive internal state experienced during play (e.g., self-rewarding) (Boissy et al. 2007; Waller and Cherry 2012; Bekoff 2015). Other researchers, on the

contrary, claim that the PF is used to communicate information to the playmate about the non-serious intent of the interaction (Mancini et al. 2013a; Demuru et al. 2015).

Rapid Facial Mimicry (RFM) implies the unconscious and rapid (< 1 s) activation of a congruent facial expression in response to the detection of others' facial expressions (Palagi et al. 2020). RFM of PFs has been found during play in different social mammals (*Pongo pygmaeus*, Davila-Ross et al. 2008; *Theropithecus gelada*, Mancini et al. 2013b; *Canis lupus familiaris*, Palagi et al. 2015). Observing an emotionally valent facial expression may activate the motor programs involved in producing the same expression, inducing an experience of the emotional state underlying that facial expression. This can be seen as a 'same face, same emotion' process (Pfeifer et al. 2008; Palagi et al. 2020; Paul et al. 2020). However, it is difficult to disentangle motor mimicry of facial muscular movements from emotional mimicry of the affective state conveyed by the facial expression (Hess and Fischer 2022). Nevertheless, the importance of RFM in sharing the playful mood and synchronizing motor actions has become evident from findings revealing a linkage between facial mimicry and the duration of playful interactions (Mancini et al. 2013a; Palagi et al. 2015; Scopa and Palagi 2016).

Despite the positive valence generally ascribed to play, the behaviour can be risky due to the possibility of aggressive escalation in absence of proper regulation, facilitated by the similarity between the playful and aggressive patterns (Palagi 2018). Moreover, species tolerance and cooperation degree can affect the presence and distribution of social play, as play among adults is observed mostly in tolerant societies (Palagi 2023; Burghardt et al. 2024). These aspects make the *Macaca* genus highly suitable to study play fighting and its communicative modules. Although macaque species share the same social organization and dispersal patterns (multi-male/multi-female groups of variable size with male dispersal and female philopatry, Thierry 2007), they can be arranged according to a continuum of social tolerance (de Waal and Luttrell 1989; Thierry 2000). Tolerant macaques are found to be more playful at any age with high rates of vigorous play fighting and physical contact, often involving more than two playmates (Caine and Mitchell 1979; Petit et al. 2008; Reinhart et al. 2010; Ciani et al. 2012; Yanagi and Berman 2017). In despotic-intolerant species, social relationships develop around the pillars of hierarchy and nepotism (Thierry 2007). In despotic-intolerant species, unlike their tolerant counterparts, social play is nearly absent in adulthood (Palagi 2023). The mere presence of adults inhibits social play between young individuals (Bernstein and Draper 1964). Variations in social style also correspond to differences in communication, where tolerance levels are positively correlated with facial expression (Freeberg et al. 2012; Rincon et al. 2023) and vocal signal variability

(Rebout et al. 2020, 2022). This seems to apply also to the social play sphere, as differences in play style also imply differences in communication during play (Palagi et al. 2016). In despotic-intolerant groups, the outcomes of social interactions are more predictable compared to those of tolerant species, making the use of formalized and stereotyped context-specific signals (also in play fighting) highly adaptive (Preuschoft and van Schaik 2000; Flack and de Waal 2004). In the only study comparing RFM in two macaque species, the highly tolerant *M. tonkeana* and the highly intolerant *M. fuscata*, the phenomenon was found in the former but not in the latter (Scopa and Palagi 2016). According to the authors, the greater variability of facial expressions used in play by tolerant macaques, which results from more uncertain interactions due to less fixed social relationships, might have positively selected mechanisms (e.g., RFM) to canalize playful communication (Scopa and Palagi 2016). However, it remains unclear why such phylogenetically close species should show differences in the presence of a cognitively automatic and low-level phenomenon (de Waal and Preston 2017). In fact, other mimicry phenomena such as vigilance (Iki and Kutsukake 2021) and scratching contagion (Nakayama 2004; Feneran et al. 2013) are present in despotic-intolerant macaques, and, moreover, RFM could be beneficial in managing risky interactions, especially in these species. To fill the gap, we focused on a despotic-intolerant macaque species (*Macaca mulatta*) to test non-mutually exclusive hypotheses on play communication and, in particular, on RFM.

Mimicry phenomena, including Rapid Facial Mimicry (RFM), are effective mechanisms in increasing affiliation during uncertain interactions (Palagi and Mancini 2011; Roth et al. 2021; Poole and Henderson 2023). In this view, RFM during play fighting can be important in societies with strict dominance relationships, where the necessity of playmate synchronization is particularly high (Demaria and Thierry 2001; Sueur et al. 2011) (*Hypothesis 1*). Thus, we expect RFM to be present in *M. mulatta* (*Prediction 1a*) and to be particularly frequent towards high-ranking subjects (*Prediction 1b*) or between subjects sharing a relatively low level of play bond strength (*Prediction 1c*). If mimicking the partner playful facial expressions improves communication and increases the affective arousal of the playmates (Palagi and Mancini 2011), RFM events should lead to longer play sessions (*Prediction 2a*) and to shorter breaks when play is punctuated by pauses (*Prediction 2b*).

The most rewarding sessions are those in which playmates match in physical abilities or playful style (e.g., similar levels of competitive-cooperative patterns used in play fighting) (Bresciani et al. 2022; Iki and Kutsukake 2023; Ham et al. 2024). In such cases, play can however become more competitive because animals are less prone to engage in self-restraining (Pereira and Preisser 1998), making the

recruitment of communicative strategies more important (*Hypothesis 3*). In this framework RFM should be more frequent in sessions involving playmates that are similar in age (proxy for size) (*Prediction 3*).

In humans, watching a film, reading a book, or attending a theatre piece can evoke an emotional involvement in the subject (de Waal 2009). Testing the “same face-same emotion” hypothesis (Palagi et al. 2020) requires verifying if a facial expression can evoke a congruent response in an observer, even when it is not directly involved in the ongoing social interaction. This approach allows to disentangle the playful mood evoked in the observer from simply perceiving others’ PFs from that caused by the active participation in play fighting. If “same face-same emotion” hypothesis is valid (*Hypothesis 4*), we expect that also bystanders can respond after perceiving PFs of the playing agents engaging in RFM (*Prediction 4*).

Methods

Study group, data collection and video coding

The study group was housed at Planète Sauvage (Port-Saint-Père, France) in a 6110-m² enclosure, composed of a grassy area with high trees connected through a system of ropes, rope nets, and wood/metal shelters. Animals were fed at 9:30am with commercial primate pellet, and at 2.30 pm with fruits, vegetables, and bread. Water was available ad libitum. During data collection (August–October 2022), the group was composed of captive-born 122 macaques (59 males, 63 females, see Table S1) and was stable as no new animals were introduced in the previous 2 years. Animals were recorded (Panasonic full-HD HC-V785 25x, HC-V180 200x) in the morning (9:00–13:00) and afternoon (13:00–17:00). Before data collection, the observers underwent a training period (by EP) to become proficient in animal and behavior recognition. All 122 subjects were recognized based on facial and body characteristics (e.g., hair/skin color, scars, tail shape, size). Macaques were classified into three age categories, based on partial birth data provided by the zoo staff, as well as the following criteria: i) Adults: individuals with developed and clearly visible sexual traits (≥ 6 years old for males, > 5 years old for females, Liao et al. 2018); ii) Subadults: completely developed individuals never observed in nipple contact with their mothers, typically smaller in size than adults ($3 \leq$ years old < 6 for males, $3 \leq$ years old ≤ 5 for females, Liao et al. 2018); iii) Juveniles: individuals typically smaller in size than subadults who spent most of their time close to the mother and that were observed at least once during the data collection in nipple contact with the mother (0–2 years old, Liao et al. 2018) (Hudson et al. 1996; Berghänel et al. 2016; Liao et al. 2018).

