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Analytical sensitivity in the study of rapid facial mimicry: evidence from orangutan play

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Abstract

Rapid facial mimicry (RFM) is the rapid (<1 s), automatic replication of others' facial expressions, thought to promote emotional sharing and social coordination. Although RFM has been reported in several species, its detection in non-human animals relies on different analytical approaches whose relative sensitivity has never been directly compared. Here, we examined how methodological approaches affect RFM detection in orangutans (*Pongo pygmaeus* and *Pongo abelii*) during social play. Using the same naturalistic video dataset, we applied three established approaches that differed in their control conditions, behavioural comparisons and analytical design: (1) a detectability-based comparison of perceived versus non-perceived expressions, (2) a comparison between communicative playful facial expressions (Play Face/Full Play Face) and a morphologically similar but non-communicative action (Attempt to Bite) and (3) a comparison between display and matched neutral scenes using multiple statistical procedures. Evidence for RFM emerged only under the second approach: orangutans were significantly more likely to produce playful facial expression after perceiving a Play Face than after perceiving an Attempt to Bite. No evidence for RFM was found using detectability-based or display/neutral comparisons. These findings show that the detection of RFM in orangutans is highly sensitive to analytical design, particularly to the choice of control condition. The emergence of mimicry when communicative and non-communicative facial actions are contrasted suggests that communicative relevance is key in

eliciting RFM. Our findings therefore complement existing methodological frameworks by demonstrating that the application of multiple analytical approaches can reveal differences in analytical sensitivity and improve the interpretation of RFM across biological contexts.

Keywords
emotional contagion, facial communication, methodological comparison, non-human primates, play face, *Pongo* spp., social play.

1. Introduction

Rapid facial mimicry (RFM) is an automatic and involuntary response in which an individual replicates others' facial expression (Dimberg & Thunberg, 1998; Hess & Fisher, 2013; Palagi et al., 2020a). This phenomenon is distinct from voluntary or cognitive imitation due to its rapidity (<1 s) and the exclusive involvement of the face (Dimberg et al., 2000, 2002; Iacoboni, 2009; Nakamura & Tanaka, 2026). RFM has been extensively documented in both children (Beall et al., 2008; Jones, 2009; Isomura & Nakano, 2016) and adults (Dimberg et al., 1997, 2002; Hess & Fisher, 2013), with evidence showing that congruent facial reactions occur more frequently and quickly in response to dynamic rather than static facial expressions (Sato & Yoshikawa, 2007).

This phenomenon is not a human prerogative, as RFM of playful facial expressions has been found mostly during social play in several species of mammals (Davila-Ross & Palagi, 2022; Diana & Kret, 2025; Sandars & Clay, 2025; Wu et al., 2025) such as great apes (orangutans, *Pongo pygmaeus*, Davila-Ross et al., 2008; chimpanzees, *Pan troglodytes* and gorilla, *Gorilla gorilla gorilla*, Palagi et al., 2019a, bonobos, *Pan paniscus*, Palagi et al., 2020b; Bertini et al., 2022), Old World monkeys (rhesus macaques, *Macaca mulatta*, Facondini et al., 2024; Tonkean macaques, *Macaca tonkeana*, Scopa & Palagi, 2016; geladas, *Theropithecus gelada*, Mancini et al., 2013; Gallo et al., 2022), New World monkeys (brown-headed spider monkeys, *Ateles fusciceps fusciceps*, brown spider monkeys, *Ateles hybridus and* red-faced spider monkeys, *Ateles paniscus*, Cordoni et al., 2024), bottlenose dolphins (*Tursiops truncatus*, Maglieri et al., 2024) and several carnivore species (wolves, *Canis lupus italicus*, Maglieri et al., 2025; domestic dogs, *C. l. familiaris*, Palagi et al., 2015; meerkats, *Suricata suricatta*, Palagi et al., 2019b; sun bears, *Helarctos malayanus*, Taylor et al., 2019).

RFM likely arises from automatic perception-action coupling in motor brain areas (de Waal & Preston, 2017), supported by mirror neurons that

respond to both action and observation. In humans, seeing facial emotions activates motor regions involved in expression and empathy (di Pellegrino et al., 1992; Ferrari et al., 2003), suggesting RFM supports emotional connection (Oberman et al., 2007; Prochazkova & Kret, 2017; Liu et al., 2025; Nakamura & Tanaka, 2026). It occurs more often among friends and kin, highlighting its role in social bonding and affiliative behaviour (McIntosh, 2006; Liu et al., 2025). Even if distinguishing the mere motor mimicry of facial muscle movements and the emotional mimicry of the affective state conveyed by the expression remains challenging especially in nonhuman species (Hess & Fischer, 2022), research underscores the significance of RFM in sharing emotional states, synchronising motor actions and reinforcing social bonds (Mancini et al., 2013; Palagi et al., 2015; Scopa & Palagi, 2016). Nevertheless, alternative perspectives view RFM as a strategy to reduce risk and improve the predictability of partners' behaviour (Hale & Hamilton, 2016; Diana & Kret, 2025). This interpretation is supported by recent findings in more despotic species showing that RFM is more frequently used when play-fighting with dominant group members (Facondini et al., 2024) and in interactions involving males, where it is associated with stronger engagement (Pedruzzi et al., 2025).

Methodologically, RFM has been investigated in humans using high-speed video analysis, facial electromyography (EMG) and eye-tracking while participants observe static or dynamic emotional facial expressions (Dimberg & Thunberg, 1998; Isomura & Nakano, 2016; Murata et al., 2016; Thompson et al., 2024; Seikavandi et al., 2025). High-speed video analysis, often combined with automated facial coding systems such as the Facial Action Coding System (FACS; Ekman & Friesen, 2002), allows researchers to detect rapid facial responses occurring within a few hundred milliseconds. EMG provides fine-grained physiological evidence of facial muscle activation associated with specific emotional expressions, whereas eye-tracking reveals how visual attention to expressive faces influences the likelihood and timing of facial mimicry (Thompson et al., 2024).

