

1 **Playful interactions and facial mimicry in infant bonobos (*Pan paniscus*)**

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3 MARTA BERTINI¹, GIULIA ANNICCHIARICO¹, CHIARA BRESCIANI¹, GIADA CORDONI¹ and

4 ELISABETTA PALAGI^{1,2,*}

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6 ¹*Natural History Museum, University of Pisa, Via Roma 79, 56011 Calci (Pisa), Italy*

7 ²*Department of Biology, Unit of Ethology, University of Pisa, Via A. Volta 6, 56126 Pisa, Italy*

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10 *Corresponding author: Elisabetta Palagi, Dipartimento di Biologia, Unità di Etologia,
11 Università di Pisa, Via A. Volta 6, 56126 Pisa, Italy (E-mail: elisabetta.palagi@unipi.it).

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13 **Highlights**

- 14 • Both Rapid and Delayed Facial Mimicry are present during infant play in bonobos
- 15 • Face-to-face interactions between infant playmates enhances mimicry response
- 16 • Mimicry phenomena do not have any effect in prolonging the play session
- 17 • Mimicry phenomena are not probably recruited for managing sessions but simply for
- 18 boosting playful mood sharing

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26 The capacity to promptly and congruently respond to others' facial signals has at its basis a
27 mirror neuron mechanism. In Rapid (< 1 sec, RFM) and Delayed (1-5 sec, DFM) Facial Mimicry
28 the expression emitted by an individual (trigger) is perceived and replicated by an observer. The
29 occurrence of mimicry phenomena has been demonstrated almost exclusively in the play domain.
30 Here, we aim at evaluating the presence of RFM/DFM during playful interactions between infant
31 bonobos (*Pan paniscus*), one of the most playful primate species. We video-recorded 435 play
32 sessions between five infants (< 48 months of age) belonging to the bonobo colony hosted at the
33 Wilhelma Zoo (Germany). Via a frame-by-frame video-analysis, we demonstrated the presence of
34 both RFM and DFM. These two phenomena were enhanced by face-to-face interactions between
35 playmates. Hence, the access to others' faces allows the player to perceive, decode and replicate
36 signals thus promoting a mutual intersubjective engagement with the partner. The occurrence of
37 DFM suggests that in bonobos, as in chimpanzees, such mirror event is present just starting from
38 infancy. The less automaticity characterizing DFM compared to RFM could be due to the
39 involvement of more complex and time-demanding cognitive processes. Neither RFM nor DFM
40 increased the duration of play sessions. Probably, the mimicry phenomena in infant bonobos are not
41 recruited for manipulating the sessions, which are highly balanced and fair, but possibly for sharing
42 the playful mood between interacting subjects thus increasing their level of familiarity and
43 affiliation.

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45 KEY WORDS: play face, face engagement, ontogenetic pathways, playful mood, symmetric
46 play, *Pan paniscus*.

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48 **Running Title:** Facial mimicry in play of infant bonobos

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INTRODUCTION

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53 Mirror Neurons (MNs) provide motor neural template through which the visual and/or
54 auditory perception of others' behaviour activates in the observer the same motor action
55 representation underpinning the execution of that behaviour (di Pellegrino et al. 1992; Gallese et al.
56 1996). As a whole, the sensory information coming from others' actions are strictly linked with
57 their internal cortical motor representation (Coudé & Ferrari 2018). Recently, Ferrari et al. (2017)
58 suggested that the MN system is composed by two different anatomical pathways connected with
59 sensorimotor transformation of reaching/grasping action and mouth/face motor control,
60 respectively. The mouth/face pathway includes the anterior cingulate and orbitofrontal cortex,
61 anterior insula, and basolateral amygdala; these brain areas are involved in the perception and
62 imitation of facial expressions (Carr et al. 2003; Singer et al. 2004) and in reward processes (Azzi et
63 al., 2012). In this view, it has been proposed that mouth/face MN network can have a role in
64 evolutionary processes that have connected emotional communication with facial expressions
65 (Ferrari et al. 2017; Coudé & Ferrari 2018). In a wider and more integrative approach Waller et al.
66 (2017) proposed that the observation and reproduction of facial expressions represent a multimodal
67 system in which communication, emotional experience and cognition work in synergy within the
68 social domain.