Via all-occurrences sampling (Altmann 1974), we recorded all the social interactions (e.g., social play, aggression, affiliation, proximity, resting periods) by randomly following subgroups of subjects that were visible to the observers. When recording, the researchers followed the subjects to film the interaction throughout its entire length. Significantly, the two observers concurrently recorded from various sections of the enclosure distinct subgroups of animals. These subgroups exhibited frequent and fluid changes in their composition, enabling the collection of data on a substantial number of playful pairings. By the conclusion of the fieldwork, video recordings were relatively uniform distribution among subjects.

We calculated the observation time for each subject through the scan sampling method (Altmann 1974). During video analysis, we stopped the video every 5 min and coded all the IDs of the macaques present in the frame (ranging from 2 to 10 animals). Then, we summed up all the scans for each subject and estimated the individual observation time (e.g., 50 scans in which a subject was observed = 250 min observation; mean obs. time \pm SE: 3.47 ± 0.16 h). A total of more than 120 h of videos were collected.

Video analysis of dyadic playful interactions was conducted frame-by-frame (GF, SA, LP) using PotPlayer© to record the exact occurrence and duration of each behavioral pattern (accuracy: 0.02 s). For the behavioral coding we used the ethograms already available for macaques (Thierry et al. 2000; Partan 2002; Yanagi and Berman 2014;) and other cercopithecoid species (Palagi and Mancini 2011; Gallo et al. 2022) (all behaviours coded in Table S2a). The initiation of a playful bout occurred when an individual exhibited a

playful pattern towards another and the partner reciprocally responded with another playful pattern (Gallo et al. 2022). A play session was defined as a play bout lasting at least 5 s and when playmates ceased exhibiting playful patterns for at least 10 s the session was coded as concluded (Palagi and Mancini 2011; Mancini et al. 2013a; Bresciani et al. 2022). For each play session, we coded the playmates' identity (ID, sex, age category) and the exact sequence of the behavioural patterns and PFs (Table S2 for definitions). Here, we only consider dyadic play sessions (e.g., play sessions involving two subjects).

Operational definitions

Rapid facial mimicry (RFM)

To assess the receiver's possibility to detect playmate PF, we considered the orientation of the head of the two agents (Demuru et al. 2015; Scopa and Palagi 2016). We considered the PF as detected when triggers and receivers were in direct visual contact within the range of their stereoscopic view, see Fig. 1a (Gallo et al. 2022). All instances of uncertainty (e.g., lateral views) were discarded for parsimony. When PFs were detected and replicated within one second (starting from detection and ending with the PF emitted by the receiver, Palagi et al. 2020), we coded such event as RFM (Fig. 1b). To ensure a reliable evaluation that the observer's PF was genuinely prompted by the trigger's PF, we focused solely on interactions where the observer gazed at the trigger's face and exhibited no facial expressions in the 1-s period leading up to the trigger's stimulus. Each play session

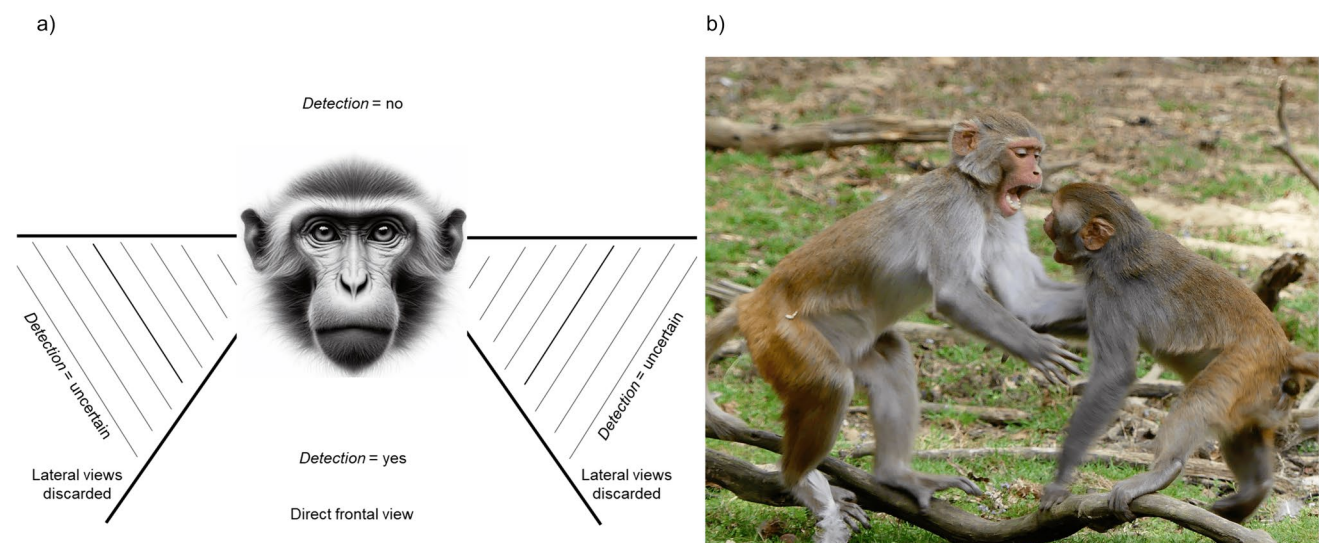


Fig. 1 Illustration depicting potential visual scenarios during the production of play faces (PFs). **a)** In our analyses, a PF was categorized as detected only when subjects were in the condition of direct visual contact. Cases of uncertainty (e.g., lateral view) were excluded from

the analyses. **b)** Picture depicting two young rhesus macaques showing Rapid Facial Mimicry during play fighting. Photo credits Elisabetta Palagi

was categorized as: i) without PFs, ii) with PFs emitted but not replicated (absence of RFM), iii) with at least one RFM event. For each play session, we counted the number of PFs and RFM events. We calculated the *Proportion of RFM* for each play session as follows: (PFs produced by A and replicated by B / PFs produced by A and detected by B) + (PFs produced by B and replicated by A / PFs produced by B and detected by A).

Play bond strength

We calculated for all the dyads of players the index *Play bond strength* as the ratio between the time two macaques spent playing together (sec) on the total time they were observed together (sec, obtained from 5-min scan sampling). The index gives a proxy for the likelihood of two subjects to play together when they are in proximity by, providing us with a measure of “social bonding” based on social play, a behaviour more frequent and possibly suitable for immatures compared to grooming (Palagi 2023).