In non-human animals, demonstrating RFM is challenging because invasive methods cannot be applied, as they would influence the animal's behaviour and obscure the phenomenon. Such methods would interfere with the animal's emotional system, leading to unreliable responses. For this reason, research on non-human animals has so far relied on naturalistic approaches. RFM in non-human animals has been investigated primarily

Table 1.
Resuming table showing the methods with which Rapid Mimicry in response to facial expressions has been investigated across non-human species.

Species	Reference	Perception (yes/no)	Similar display (ATB)	Display vs neutral scene
Chimpanzee	Palagi et al. (2019a); Austry et al. (2026)	Yes	N/A	Yes
Gorilla	Palagi et al. (2019a)	Yes	N/A	N/A
Bonobo	Palagi et al. (2020); Bertini et al. (2022); Francesconi et al. (2026)	Yes	N/A	N/A
Orangutan	Davila-Ross et al. (2008); Austry et al. (2026)	N/A	N/A	Yes
Tonkean and Japanese macaque	Scopa & Palagi (2016)	Yes	Yes	N/A
Rhesus macaque	Facondini et al. (2024); Pedruzzi et al. (2025)	Yes	N/A	N/A
Gelada baboon	Mancini et al. (2013); Gallo et al. (2022)	Yes	Yes	N/A
Brown, brown-headed and red-faced spider monkeys	Cordoni et al. (2024)	Yes	N/A	N/A
Wolves	Maglieri et al. (2025)	N/A	Yes	N/A
Dogs	Palagi et al. (2015)	N/A	Yes	N/A
Meerkats	Palagi et al. (2019b)	Yes	N/A	N/A
Sun bears	Taylor et al. (2019)	N/A	N/A	Yes
Dolphins	Maglieri et al. (2024)	Yes	N/A	N/A
Dog–horse	Maglieri et al. (2020)	N/A	Yes	N/A

N/A, not available.

during playful interactions (e.g., primates: Play Face/Full Play Face; carnivores: Relaxed Open Mouth, Davila-Ross & Palagi, 2022) and only recently during sexual interactions (bonobos, *Pan paniscus*, Palagi et al., 2020a; Francesconi et al., 2026). The phenomenon has been explored through three distinct analytical approaches (Table 1) applied to naturalistic video-recorded behaviours. Although all approaches focus on the replication of playful facial expressions, they differ not only in the control condition adopted, but also in the behavioural events selected for analysis, the construc-

tion of the analytical dataset and the statistical framework used to evaluate RFM (Table 1).

In orangutans and sun bears (Table 1), RFM has been investigated by comparing the likelihood of producing a playful facial expression in response to observing the display of the same expression and a neutral face (Display/Neutral Scene comparison; Davila-Ross et al., 2008; Taylor et al., 2019).

In several primates and non-primate species researchers adopted a *perceived/not perceived* design, comparing the probability of emitting a playful facial expression after observing the same display, to the probability of doing so in the absence of visual access to the playmate's expression (see Table 1 for the complete list of the species studied). In the last approach to explore RFM, researchers evaluated the probability of emitting a playful facial expression after perceiving the same expression with the probability of emitting a playful facial expression after perceiving a morphologically similar facial behaviour, which does not typically function as a communicative signal (e.g., Play Face vs Attempt to Bite; Mancini et al., 2013; Palagi et al., 2015; Scopa & Palagi, 2016; Maglieri et al., 2020, 2025). This approach isolates the communicative relevance of the expression, testing whether mimicry occurs specifically in response to socially meaningful signals. Together, these complementary methods have consistently provided evidence for RFM across a broad range of mammalian species, supporting the robustness of the phenomenon despite differences in analytical design.

Recent work has highlighted that facial mimicry in great apes may depend not only on the presence of a playful facial expression, but also on the specific facial variant and the social context in which it is expressed (Palagi et al., 2019a; Austry et al., 2026). In orangutans and chimpanzees, exact facial replications were found to occur preferentially for particular *laughface* variants, suggesting that the occurrence and expression of mimicry may vary according to the communicative characteristics of the triggering signal. These findings also indicate that evidence for facial mimicry may be influenced by the behavioural features included in the analysis and, therefore, that methodological comparisons should be interpreted within the biological and social context in which data are collected. Accordingly, comparisons among analytical approaches should be interpreted cautiously, as their relative performance may vary across study populations, species and observational contexts. This raises the question of whether the currently available analytical

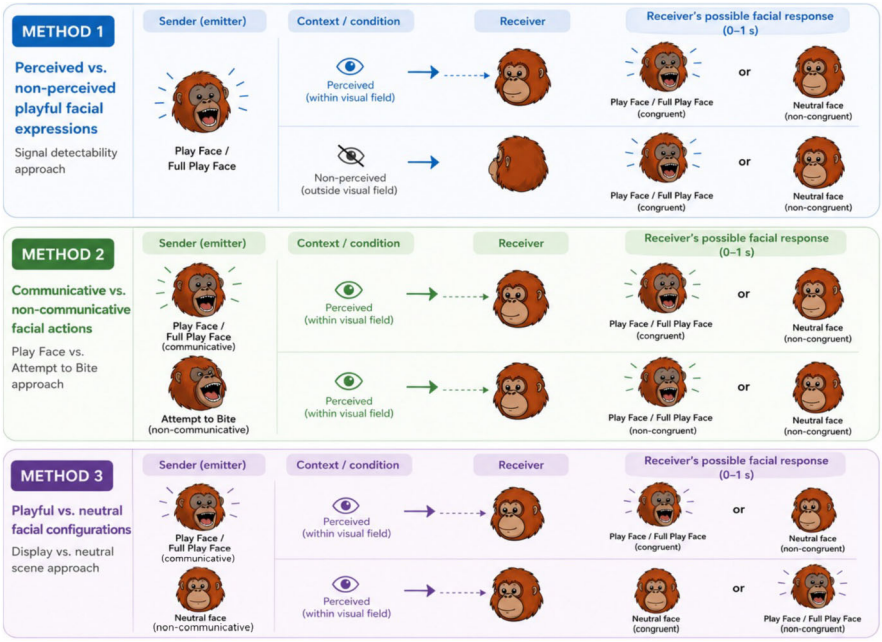

Figure 1. Schematic representation of the three methodological approaches used to investigate rapid facial mimicry (RFM) in orangutans during social play. Method 1 compares receivers' playful facial responses after perceiving versus not perceiving a partner's playful facial expression (Play Face/Full Play Face). Method 2 compares receivers' responses following the perception of a communicative playful facial expression versus a morphologically similar but non-communicative facial action (Attempt to Bite). Method 3 contrasts receivers' facial responses during playful facial display scenes and neutral facial configurations. Facial responses emitted within 1 s from the onset of the sender's facial display were considered potential cases of RFM. Stylised orangutan facial icons were generated with the assistance of OpenAI ChatGPT image-generation tools and subsequently modified by the authors.

approaches differ in their ability to detect RFM when applied to the same naturalistic dataset.

Here, we applied the complete array of methodological approaches to explore the RFM during social play in orangutans, the first non-human species in which RFM was originally described (Davila-Ross et al., 2008). By applying multiple analytical frameworks to the same dataset (Figure 1), we aimed to assess whether different methodological choices may lead to converging or diverging outcomes and to what extent the detection of RFM depends on the structure of the control condition, focusing specifically on naturalistic observational methods rather than experimental approaches (e.g.,

video stimuli paradigms). This comparative perspective allows us to assess the relative analytical sensitivity of currently available approaches and to evaluate how methodological choices influence the detection and interpretation of RFM under naturalistic conditions. Understanding differences in analytical sensitivity is crucial because approaches with different degrees of analytical sensitivity may be suited to different research objectives. More conservative approaches may be particularly appropriate for establishing the occurrence of RFM across species or study contexts, whereas more lenient approaches that are more sensitive in detecting RFM may facilitate investigations of RFM in biologically or socially challenging situations.

2. Methods

2.1. Ethic statement

The research was entirely observational and did not involve any contact with animals. As a result, the Animal Care and Use Committees of the University of Pisa and the University of Lethbridge waived the requirement for approval, although it should be noted that the research offices of the Zoos involved evaluated and endorsed the data collection.

2.2. Data collection and subjects

Observations were conducted on three different groups of captive orangutans, for a total of 22 subjects: two colonies of *Pongo pygmaeus* hosted at the ZooParc de Beauval, France (from October–December, 2015; 3 females, 3 males), at the Zoo de La Boissière du Doré, France (March 2022, 6 females, 2 males) and one colony of *Pongo abelii* housed at the Chester Zoo, Chester, UK (from July, 2010; 8 subjects). All the subjects were individually identified by distinctive features such as face shape, size, fur colour, scars or missing fur patches (Table 2).

2.3. Operational definitions and video analysis

Video analysis was carried out by two operators (VM and FF), who cross-checked 15% of the videos. Reliability is reported under each section.

2.3.1. Playful context

A social play session starts when one individual directed a playful action towards another individual that responded in a congruent way. The session began with the first playful action exchanged between the two individuals

Table 2.
Composition of the groups.

Subject	Sex	Age category	Group
Bayu	Male	Adult	Beauval
Belayan	Male	Juvenile	Beauval
Christina	Female	Adult	Beauval
Dayak	Male	Juvenile	Beauval
Janah	Female	Adult	Beauval
Manis	Female	Adult	Beauval
Saba	Unknown	Infant	Beauval
Muda	Male	Adult	Beauval
Becky	Female	Adult	Boissiere
Jane	Female	Adult	Boissiere
Jaya	Male	Adult	Boissiere
Joko	Male	Adult	Boissiere
Moni	Female	Adult	Boissiere
Taurà	Female	Infant	Boissiere
Fem1	Female	Juvenile	Chester
Fem2	Female	Adult	Chester
Fem3	Female	Adult	Chester
Inf1	Female	Infant	Chester
Inf2	Female	Infant	Chester
Male1	Male	Adult	Chester
Male2	Male	Juvenile	Chester
Male3	Male	Juvenile	Chester

and ended when play actions stopped for 10 s or more or when a third subject interfered (Davila-Ross et al., 2008; Scopa & Palagi, 2016; Facondini et al., 2024). The classification of the playful actions was made following existing play ethograms for great apes (Flack et al., 2004; Palagi et al., 2019a; Mielke & Carvalho, 2022). Playful actions included pattern such as jumps, gentle bites and ambushes (Table S1 in the Supplementary material).

2.3.2. Playful facial expressions

All occurrences of Play Faces and Full Play Faces were recorded, following established ethological criteria described in previous studies on great apes (Palagi, 2006; Parr et al., 2007; Davila-Ross et al., 2008, 2011; Waller & Cherry, 2012). Typically, during a playful facial expression, the signaller keeps the mouth open showing both the lower and upper teeth (Full Play Face) or only the lower teeth (Play Face), avoiding any actual mouth-to-body contact, even in instances where the partner's body part enters the oral range

of the emitter. This suggests a clear pattern of mouth restraint during playful facial expressions, in which the subject deliberately avoids making contact between its mouth and the partner's body (Cohen's $K = 0.94$).