Type of PF receiver

For each PF displayed during a play session, we recorded the identity of all potential receivers both involved (*player*) or not involved in the play session (*bystander*). The *bystander* was an individual observing the play session at no more than 4-macaque-body length apart from the playing dyad. For both types of receivers, we coded the exact time of detection, response and, in this last case, the latency (time difference between the first frame when the receiver’s lips part and the first frame from the detection of the previous PF).

Latency to re-start playing

Independently from the definition of “play session” (see above), for all the pauses longer than 3 s occurring during a playful interaction, we indicated whether the break was due to internal (*int*) or external (*ext*) factors. We used a minimum of 3 s empirically considering this as a reasonable time window required for an individual to stop all play patterns and movements and divert attention from the activity, the same criterion has been used by Heesen et al. (2021) in

their study on great apes. The *int* factors refer to the motivation originating within the dyad itself, without apparent influence from the environment or individuals external to the dyad. The *ext* factors could be nearby aggression, loud noises, feeding times, or the intervention of a third party. External interventions could result in different outcomes: joining the interaction (*j*), replacing one player (*r*), or ending the play session (*e*). In each of these cases, we specified the names of the subjects involved. All cases coded as *j*, *r*, *e* were excluded from the analyses to only account for breaks caused by internal factors. We coded all the play resumptions occurred between the two initial subjects; these had to continuously remain visible during the break and must not have interacted with other group members. Moreover, instances of overt play invitations (e.g., peek-a-boo, object throwing) were discarded from the analysis. We also noted the latencies (sec) to restart playing (the latencies observed ranged from 3 to 150 s). As our analyses focus on the latency to re-start playing, all cases without apparent resumption such as those due to the video ending or to animals getting far from the observers were not object of the study.

Play asymmetry index

To assess the level of balance of each play session, we adopted the commonly used Play Asymmetry Index (PAI, Gallo et al. 2022) calculated as follows: we added the number of advantageous patterns directed by A towards B to the number of disadvantageous patterns performed by B towards A. We then subtracted the number of advantageous patterns directed by B toward A from the number of disadvantageous patterns performed by A toward B. This was divided by the total number of playful patterns observed during the session. All those patterns not included in the previous categorization were coded as neutral. We considered as advantageous those play patterns helping the player to get “the upper hand” in the interaction (e.g., biting the playmate), whereas disadvantageous patterns are those putting the player in a less favourable or weaker position with respect to the playmate (e.g., laying on the back). The PAI ranges from -1 (indicating a perfect skew towards player B) to +1 (indicating a perfect skew towards player A), with a value of zero denoting a completely symmetrical session. See Table S2 for the classification of the playful patterns used.

$$PAI = \frac{(advantageous_{A \rightarrow B} + disadvantageous_{B \rightarrow A}) - (advantageous_{B \rightarrow A} + disadvantageous_{A \rightarrow B})}{(advantageous_{A \rightarrow B} + disadvantageous_{B \rightarrow A}) - (advantageous_{B \rightarrow A} + disadvantageous_{A \rightarrow B}) + neutral_{A+B}}$$

Dominance hierarchy

The individual dominance rank was determined using the Average Dominance Index (ADI, Saccà et al. 2022). The ADI, ranging from 0 to 1, serves as a suitable metric for

assessing hierarchies within large groups, especially when numerous dyads may lack direct interactions (Saccà et al. 2022). For all agonistic encounters, we recorded the identities of both the victim and aggressor of agonistic encounters,

along with the behavioural patterns and the timing of each interaction (e.g., avoidance, bite, chase, open mouth bared teeth, presenting, run after, threat, Thierry et al. 2000; Partan 2002, all behaviours used listed in Table S2b). All instances with unclear winner/loser roles (e.g., retaliation or counterattack, absence of flee behaviour or submission by the victim) or uncertain valence were excluded from the matrix analysis.

Inter-observer agreement

As our study involved focal animals in the field, it was not possible to record data blind. Nevertheless, interobserver reliability for behaviour coding was assessed on about 15% of the videos independently coded by GF and SA using Cohen's Kappa coefficient (Cohen 1968), which was always higher than 0.80 (subject identification, $k=0.94$; playful patterns $K_{\min}=0.82$, $K_{\max}=0.87$; PFs, detection, RFM $K_{\min}=0.81$, $K_{\max}=0.91$; agonistic patterns and winner/loser roles: $k_{\min}=0.87$, $k_{\max}=0.96$).

Statistical analyses

Distribution of social play To investigate the distribution of social play according to age (Juvenile vs Subadult vs Adult) and sex (Female vs Male), we ran a Generalized Linear Mixed Model (GLMM, R package: glmmTMB) with the total time spent by each animal in play fighting (seconds) as response variable (each subject as an observation in the model) and *Age*Sex* as fixed factors. As $n=49$ subjects never engaged in play we used a model for zero-inflated data (allowing the number of extra zeros to depend on *Age*Sex*). We modelled the data using the negative binomial distribution (Brooks et al. 2017), after checking the overdispersion of the response variable and the non-normality of its distribution through Shapiro–Wilk tests (Ghasemi and Zahediasl 2012) and visual inspection (e.g., histograms). Since our response variable was over dispersed, we modelled the data using a negative binomial distribution, adapting a distribution generally used in more ecological studies for count data on time spent in social play (seconds, considered here as count). Models using negative binomial distribution are better suited when dealing with overdispersion and using such distribution can indeed be a solution for overdispersion (Brooks et al. 2017). Importantly, to check for biases due to differences in individual recording time, we included in the model the total time (minutes) of observation for each animal as *offset*.

RFM (Prediction 1, 4, 5) To understand which factors affected the likelihood of responding to a PF with a congruent PF within 1 s, we ran a GLMM with RFM as response variable (presence/absence, binomial error distribution). The interaction between *Trigger* and *Receiver* subjects as well as the *Progressive number of sessions* were included as random

factors to cope with pseudo-replication issues. The fixed factors considered were: i) *Detection* (Yes/No), ii) *Play bond strength*, iii) *Age combination* (juvenile-juvenile/juvenile-subadult/subadult-subadult), iv) *Sex combination* (male-male/male-female/female-female), v) The difference in ADI between the trigger and the receiver (*diffADI_{t-r}*) and the vi) *Type of receiver* (player/bystander) of the PF.

Play session length (Prediction 2) To understand which factors affected the duration of the play sessions, we ran a Linear Mixed Model (LMM, glmmTMB 1.2.5042) with *Play session length* (seconds, log-transformed to apply Gaussian distribution) as response variable. The interaction *Player A * Player B* was included as random factor. The fixed factors considered were: i) the absolute value of the Play Asymmetry Index (*lPAI*), ii) presence of RFM during the play session (*Presence of RFM*: No PFs displayed by players / PFs displayed by players but no RFM / presence of at least one RFM), iii) the *Age combination* (j-j/j-s/s-s) of the dyad, iv) the *Sex combination* (m-m/m-f/f-f) of the dyad, and v) the absolute value of the difference of the two subjects' ADIs (*ldiffADI*). We also included the number PFs produced/session duration (*Frequency of PFs*), and the total number of patterns used in the play session (*Number of patterns*) as control factors.