In contrast, during an attempt to bite (ATB), the subject opens its mouth and quickly snaps it shut while thrusting toward the partner, actively trying to grasp or contact their body or skin. Although receivers may use evasive movements during fast-paced interactions to avoid being bitten, the biting motion consistently concludes with a rapid jaw closure directed at the target area, without reaching it (Cohen's $K = 0.87$). Actual play bites were not included because once mouth-to-body contact occurred, the behaviour was no longer morphologically comparable to a Play Face, making it unsuitable as a morphological control. We therefore restricted the analysis to attempted bites, whose initial facial configuration closely resembles that of playful facial expressions while differing in communicative function. All Attempt to Bite events included in the analyses occurred during ongoing social play sessions and therefore represent playful biting attempts rather than aggressive bites.

For each PF and FPF displayed and for each ATB, we noted: (i) the identity, (ii) sex and (iii) age of both the emitter and the receiver, (iv) the exact onset (first frame in which the lips of the emitter started to separate) and offset (first frame in which the lips of the emitter where closed again after the emission of the facial event and (v) the detectability of the facial expression (in/out the field of view of the receiver; Cohen's $K = 0.91$).

We defined as "Neutral Face" a relaxed face with the mouth closed, not corresponding to any of the facial movements reported for this species in the literature (Caeiro et al., 2013). Moreover, the individual was neither chewing nor performing any other movements involving the mandible/jaw or the opening of the mouth.

2.3.3. Detectability

No data are available on the visual field angle of orangutans. In humans, the binocular field of view is 140° (Heesy, 2004). Given that orangutans share similar morphological features and live in complex arboreal habitats, we conservatively estimated that their binocular field of view would at least around 120°. We classified as "in the field of view" all cases in which the emitter of the facial expression and the receiver were face to face. We classified as "out of the field of view" all cases in which the receiver's face was not oriented towards the emitter (i.e., turned away or with no access to the emitter's

face because their back was facing the emitter). We discarded all ambiguous cases in which the receiver was positioned to the side of the emitter, making it difficult to determine whether the expression had been perceived.

2.4. Investigating the presence of rapid facial mimicry

To investigate which factor could influence the emission of a playful facial expression in/out the field of view of the receiver we ran a Generalised Linear Mixed Model (GLMM) setting as response variable the detectability of the facial expression (in/out the receiver field of view, binomial error distribution). The fixed factors were the age (infant/juvenile/adult) and the sex of both the emitter and the playmate and the type of facial expression (PF/FPF). The identities of the players and the colony (CHESTER/BEAUVAL/BOISSIERE) were set as random factors.

To assess whether there was individual variability in the emission of facial expressions inside and outside the receiver's field of view, we performed a binomial test in R for each subject who had produced at least 10 expressions of a given type (PF or FPF).

2.4.1. Method 1$_{DETECTABILITY}$

Hypotesis: If orangutans show RFM, they should be significantly more likely to produce PFs when the signal is emitted in their field of view compared to when the signal is emitted out of their field of view (a proxy for signal detectability) (Figure 1, Table 3).

To explore the presence of RFM by applying the detectability method, we built a GLMM (glmmTMB R-package; Brooks et al., 2017; Version 1.4.1717) setting the replication of the facial expression (absence/presence) as response variable. We included as fixed factors the age class (infant/juveniles/adult) of the two players ($AGE_{PLAYER1}$ and $AGE_{PLAYER2}$), the sexes of the two players ($SEX_{PLAYER1\ and}$ $SEX_{PLAYER2}$) and the detectability of the facial expression (in/out of the receiver field of view). We included as random factors the interaction between the identity of the two players (ID_{ACTOR}*$ID_{RECEIVER}$) and the colony (Beauval/Chester/La Boissiere). Using a Likelihood Ratio Test (LRT, Dobson & Barnett, 2018), we tested the significance of the full model (Forstmeier & Schielzeth, 2011) by comparing it against a control model including the random and the fixed factors but the detectability of the facial expression.

Table 3.
Summary of the three analytical approaches used to investigate rapid facial mimicry (RFM), summarising the control condition, behavioural comparison, dataset construction, statistical approach, and the main methodological strengths and limitations of each method.

Feature	Method 1	Method 2	Method 3
Control condition	Perceived vs not perceived	Play Face vs Attempt to Bite	Display vs Neutral
Behavioural comparison	Same expression	Communicative vs Non-communicative	Communicative vs Neutral
Dataset construction	All facial events	Only detectable PF/ATB events	Matched detectable Display/Neutral scenes
Statistical approach	GLMM	GLMM	McNemar + Wilcoxon + GLMM
Main focus	Signal detectability	Communicative relevance	Display vs neutral facial state
Potential limitation	Detectability as proxy	Restricted event selection	Individual-level aggregation, matched-scene design

2.4.2. *Method 2*$_{PLAY\ FACE/ATTEMPT\ TO\ BITE}$

Hypotesis: If orangutans show RFM, they should be significantly more likely to produce PFs after perceiving a PF compared to after perceiving another facial pattern such as an ATB, a pattern similar to a PF in the motor execution (Figure 1 and Table 3).

In the method play face/attempt to bite, we built a GLMM setting as response variable play face emission (absence/presence) by the receiver within 1 s of perceiving a Play Face (PF) or an attempt to bite (ATB). We considered only those cases in which the receiver could perceive the facial display emitted. We included as fixed factors the age class (infant/juveniles/adult) of the two players ($AGE_{PLAYER1}$ and $AGE_{PLAYER2}$), the sexes of the two players ($SEX_{PLAYER1\ and}$ $SEX_{PLAYER2}$) and the type of facial display perceived (ATB or FPF/PF). We included as random factors the interaction between the identity of the two players (ID_{ACTOR}*$ID_{RECEIVER}$) and the colony (Beauval/Chester/LA Boissiere). We tested the significance of the full model by comparing it against a control model including the random factors and the fixed factors, but the type of facial display perceived. Then, the p-values for the individual predictors were calculated using the R-function Anova in the R-package car 3.0-10 (Fox & Weisberg, 2019).

2.4.3. Method 3$_{DISPLAY\ SCENE/NEUTRAL\ SCENE}$

Hypothesis: If orangutans show RFM, they should be significantly more likely to produce PFs in the Display Scene (DS) compared to the Neutral Scene (NS) (Figure 1, Table 3).

In the display/neutral scene method we built a dataset by identifying two different scenarios: the player can direct a play face (PF/FPF, DS) or a neutral face (NS) to the playmate. Both scenes could occur at any point during a play session. To ensure accurate assessment, we only considered PF/FPF emitted within the receiver field of view and where both players' faces were clearly visible to the video-coders. Both players had to show a neutral face for at least one second before the scene began. After identifying a DS, we searched for a corresponding NS for the same dyad in a different play session. The starting point for locating a NS was at least 5 s following a DS. If the playmate was not displaying a neutral scene, the search was continued linearly until a neutral scene was found. Scenes involving ambiguous facial transitions were excluded to minimise coding uncertainties.

Method 3a — DS and NS resulted in four possible scenarios: the receiver produces a PF only in DS, the receiver produces a PF only in NS, the receiver produces a PF in both scenes and the receiver never produces a PF. Then, as already done for orangutans (Davila-Ross et al., 2008) and sun bears (Taylor et al., 2019) we applied the McNemar test, placing the four possible scenarios into a 2 × 2 contingency table.

Method 3b — For each subject we calculated the number of congruent and non-congruent responses for both the DS and NS. Then, using the Exact Wilcoxon Signed Rank Test, we compared the number of congruent responses (PF → PF in the Display Scene; Neutral Face → Neutral face in the Neutral Scene) with the number of incongruent ones (PF → NF in the Display Scene; Neutral Face → PF in the Neutral Scene).

Method 3c — From the total of DS and randomly selected NS, we built a GLMM setting the occurrence of a play face (absence/presence; binomial error distribution) by the receiver within 1 s of the scene onset (DS/NS). We included as fixed factors the age class (infant/juveniles/adult) of the two players ($AGE_{PLAYER1}$ and $AGE_{PLAYER2}$), the sexes of the two players ($SEX_{PLAYER1\ and}$ $SEX_{PLAYER2}$) and the type of scene (Display/Neutral). We included as random factors the interaction between the identity of the two players (ID_{ACTOR}*$ID_{RECEIVER}$) and the colony (Beauval/Chester/La Boissiere). We tested the significance of the full model by comparing it

Table 4.
The PF and FPF emitted by each subject inside and outside the receiver's field of view and the results of the binomial test.

Subject	PF emitted in receiver the field of view	PF out	Binomial test PF	FPF in	FPF out	Binomial test FPF
Belaian	16	48	<0.001	46	82	0.001
Cristina	28	29	1.000	10	10	1.000
Diac	10	17	0.576	34	22	0.141
Manise	10	40	<0.001	11	16	0.442
Becky	3	0	N/A	1	0	N/A
Jaya	0	3	N/A	2	0	N/A
Jane	5	6	0.996	7	5	0.774
Joko	1	2	N/A	0	0	N/A
Taurà	2	10	0.038	7	9	0.804
Fem1	36	36	1.000	85	76	0.529
Fem2	0	3	N/A	1	5	N/A
Fem3	2	2	N/A	0	0	N/A
Inf1	4	1	N/A	0	0	N/A
Inf2	2	14	0.004	2	36	<0.001
Male1	1	0	N/A	0	0	N/A
Male2	5	7	0.774	17	31	0.060
Male3	3	6	N/A	26	43	0.053

A significant p-value ($p < 0.05$) indicates a higher probability of a playful expression being emitted outside the receiver's field of view than inside it.

against a control model including the random and the fixed factors but the type of scene.

3. Results

We recorded a total of 584 FPFs (from 14 subjects) and 352 PFs (from 17 subjects). Of the total facial expressions recorded, 249 FPFs (43%) and 128 PFs (36%) were emitted in the field of view of the receiver.

The model built to investigate which factor could influence the emission of a PF/FPF in or out of the field of view of the receiver did not differ from the null model including only the random factors ($\chi^2_7 = 7.372$, $P = 0.391$; $N_{cases} = 936$). Fixed factors showed no collinearity ($VIF_{min} = 1.04$; $VIF_{max} = 2.79$). Table 4 shows the individual results of the binomial test.

Table 5.
Results of the GLMM testing the effect of display type (Playful facial expression/Play bite) on the occurrence of RFM.

Fixed effect	Coeff	SE	χ^2	df	*P*
Tested variable					
Intercept	−1.930	0.562	N/A	N/A	N/A
Stimulus perceived	2.157	0.500	18.588	1	<0.001
Control variables					
$AGE_{RECEIVER}$	−0.284	0.494	0.331	1	0.565
$AGE_{EMITTER}$	0.477	0.601	0.629	1	0.428
$SEX_{RECEIVER}$	−0.711	0.536	1.759	1	0.185
$SEX_{EMITTER}$	−1.580	0.614	6.626	1	0.010

Chi-square tests refer to likelihood ratio tests. Variance for the random factors: $ID_{RECEIVER} = 7.621e^{-2} \pm 6.277e^{-6}$, $N_{RECEIVER} = 20$; $ID_{EMITTER} = 7.621e^{-2} \pm 0.276$, $N_{EMITTER} = 17$; $ID_{EMITTER:RECEIVER} = 6.334e^{-9} \pm 7.959e^{-5}$, $N_{EMITTER:RECEIVER} = 30$; $ID_{GROUP} = 4.389e^{-14} \pm 2.095e^{-7}$, $N_{GROUP} = 3$

3.1. Method 1 DETECTABILITY

The full model did not differ from the control model ($\chi^2{}_1 = 1.781$, $P = 0.182$; $N_{cases} = 309$). Fixed factors showed no collinearity ($VIF_{min} = 1.01$; $VIF_{max} = 2.60$).