To understand whether not just the presence but also the frequency of RFM events could influence the duration of the play session, we tested which factors affected the duration of play sessions with at least one mimicry event. We ran a LMM with *Play session length* (seconds, log-transformed) as response variable. The interaction between *Player A* and *Player B* was included as random factor. The fixed factors considered were: i) the absolute value of the Play Asymmetry Index (*lPAI*), ii) the RFM events during the session (*Proportion of RFM*), iii) the *Age combination* (j-j/j-s/s-s) of the dyad, iv) the *Sex combination* (m-m/m-f/f-f) of the dyad, and v) the absolute value of the difference of the two subjects' ADIs (*ldiffADI*). Again, we included the number PFs produced/session duration (*Frequency of PFs*), and the total number of patterns used in the play session (*Number of patterns*) as control factors.

Role of RFM in resuming play fighting after breaks (Prediction 3)—To understand the possible role of RFM on shortening play breaks, we ran a GLMM with *Latency to re-start playing* (seconds, negative binomial distribution) as response variable. We chose this distribution as the variable did not fulfil the assumptions of either Gaussian or Poisson distributions (e.g., normality, no overdispersion, Brooks et al. 2017). As reported above (see *Distribution of social play*) also the variable *Latency to re-start playing* was over dispersed, thus we modelled the data using a negative binomial distribution, adapting a distribution generally used in

ecological studies for count data on the latency to restart playing (seconds, considered here as count). The interaction between *Player A* and *Player B* was included as random factor. The fixed factors considered in were: i) the *Presence of RFM before the interruption* (yes/no), ii) *Play bond strength*, iii) *Age combination* (j-j/j-s/s-s), and iv) *Sex combination* (m-m/m-f/f-f) of the dyad, and iv) the absolute value of the difference of the two subjects' ADIs (*diffADI*). Moreover, we included in the model the duration (seconds) of the play bout preceding the break (*Length of play before break*) as control factor.

All the analyses were carried out using RStudio (<http://www.r-project.org>). Multicollinearity in the GLMMs was assessed by employing the *check_collinearity* function (package *performance* 0.4.4) through Variance Inflation Factors (VIFs). *Low correlation* was found for all the fixed factors included in the models (VIF: 1.01–1.96). The significance of the models was evaluated by comparing the full model against a null model consisting only of random effects using the Likelihood Ratio Test (LRT) with the *Chisq* test argument (Dobson and Barnett 2018). To determine the predictors p-value, LRTs were conducted between the full model and a model lacking that specific predictor, using *Anova* function (Barr 2013). To assess model fit and potential overdispersion issues, we used version 0.3.3.0 of *DHARMA* package (Hartig 2020) (nonparametric dispersion test, dispersion range: 0.165–0.198, p-value range: $p = 0.99$ –1). To calculate marginal and residual R^2 values, we used the *MuMIn* package version 1.43.17 (Bartoń 2020). Marginal R^2 quantifies the proportion of variance in the response variable explained by the fixed factors alone, while residual R^2 captures the portion explained by both fixed and random factors (Nakagawa and Schielzeth al. 2013). In models using binomial distribution, relative odds ratios were used to illustrate the impact of estimated effects, using the *confint()* function, where odds ratios (OR) represent the expected change in odds when all variables are held at reference values, and the fixed factor increases by one unit or change categorical level. For pairwise comparisons with factors with more than two levels, we used the package *emmeans* to perform the Tukey test (Bretz et al. 2016; Lenth 2021).

Results

Distribution of social play 72 out of 122 macaques of the group engaged in social play fighting, with an average frequency of 1.16 min/hour (SD: 1.71 min/hour) (Table S1 for full data and Fig. S1 for graphical representation of play frequencies in relation to age and sex classes). The full model investigating the time spent in social play significantly differed from the null one only including the *offset* ($X^2_7 = 180.73$, $p < 0.0001$, full outputs of conditional and zero-inflated models in File S1). Males spent more time in play fighting than females ($X^2 = 33.70$,

$p < 0.0001$), and juveniles and subadults both spent more time in play than adults ($X^2 = 69.56$, $p < 0.0001$, Tukey test results: $df = 113$, juvenile vs adult: t-ratio = -7.84, $p < 0.0001$; sub-adult vs adult: t-ratio = -7.43, $p < 0.0001$; subadult vs juvenile: t-ratio = 0.810, $p = 0.698$). Actually, as adult-adult play fighting was never observed and adults hardly ever engaged in play with non-adult animals (Fig. S1b, Table S1), we focused the analyses on non-adult macaques ($n = 63$).

RFM (Prediction 1a, 1b, 1c, 3) The full model investigating the factors affecting the likelihood of RFM significantly differed from the null one ($X^2_8 = 588.13$, $p < 0.0001$, marginal $R^2 = 0.64$, R^2 conditional $R^2 = 0.68$). The variables *Detection*, *Age combination*, *diffADI_{t,r}*, and *Type of receiver* had a significant effect on RFM. Specifically, the likelihood of RFM was more than six times higher (odds ratio = 6.17) after detecting than after not detecting a PF ($X^2 = 82.32$, $p < 0.0001$, Fig. 2a, Table 1). Moreover, the likelihood of RFM was highest when the playmates were both subadults compared to mixed-age dyads ($X^2 = 15.75$, $p < 0.001$, Tukey test results: $df = 1291$, s-s vs j-s: t-ratio = -3.82 $p = 0.0004$, j-j vs j-s: t-ratio = 2.022, $p = 0.107$; s-s vs j-j: t-ratio = -0.772, $p = 0.72$; Fig. 2b, Table 1). Importantly, the more dominant the trigger subject compared to the receiver, the higher the probability of mirroring trigger play faces ($X^2 = 6.11$, $p = 0.013$, Fig. 2c, Table 1). Finally, RFM was much more frequent when the receiver was one of the players rather than a *bystander* ($X^2 = 73.71$, $p < 0.0001$, odds ratio = 224.14, Fig. 2d, Table 1). It must be noted that we never recorded a congruent facial expression in bystanders after detecting others' PFs. *Play bond strength* and *Sex combination* did not affect the likelihood of RFM (Table 1).

Play session length (Prediction 2a) The full model investigating the factors affecting the length of social play sessions ($n = 587$, bouts lasting < 5 s discarded) significantly differed from the control one ($X^2_7 = 129.44$, $p < 0.0001$, marginal $R^2 = 0.59$, conditional $R^2 = 0.62$). The variables, *lPAI*, *Age combination*, and *Presence of RFM* had a significant effect on the length of playful interactions. The longer the *lPAI*, the longer the play session ($X^2 = 5.33$, $p = 0.021$, Fig. 3a); mixed-sex dyads of players had on average longer sessions compared to subadult-subadult dyads ($X^2 = 7.16$, $p = 0.028$, Tukey test: $df = 573$, j-s vs s-s: t-ratio = 2.570, $p = 0.028$; j-j vs j-s: t-ratio = -1.160, $p = 0.478$; j-j vs s-s: t-ratio = 0.912, $p = 0.633$; Fig. 3b). The presence of at least one event of RFM prolonged the play session ($X^2 = 109.92$, $p < 0.0001$, Tukey test: $df = 573$, No play faces vs Play faces but no RFM: t-ratio = -4.162, $p = 0.0001$; No play faces vs RFM: t-ratio = -10.157, $p < 0.0001$; Play faces but no RFM vs RFM: t-ratio = -6.853, $p < 0.0001$, Fig. 3c). The *diffADI* and *Sex combination* did not affect the likelihood of RFM (Table 2a).

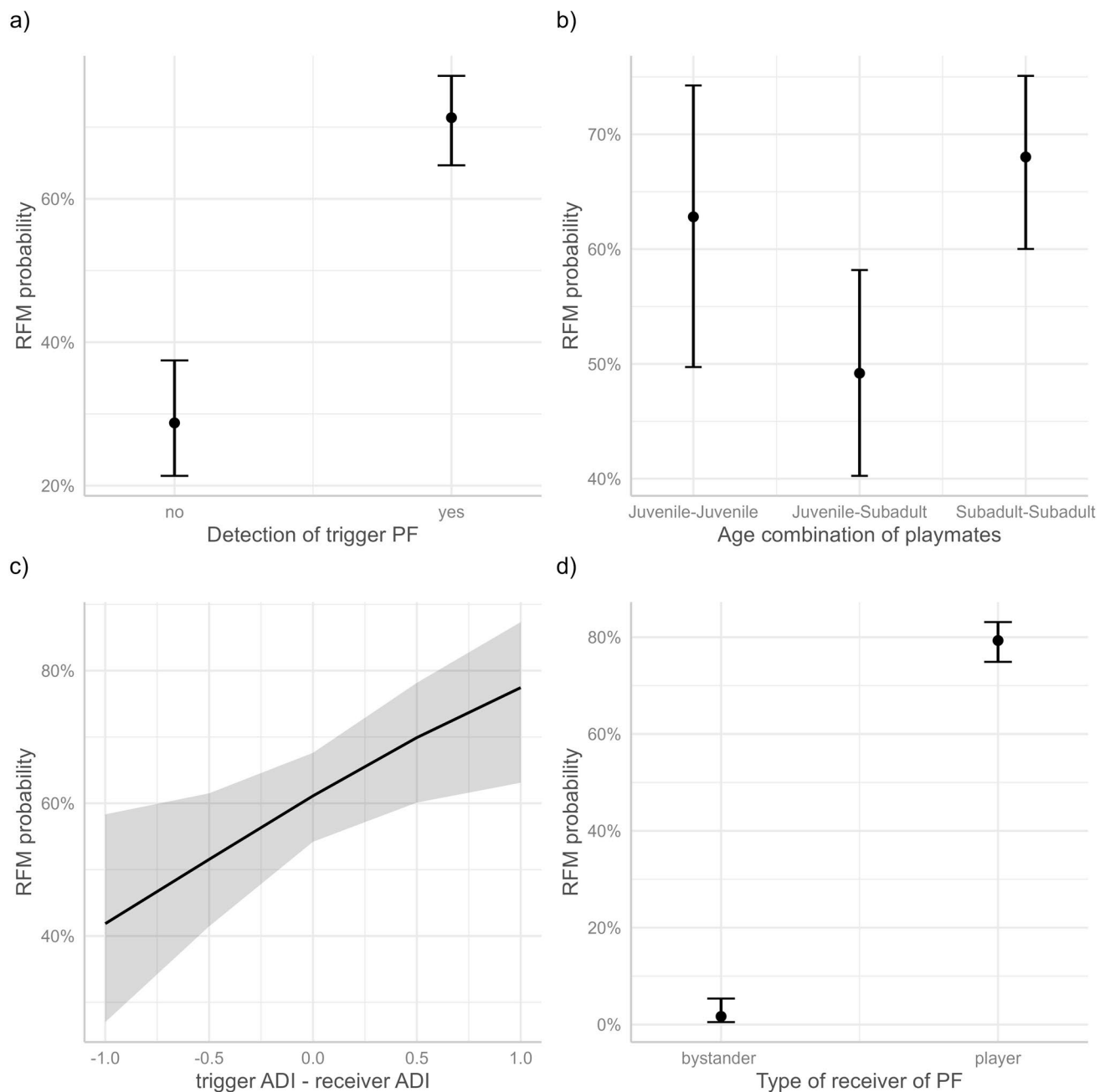


Fig. 2 Effect plot showing the significant effect of **a)** the *Detection* of trigger PF on the probability of RFM, **b)** the *Age combination* of playmates, **c)** the difference in ADI between the trigger and receiver of the play face, and of **d)** the *Type of receiver* of PF on the RFM

probability. Error bars and shaded areas represent confidence intervals. PF=play face; RFM=Rapid Facial Mimicry; ADI=Average Dominance Index

Focussing on sessions with at least one RFM event ($n = 336$), the full model significantly differed from the control one ($X^2_6 = 30.93$, $p < 0.0001$, marginal $R^2 = 0.72 = \text{conditional } R^2$). The variables *Frequency of RFM*, *Sex combination* and *Age combination* had a significant effect on the length of playful interactions. We found that the higher the *Frequency of RFM*, the longer the play session ($X^2 = 19.36$, $p < 0.0001$, Fig. 3d, Table 2).

Male-male players had longer play sessions compared to mixed-sex dyads ($X^2 = 6.26$, $p = 0.044$; Tukey test: $df = 323$, m-f vs m-m: t-ratio = -2.50, $p = 0.035$; f-f vs m-f: t-ratio = 0.987, $p = 0.58$; f-f vs m-m: t-ratio = -0.458, $p = 0.891$, Table 2) and mixed-age dyads played for longer compared to dyads composed by subadult playmates ($X^2 = 6.26$, $p = 0.013$; Tukey test: $df = 323$, j-j vs j-s: t-ratio = -1.123, $p = 0.501$; j-j vs s-s: t-ratio = -1.062;

Table 1 Estimated parameters (Coeff), Standard Error (SE), and results of the likelihood ratio tests (χ^2) of the Generalized Linear Mixed Model (binomial error distribution) with Rapid facial Mimicry (RFM) as response variable. The *Interaction between Trigger* (59 subjects) and *Receiver* (59 receivers) and the *Progressive number of sessions* (477 different play sessions) were included as random factors. From the total observations ($n = 1801$ dyads of trigger-receiver of play faces) we excluded all cases with uncertain detection and/or response as well as cases involving adult subjects, due to the very small sample size (64/1801 cases). This led us to a total of $n = 1303$ observations. Significant values are in bold. diffADI_{t-r} = difference in Average Dominance Index between trigger and receiver

Fixed Effects	Coeff	SE	χ^2	df	P
Rapid Facial Mimicry (Prediction 1a, 1b, 1c; Prediction 3; Prediction 4)					
Intercept	-5.222	0.811	-	-	-
Tested variables					
diffADI_{t-r}	0.781	0.316	6.112	1	0.013
Age combination ^a			15.757	2	0.000
Age combination (js)	-0.557	0.275			
Age combination (ss)	0.275	0.299			
Detection (Yes) ^a	1.818	0.200	82.316	1	0.000
Play bond strength	1.323	1.327	0.996	1	0.318
Sex combination ^a			0.260	2	0.878
Sex combination (mf)	-0.111	0.608			
Sex combination (mm)	-0.237	0.544			
Type of receiver (player) ^a	5.412	0.630	73.712	1	0.000

$N_{\text{observations}} = 1303$, $N_{\text{trigger}} = 59$, $N_{\text{receiver}} = 59$, $N_{\text{session}} = 477$. Random factors: Trigger, Variance=0.024, SD=0.154; Receiver, Variance=0.077, SD=0.277; Number of session, Variance=0.364, SD=0.603

^aThese predictors were dummy coded, with “Age combination (jj)”, “Detection (No)”, “Sex combination (ff)”, “Type of player (bystander)” being the reference categories

$p = 0.539$; j-s vs s-s: t-ratio = -2.50, $p = 0.0095$, Table 2). The $|\text{diffADI}|$ and $|PAI|$ did not affect the duration of the play session (Table 2b).