3.2. Method 2 PLAY FACE/ATTEMPT TO BITE

The full model significantly differed from the control model ($\chi^2{}_1 = 26.016$, $P < 0.001$; $N_{cases} = 236$; Table 5, Figure 2). The resulting dataset included 17 emitters and 20 receivers (Table 5). Fixed factors showed no collinearity ($VIF_{min} = 1.10$; $VIF_{max} = 2.18$). The probability of a playful facial expression emission was 8.64 times higher when the receiver perceived a playful facial expression (both PF and FPF) compared to when the receiver perceived an ATB.

As further evidence, if we look at the ATB emission there were only 9 replication cases out of 206 (8 ATB → ATB out of 96, 1 Playful expression → ATB out of 110). Since the number of replication cases was so low, the model failed to converge and we decided not to proceed further.

3.3. Method 3 DISPLAY SCENE/NEUTRAL SCENE

To test for facial mimicry, we examined whether subjects were more likely to produce a PF as a response to the PF of the playmate than as a response

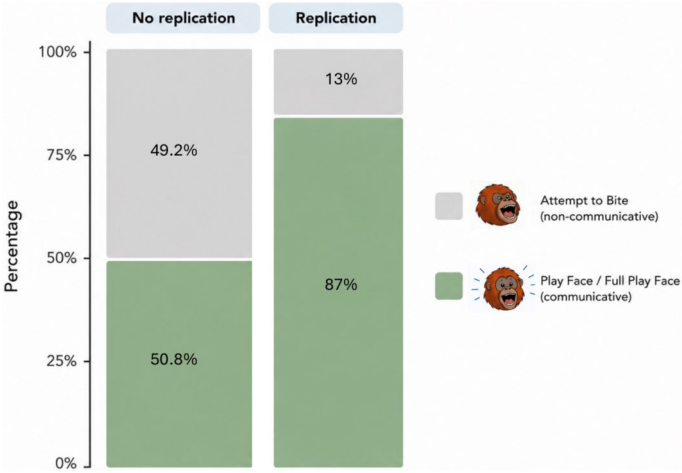

Figure 2. Plot representing the proportion of replication and no-replication responses following the perception of Play Face/Full Play Face and Attempt to Bite displays, respectively. Replication was defined as the emission of a playful facial expression by the receiver within 1 s from the onset of the sender's facial display. Stylised orangutan facial icons were generated with the assistance of AI-based illustration tools and subsequently edited by the authors.

to a neutral face. Subjects showed no significant differences between the two conditions (one-tailed McNemar test, $\chi^2 = 0.877$, $p = 0.349$).

In the Display Scene, receivers showed significantly more neutral face than playful facial expressions after perceiving a playful expression (both PF and FPF; Wilcoxon-signed ranks test: $Z = -2.879$; ties $= 1$; $N = 13$; $p = 0.004$).

In the Neutral Scene, receivers showed significantly more neutral faces than playful facial expressions after perceiving a neutral face from the playmate (Wilcoxon-signed ranks test: $Z = -3.055$; ties $= 1$; $N = 13$; $p < 0.001$).

The full model did not differ from the control model (${\chi^2}_1 = 3.565$, $P = 0.059$; $N_{\text{cases}} = 262$). Fixed factors showed no collinearity ($\text{VIF}_{\text{min}} = 1.11$; $\text{VIF}_{\text{max}} = 1.95$).

4. Discussion

By applying three complementary methodological approaches to the same dataset of orangutan play interactions, this study examined how methodological choices influence the detection and interpretation of rapid facial mimicry

(RFM). Our results show that evidence for RFM depends on the analytical approach adopted, highlighting the strengths and limitations of current methods.

The three approaches adopted in this study differed substantially in the type of control condition used. *Method 1* contrasted perceived versus non-perceived playful facial expressions, using signal detectability as a proxy for social perception (Facondini et al., 2024; Maglieri et al., 2024). *Method 2* compared responses to a communicative facial signal (Play Face/Full Play Face) with responses to a morphologically similar but non-communicative facial action (Attempt to Bite) (Scopa & Palagi, 2016; Palagi et al., 2019b; Maglieri et al., 2020, 2025; Gallo et al., 2022). Method 3 contrasted playful facial expressions with neutral facial configurations (Davila-Ross et al., 2008; Taylor et al., 2019) using three complementary statistical strategies. Among these approaches, only the comparison between playful facial expressions and attempts to bite (Method 2) yielded evidence consistent with the presence of RFM.

The fact that mimicry emerged only when a communicative signal was contrasted with a morphologically similar but non-communicative display suggests that communicative relevance may be a key factor in eliciting RFM in orangutans. Playful facial expressions are widely considered ritualised signals that convey playful intent and reduce ambiguity during rough-and-tumble interactions, which often include actions typical of agonistic contexts (Flack et al., 2004; Palagi et al., 2019). To explain how communicative signals evolve, Tinbergen (1952) proposed the theory of ritualisation, suggesting that signals originate from functional behaviours (e.g., play bite) which, over time, become increasingly stereotyped in their motor patterns to enhance their effectiveness in a new communicative role. Through ritualisation, behaviours are exaggerated, formalised and modified to capture the receiver's attention and clarify intent (Laidre & Johnstone, 2013), increasing their effectiveness as social signals (Hebets & Papaj, 2005). Within this framework, the selective replication of Play Faces, but not attempts to bite, supports the interpretation of RFM as a mechanism involved in the sharing and synchronisation of motivational states, thereby facilitating the regulation of playful interactions and reducing the risk of escalation (Hebets & Papaj, 2005).