Role of RFM in resuming play fighting after breaks (Prediction 2b) The full model significantly differed from the null model ($X^2_7 = 123.44$, $p < 0.0001$, marginal $R^2 = 0.33$, conditional $R^2 = 0.45$). The variables *Sex combination* and *Presence of RFM before* had a significant effect on the latency to re-start playing. Specifically, if before the break at least one RFM event occurred, the latency to re-start playing was significantly shorter ($X^2 = 111.027$, $p < 0.0001$, Fig. 4, Table 2). The shortest latencies occurred between male-male players ($X^2 = 10.52$, $p = 0.0052$; Tukey test, $df = 356$, f-f vs m-f: t-ratio = -2.124, $p = 0.087$; f-f vs m-m: t-ratio = 0.685, $p = 0.772$; m-f vs m-m: t-ratio = 3.169, $p = 0.0047$, Table 2). The $|\text{diffADI}|$, *Play bond strength*, and the *Age combination* did not affect the latency to re-start playing (Table 2c).

Discussion

In contrast to the existing literature on despotic-intolerant macaque species (Scopa and Palagi 2016), Rapid Facial Mimicry (RFM) was present during social play in our group of rhesus macaques, supporting *Prediction 1a*. Mimicry was more likely directed from subordinate towards more dominant subjects (*Prediction 1b* supported, *Prediction 1c* not supported) and when both playmates were subadults (*Prediction 3* supported). Interestingly, as found in the case of tolerant Tonkean macaque, the presence and frequency of RFM events prolonged the playful sessions (*Prediction 2a* supported). Notably, we also found that RFM had an effect on shortening play breaks, possibly renewing the motivation of the two agents to play and signalling arousal (*Prediction 2b* supported, Fig. 3b). RFM was basically absent in bystanders who were not directly involved in the playful interaction (*Prediction 4* not supported). Table 3 summarizes all the outcomes.

Living in a despotic group implies high risks of aggressive escalation in contexts characterized by a high level of competition and emotional arousal such as play fighting (Palagi et al. 2016). This aspect, first and foremost, and the subsequent need to downgrade such risk, may explain the presence of RFM in our group, observed for the first time in the species and, more generally, in a despotic macaque.

The PF conveys a positive message and mirroring such facial expression can inform the sender about the proper perception and de-codification of the signal, limiting uncertainty possibly caused by incongruent or absent responses to one’s play face (Kavanagh and Winkielman 2016; Prochazkova and Kret 2017; Bresciani et al. 2022). Importantly, this function is highlighted by the hierarchical modulation of the phenomenon found here; as interactions with higher-ranking playmates are more uncertain and possibly riskier, mimicking their playful facial expression may clarify the receiver intentions and increase coordination with socially relevant groupmates (Roth et al. 2021). In this way, RFM facilitates communication and helps limit misunderstanding (Scopa and Palagi 2016). Thus, the presence of RFM in a despotic species is in line with the role and function of the phenomenon in easing mood synchronization and promoting behavioural coordination with the counterpart (Palagi et al. 2020).

This finding is only apparently in contrast with previous evidence indicating the absence of RFM in another despotic-intolerant macaque species, *M. fuscata* (Scopa and Palagi 2016). Probably, the large number of juvenile and subadult subjects engaging in many play sessions and, consequently, facial expressions, allowed unveiling the presence of the mimicry phenomenon in our group.

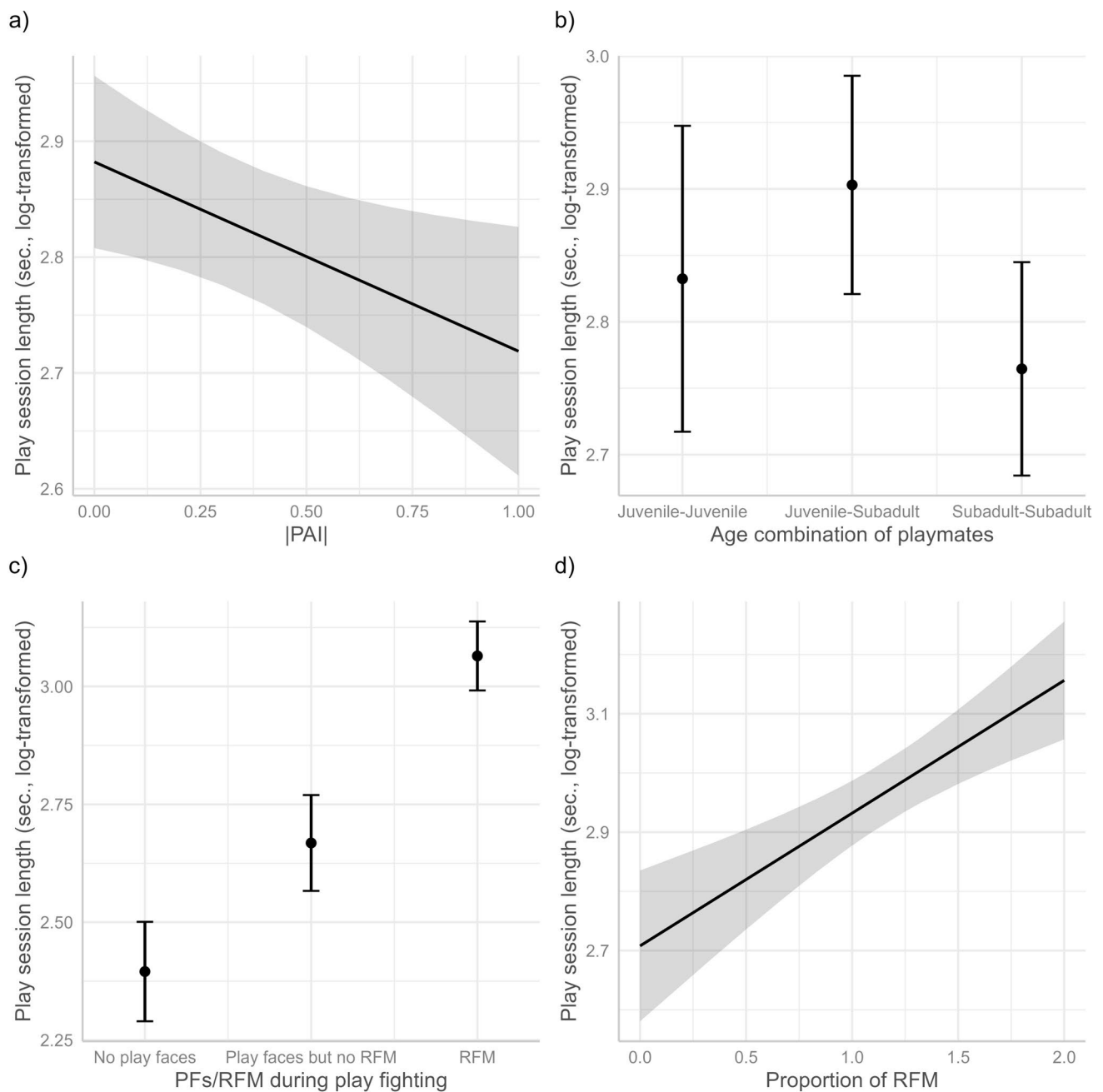


Fig. 3 Effect plot showing the significant effect of **a)** the $|PAI|$, **b)** the *Sex combination* of playmates, **c)** the presence of Rapid Facial Mimicry (*Presence of RFM*), as well as **d)** the *Proportion of RFM*

on Play session length (sec., log-transformed). Error bars and shaded areas represent confidence intervals. PAI=Play Asymmetry Index; PF=play face; RFM=Rapid Facial Mimicry

Another possible explanation resides in the fact that, in large groups, subjects can play with many different fellows thus facing more social challenges. Indeed, changing frequently the playmate requires fine and flexible communicative strategies more typical of “tolerant” groups, where social relationships are less formally established and fixed. This does not mean that our group is an exception, because our analysis of play distribution reflects that reported for

despotic-intolerant species (Liao et al. 2018; Palagi 2023) with play fighting being more widespread among immature males (Ciani et al. 2012; Kulik et al. 2015) that also played for longer possibly due to their need to acquire sex-specific competences.

Our findings also show that the more similar the age of the playmates (proxy of size), the higher the probability of RFM, particularly for subadults playing together compared

Table 2 Estimated parameters (Coeff), Standard Error (SE), and results of the likelihood ratio tests (χ^2) of the Generalized Linear Mixed Models. For **a**) and **b**), among all play bouts coded ($n = 884$), we considered only play sessions lasting more than 5 s, then we excluded the cases where it was not possible to calculate the PAI ($n = 222$), the few sessions where adults were included ($n = 26$), and those play sessions where PFs were produced but never perceived ($n = 28$). This led us with a total of 587 observations for **a**) and 336 (play sessions with at least one RFM event) for **b**). Significant values are in bold. diffADI_{t-r} = difference in Average Dominance Index between trigger and receiver; PAI = Play Asymmetry Index; PF = play face; RFM = Rapid Facial Mimicry

Fixed Effects	Coeff	SE	χ^2	df	P
a) Play session length (Prediction 2a supported)					
Intercept	2.283	0.096	-	-	-
Tested variables					
ldiffADII	0.043	0.506	0.1367	1	0.711
Age combination ^a	-	-	7.159	1	0.028
Age combination (js)	0.071	0.061	-	-	-
Age combination (ss)	-0.068	0.074	-	-	-
IPAI	-0.163	0.071	5.332	1	0.021
Presence of RFM ^a	-	-	109.921	2	0.000
Presence of RFM (PF but no RFM)	0.273	0.065	-	-	-
Presence of RFM (RFM)	0.669	0.066	-	-	-
Sex combination ^a	-	-	4.954	2	0.084
Sex combination (mf)	-0.081	0.092	-	-	-
Sex combination (mm)	0.071	0.094	-	-	-
Control variables					
Number of patterns	0.074	0.004	366.682	1	0.000
Frequency of PFs	-2.138	0.143	222.839	1	0.000
b) Play session length (Prediction 2a supported)					
Intercept	2.720	0.157	-	-	-
Tested variables					
ldiffADII	0.005	0.127	0.002	1	0.965
IPAI	-0.020	0.090	0.048	1	0.826
Proportion of RFM	0.224	0.051	19.361	1	0.000
Age combination ^a	-	-	8.704	2	0.013
Age combination (sj)	0.082	0.073	-	-	-
Age combination (ss)	-0.079	0.074	-	-	-
Sex combination ^a	-	-	8.704	1	0.013
Sex combination (mf)	-0.160	0.162	-	-	-
Sex combination (mm)	0.067	0.147	-	-	-
Control variables					
Number of patterns	0.0706	0.004	296.309	2	0.000
Frequency of PFs	-2.241	0.138	262.258	1	0.000
c) Latency to restart playing (Prediction 2b supported)					
Fixed Effects					
Intercept	2.847	0.185	-	-	-
Tested variables					
ldiffADII	-0.136	0.257	0.278	1	0.598
Presence of RFM ^a (presence)	-0.892	0.085	111.027	1	0.000
Play bond strength	0.843	0.720	1.372	1	0.241
Age combination ^a	-	-	0.799	2	0.671
Age combination (sj)	0.110	0.130	-	-	-
Age combination (ss)	0.124	0.158	-	-	-
Sex combination ^a	-	-	10.523	2	0.005
Sex combination (mf)	0.440	0.207	-	-	-
Sex combination (mm)	-0.137	0.200	-	-	-
Control variable					
Length of play before break	0.004	0.003	1.4267	1	0.232301 0.232

$N_{\text{observations}} = 587$, $N_{\text{playerA}} = 56$, $N_{\text{playerB}} = 57$. Random factors: Player A, Variance = 0.005, SD = 0.075, Player B Variance = 0.013, SD = 0.114; Player 2, Variance = $5.36 \cdot 10^{-2}$, SD = 0.231

$N_{\text{observations}} = 336$, $N_{\text{playerA}} = 48$, $N_{\text{playerB}} = 46$. Random factors: Player A, Variance = $3.841 \cdot 10^{-10}$, SD = 0.00002; Player B, Variance = 0.0059, SD = 0.076

$N_{\text{observations}} = 368$, $N_{\text{playerA}} = 50$, $N_{\text{playerB}} = 57$. Random factors: Player A, Variance = 0.018, SD = 0.135; Player 2, Variance = 0.072, SD = 0.268

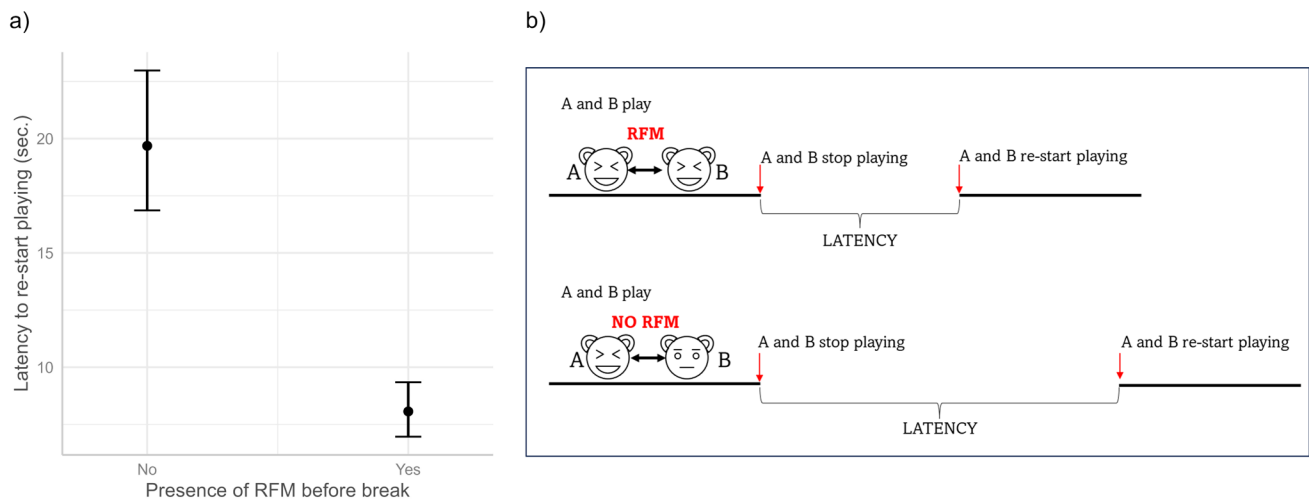


Fig. 4 a) Effect plot showing the significant effect of the *Presence of RFM before break* on the Latency to re-start playing (sec.). b) Schematic representation of different break-resumption events during a playful interaction, representing different latencies to re-start playing