The marked difference observed between responses to playful facial expressions and attempts to bite could not be interpreted solely as evidence

for the presence of RFM, but also in terms of the functional relevance of the receiver's response. Whereas Play Faces convey playful mood, an Attempt to Bite, even when occurring within a playful context, is likely to elicit a different motivational state in the receiver. In such situations, producing a playful facial expression may be not adaptive, as the receiver's priority is more likely to shift towards monitoring the playmate's actions, protecting vulnerable body parts, or preparing evasive or defensive movements, rather than emitting in playful facial expressions. Thus, the low probability of Play Face (PF) and Full Play Face (FPF) emission following the perception of an Attempt to Bite may reflect an inhibition of playful facial responses in favour of behavioural strategies aimed at self-protection and play regulation. From this perspective, Method 2 may be particularly effective in detecting RFM because it contrasts a facial signal that promotes affective alignment with a morphologically similar display that activates attentional or defensive responses. This functional incompatibility between the motivational states elicited by the two facial displays allows this approach to isolate mimicry that is selectively triggered by socially meaningful, affiliative signals rather than by facial movement per se. At the same time, alternative explanations cannot be excluded. For example, the stronger response observed following Play Faces may partly reflect differences in the behavioural consequences associated with the two facial actions, rather than communicative significance alone. Because the analytical approaches compared here differ simultaneously in several methodological features, future studies specifically manipulating individual components of the analytical design will be necessary to disentangle their relative contributions to RFM detection.

This result should be interpreted in light of the constraints inherent to the analytical approach that detected RFM. The comparison between playful facial expressions and attempts to bite necessarily focuses on a restricted subset of events, namely those in which the facial display occurred within the receiver's visual field and was clearly perceived. Interestingly, in our dataset, less than half of the PF and FPF expressions were emitted within the visual field of the potential receiver (42% of FPF and 36% of PF events), thus excluding a substantial portion of facial expressions from the dataset used to test this comparison. This observation may indicate that playful facial expressions often reflect the positive emotional state of the sender and may not always be intentionally produced to ensure visual perception by the play

partner (Waller et al., 2017; Camerlink et al., 2018). In other words, the emitter may not systematically adjust the display to ensure that it is perceivable by the play partner, suggesting a more spontaneous or emotionally driven expression, as previously proposed for playful facial expressions in great apes (Davila-Ross et al., 2008) and some other primate species (Pellis & Pellis, 2011; Pellis et al., 2011). This interpretation is also consistent with studies showing that orangutans flexibly modulate the production of playful facial expressions according to the social context in orangutans and chimpanzees (Waller et al., 2015; Crepaldi et al., 2024) and may display markers of intentional communication in bonobos (Demuru et al., 2015).

However, the lack of overt communicative intentionality does not preclude the occurrence of RFM. Mimicry may arise as an automatic response triggered by the receiver's perception of the facial expression, regardless of whether the sender actively aims to communicate it. This interpretation is consistent with perception–action coupling models and evidence for spontaneous facial mimicry in humans (di Pellegrino et al., 1992; Ferrari et al., 2003, 2009) and with evidence from humans indicating that spontaneous facial mimicry and emotional contagion can occur without conscious intent (McIntosh, 2006; Oberman et al., 2007). Thus, the low proportion of facial expressions occurring within the partner's visual field may explain why RFM was not detected under broader conditions, such as perceived versus non-perceived expressions (Method 1), while at the same time underscoring the importance of focusing on those interactions in which perception can be reliably assumed, as in the comparison between playful facial expressions and attempts to bite (Method 2).

In contrast, Methods 1 and 3 rely on broader comparative frameworks, contrasting perceived versus non-perceived facial expressions and playful versus neutral facial configurations, respectively. In principle, such approaches should be especially sensitive to RFM if it is strongly modulated by signal visibility or by the social relevance of the facial display. The absence of evidence for RFM in these broader comparisons therefore raises several non-mutually exclusive possibilities. RFM in orangutans may be more context-dependent or less frequent than previously assumed, or it may be characterised by substantial inter-individual or inter-group variability. Interestingly, recent experimental work found little evidence of play face mimicry in orangutans outside live social interactions, suggesting that RFM

in this species may strongly depend on the immediate interactional context and mutual engagement between play partners (Zijlstra et al., 2026). Differences in sampling structure, data collection protocols, or analytical resolution may also contribute to discrepancies with other studies, including the original demonstration of RFM in this species (Davila-Ross et al., 2008). Moreover, differences between orangutan groups themselves may also contribute to the inconsistent detection of RFM. Previous studies reporting positive evidence often involved groups differing in age composition, social exposure, housing conditions and play dynamics (Davila-Ross et al., 2008; Austry et al., 2026). Such differences may affect both the frequency and the communicative function of playful facial expressions, as well as the likelihood that these expressions are visually perceived and reciprocated during interactions.

Our findings should not be interpreted as indicating that any analytical approach is universally applicable or inherently more suitable than the others. Rather, the present comparison shows that different methods may vary in their sensitivity depending on the behavioural characteristics of the study population, the social context and the communicative function of the facial displays under investigation. For example, recent work by Austry et al. (2026) demonstrated that orangutans and chimpanzees selectively produced exact facial replications of particular playful facial expression variants, highlighting how subtle differences in facial morphology, social context and analytical design may influence the detection of facial mimicry. Therefore, the relative performance of different methodological approaches is likely to depend on both biological and methodological factors and future comparative studies across populations and species will be necessary to determine the generality of these patterns. A possible limitation of the present study is that all three approaches were evaluated using a single orangutan dataset. Although this design allowed a direct methodological comparison while holding the behavioural observations constant, the relative analytical sensitivity observed here may not generalise to other populations, species, or social contexts. Comparative applications across additional datasets will therefore be essential to determine the extent to which the present findings reflect general properties of the methods or characteristics of the study population.