in the presence or absence of RFM in the play bout before the break. Error bars represent confidence intervals. RFM = Rapid Facial Mimicry

to dyads of subadult-juvenile macaques. During play fighting, self-handicapping and self-restraining are less enacted when the two players are matched in size (Pereira and Preisser 1998; Power 2000; Burghardt 2005). Generally, macaques prefer to play with groupmates similar in physical abilities (Iki and Kutsukake 2023). If, on one hand, this makes the session more rewarding (Glick et al. 1986; Kuczaj and Horback 2013), on the other hand, this allows playmates to be less self-restrained thus increasing arousal. High levels of arousal during play fighting, if not accompanied by proper communication modules, can increase the risk of escalation (Palagi and Pellis 2023). In such cases (e.g., here same age subadult subjects), clarifying the positive intent through mimicry of playful signals is necessary to avoid misunderstanding (Palagi et al. 2016), especially for subjects approaching adulthood in a despotic species. Here the time spent playing together did not affect the level of RFM, suggesting that this phenomenon is functional independently from the level of “play bond strength” between the playmates involved, but rather by their relative hierarchical position. The effectiveness of RFM is particularly unveiled by one of its direct outcomes that is prolonging the duration of the session; our data confirm this function and are in line with previous studies on other mammal species (*P. troglodytes*, Davila-Ross et al. 2011, *T. gelada*, Mancini et al. 2013a, *C. l. familiaris*, Palagi et al. 2015, *M. tonkeana*, Scopa and Palagi 2016, *Suricata suricatta*, Palagi et al. 2019).

When macaques played, their playful interactions were often punctuated by break-resumption intervals. The breaks preceded by play slots including at least one event of RFM were shorter when compared with those preceded by play slots lacking RFM (Fig. 4), possibly indicating a more aroused

positive state of the playmates. Here, even though cases with overt play invitations (e.g., gestures) were discarded (see Methods), we cannot exclude that more subtle invitations (e.g., gaze) were exchanged by the two playmates during the break thus leading to play resumption. Facial mimicry, implying the activation of the same motor programs in the sender and the receiver (de Waal and Preston 2017), may lead the two agents to reciprocally share their positive arousal through PF-mediated emotional contagion (Prochazkova and Kret 2017) (A sees B’s play face → A mirrors B’s play face → A and B experience the same playful mood, in a sort of “reacting to others”). Yet, another explanation that does not imply emotional sharing is possible. Seeing the partner mimicking a previous PF can increase mutual engagement (Poole and Henderson 2023) and lead to an increased motivation to continue the interaction. This can increase the arousal experienced by both players, without implying a face-mediated emotion transmission (A sees B’s play face → A mirrors B’s play face → B sees A responding → A and B experience the same playful mood, in a sort of “reacting with others”), both becoming more motivated to restart playing. Obviously, our data do not allow us to draw conclusions on whether one of the two processes is more valid than the other. In macaques, the mere perception of PFs was not sufficient to elicit a mimicry response in subjects not directly involved in the interaction thus underlining that emotional arousal stemming from participation is fundamental to trigger RFM. Therefore, simply observing other subjects expressing a PF does not seem to evoke a playful mood in the bystander. This result indicates that the “same face-same emotion” hypothesis proposed to explain the linkage between facial mimicry and emotional contagion in humans (Olszanowski et al. 2020; Palagi et al. 2020; Paul et al. 2020) may not be

Table 3 Summary of hypotheses, predictions, and outcomes of the study. RFM = Rapid Facial Mimicry; PF = play face

Hypothesis	Prediction	Outcome
Hypothesis 1 RFM increases affiliation during uncertain interactions (Poole and Henderson 2023; Roth et al. 2021) and can be important in societies with strict dominance relationships	RFM is present in <i>M. mulatta</i> (Prediction 1) RFM is stronger towards higher-ranking triggers (Prediction 1b) RFM is stronger between subjects sharing a low level of familiarity (play bond strength) (Prediction 1c)	Supported Supported Not supported
Hypothesis 2 Mimicking the partner facial expressions improves communication and increases the affective arousal of playmates (Palagi & Mancini 2011)	Sessions with RFM last longer than those without RFM (Prediction 1d) By resuming arousal, RFM helps shorten the breaks when play is punctuated by pauses (Prediction 2b)	Supported Supported
Hypothesis 3 Play is more rewarding when playmates match in physical abilities (Bresciani et al. 2022; Iki & Kutsukake 2023; Ham et al. 2024). Play can however become more competitive as animals use less self-restraining (Pereira & Preisser 1998), making communication more important	RFM is more frequent when playmates are similar in age (proxy for body size) (Prediction 3)	Supported
Hypothesis 4 Observing a PF may induce to experience the emotional state conveyed by the PF ("same face—same emotion"; Palagi et al. 2020)	PFs should evoke congruent responses also in bystanders after perceiving PFs of the players (Prediction 4)	Not supported

supported in monkeys, possibly also going in the direction of more parsimonious approaches in the study of emotions underlying facial expressions (Waller et al. 2017). Nevertheless, this does not deny that PFs reflect a positive internal state of the sender, nor that RFM could be an indicator of emotional matching between the interacting subjects. Further comparative studies on RFM should disentangle emotional substrates evoked by being engaged in play versus observing play to unveil whether motor resonance phenomena derive from the ability to react *to* others rather than *with* others.

In conclusion, our data provide valuable insights into the communicative role of RFM during social play in despotic-intolerant macaques. Overall, we highlight the need for further comparative studies on different groups of macaques with different social styles, particularly focusing on the possible flexible communicative strategies involving motor resonance phenomena.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-024-03479-y>.

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Author contributions AL, EP, LP conceptualized the study; MB provided logistic support for the data collection; GF, SA carried out the data collection; GF, SA, LP carried out video analyses; AL, EP, LP, GF conceptualized and performed statistical analyses; GF, LP, EP, AL wrote the first draft of the manuscript.

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Data availability The dataset used for the analyses is provided as supplementary material.

Declarations

Ethics approval The study only implied the recording at distance of macaques, being purely observational and conducted without any contact or manipulation of animals. Specifically, the recording of animals adheres to the guidelines proposed by the Animal Behavior Society and by the Association for the Study of Animal Behaviour (e.g., recording distance). Therefore, the ethics committee of the University of Pisa waived the need for a permit.

Conflicts of interest The authors declare no conflict of interest of any kind.

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