Differences in analytical sensitivity should not necessarily be regarded as affecting the strengths or weaknesses of a particular approach, but rather as

reflecting different methodological trade-offs of each approach. More conservative approaches may be particularly valuable when the primary objective is to establish robust evidence for the occurrence of RFM across species or study systems. In contrast, approaches with greater analytical sensitivity may be especially useful once the phenomenon has been established, allowing researchers to investigate RFM under more challenging biological or social conditions, such as in adult individuals, less interactive groups, or species in which playful interactions are relatively infrequent. From this perspective, the three approaches should be viewed as complementary rather than competing, with each providing distinct insights into the occurrence and expression of RFM.

In the present dataset, the analytical approach adopted in Method 2 proved more sensitive for detecting RFM. However, this greater sensitivity is likely to reflect the combined influence of several methodological features, including the behavioural categories considered, the selection of response events and the analytical framework employed, rather than any single component of the method itself. In particular, approaches based on comparisons with neutral facial configurations may not fully capture the rapid, contingent dynamics of play interactions. When responses are aggregated at the individual level, moment-to-moment variability linked to interactional contingencies, partner identity, or the immediate social context may be obscured. This limitation is especially relevant for highly dynamic behaviours such as play, where facial expressions are tightly embedded within ongoing sequences of actions and mutual adjustments between partners.

Approaches based on cumulative individual-level comparisons, such as the McNemar test used in the display versus neutral scene analysis, may interact strongly with inter-group variability in play dynamics and social interaction styles. Orangutan groups can differ substantially in the structure and intensity of social play depending on factors such as age composition, social tolerance, housing conditions and partner familiarity. In some groups, play regulation may rely more strongly on facial exchanges, whereas in others alternative mechanisms such as self-handicapping, role reversals, tactile behaviours, or playful vocalisations may play a greater role in maintaining affiliative interactions and preventing escalation. Recent work on great ape laugh communication further suggests that facial replication itself may vary according to play intensity and the specific facial variants employed during play (Austry et al., 2026). Hence, methods relying on cumulative

comparisons across events may produce divergent outcomes depending on the behavioural characteristics of the groups under study and the interactional contexts sampled.

The inconsistency in detecting RFM may indicate a relatively low occurrence of the phenomenon in this species. Considering their socioecology, orangutans occupy less complex social systems relative to other primates where RFM has been consistently found and seems to have adaptive roles (e.g., other apes, Palagi et al., 2019a; macaques, Scopa & Palagi, 2016; Facondini et al., 2024; Pedruzzi et al., 2025; spider monkeys Cordoni et al., 2024; geladas, Mancini et al., 2013; Gallo et al., 2022). This reduced expression of mimicry may indicate a lower adaptive value of the behaviour in species facing fewer social challenges (e.g., less groupmates, more dominance dynamics, less differentiated relationships, Kappeler, 2019). Consistent with this interpretation, we also found no evidence for social modulation of mimicry across demographic variables (i.e., age and sex). These findings highlight the importance of carefully considering the methodological framework adopted when investigating RFM. While Method 2 yielded positive results in our study, it relies on a subset of play interactions in which the facial expression was clearly perceived by the receiver. Consequently, it does not encompass the full diversity of play interactions represented in the complete dataset. By contrast, Method 1 offers a broader comparative framework because it includes both perceived and non-perceived facial expressions, allowing the role of visual access in RFM detection to be explicitly evaluated

Our findings should not be interpreted as questioning the validity of the analytical approaches previously adopted to investigate RFM. Rather, the convergence of evidence obtained using different analytical approaches over the past two decades has substantially strengthened support for the occurrence of RFM across a wide range of non-human species. Our results instead suggest that these complementary approaches may differ in their relative analytical sensitivity depending on the biological and methodological context in which they are applied.

As a whole, we suggest that employing multiple methodological approaches within the same dataset, when feasible, may offer a more comprehensive and balanced assessment of RFM. Applying different analytical frameworks to the same interactions allows researchers not only to compare their relative analytical sensitivity, but also to disentangle methodological effects from biologically meaningful variation in social behaviour. For

example, in Maglieri et al. (2025), only Method 2 was applicable because all recorded facial expressions occurred within the receiver's visual field, rendering Method 1 inapplicable. In the present study, the divergence in outcomes across methods highlights how the detection of RFM may depend on an interaction between analytical design, sampling structure and group-specific social dynamics. Future studies across additional orangutan groups and other species would benefit from systematically comparing multiple RFM detection methods within the same datasets while also exploring hybrid analytical approaches that combine complementary features of the currently available methods. Such comparisons could help disentangle the relative contribution of individual methodological components to RFM detection, determine whether variability in outcomes reflects methodological sensitivity, genuine inter-group variation, or an interaction between the two and establish the minimum sample size required to reliably detect RFM under different analytical frameworks. Together, these advances would provide practical guidance for the design of future comparative investigations and further refine our understanding of the conditions under which RFM emerges. Integrating complementary analytical approaches may provide the most effective framework for uncovering the dynamics of RFM and clarifying the conditions under which it emerges across different biological and social contexts.

Supplementary materials

Data is available on https://doi.org/10.1163/1568539X-bja10378 under Supplementary Materials.

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Author contributions

V.M.: Conceptualisation, data collection, video coding, formal analysis, writing (original draft, review and editing). F.F.: conceptualisation, data collection, video coding, writing (review and editing). L.P.: Conceptualisation, data

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