69 The capacity to promptly and congruently respond to facial signals performed by group-
70 companions has at its basis a mirror mechanism (Coudé & Ferrari 2018). Rapid Facial Mimicry
71 (RFM) has been defined as the automatic, involuntary and fast (< 1 sec) replication by an observer
72 of a facial expression performed by a conspecific (Dimberg & Thunberg 1998; Seibt et al. 2015;
73 Prochazkova & Kret 2017; Nieuwburg et al. 2021). Up to know, this phenomenon has been
74 demonstrated in human and non-human primates and in few other social mammals (primates, for an
75 extensive review see Palagi & Scopa 2017; domestic dogs, Palagi et al. 2015; meerkats, Palagi et al.
76 2019a; sun bears, Taylor et al. 2019; dog-horse Maglieri et al. 2020).

77 Much evidence suggest that RFM can be socially modulated as its frequency arises when the
78 two interacting individuals share valuable or close social bonds (Preston & de Waal 2002). For
79 example, in domestic dogs the mimicry of open mouth display during playful interactions was more
80 frequent between "friends" than "strangers" and "acquaintances" (Palagi et al. 2015). In slender-
81 tailed meerkats (*Suricata suricatta*), the levels of fast replication of play facial expressions
82 positively correlated with the levels of affiliative interactions shared between group-companions
83 (Palagi et al. 2019a). As for primates, in geladas (*Theropithecus gelada*) during mother-infant play,
84 the RFM frequency was higher compared to the other playmate dyads, with infants responding
85 faster to mothers than other adult females (Mancini et al. 2013a). Hence, the mimicry phenomenon
86 can have a crucial role in cementing pre-existing social bonds, increasing the engagement and
87 affiliation between interacting subjects and promoting the development of inter-individual
88 communication (Carpenter et al. 2013; Sclafani et al. 2015; Murray et al. 2016). An experimental
89 study on youngster brown capuchins (*Sapajus apella*) showed an increased frequency of gazing,
90 affiliation and token exchange between study subjects and the mimic-experimenter compared to the
91 non-mimic experimenter (Paukner et al. 2009).

92 Another mirror mechanism that occurs with larger delay (1-5 sec) compared to RFM is
93 Delayed Facial Mimicry (DFM). The time clusters (RFM < 1 sec; DFM 1-5 sec) are defined based
94 on human replication latencies that are produced for positive expressions (see Dimberg & Thunberg
95 1998; Dimberg et al. 2000; Wild et al. 2003). It has been proposed that DFM may be less automatic
96 and more sensitive to audience effect thus suggesting a possible manipulative aspect of the delayed
97 phenomenon (Davila-Ross et al. 2011; Cordoni et al. 2018; Palagi et al. 2019b). In chimpanzees,
98 DFM can positively modulate playful interactions with different timing compared to RFM thus
99 intensifying and prolonging the communication of "benign intents" between playmates (Palagi et al.
100 2019b).

101 The majority of studies demonstrated the occurrence of facial mimicry (RFM and DFM)
102 within the playful context (for an extensive review see Palagi et al. 2020a). The only exception

103 comes from bonobos (*Pan paniscus*) in which the presence of RFM has been recently demonstrated
104 during adult socio-sexual interactions, where the possibility to engage in eye-to-eye contact seems
105 to foster the phenomenon (Annicchiarico et al. 2020; Palagi et al. 2020b). Since facial mimicry has
106 never been explored during playful interactions in infant bonobos, here we aim at filling the gap.

107 Play represents a fruitful domain to test the occurrence of mimicry phenomena because
108 communication between playmates has a decisive role. During play individuals have to follow rules
109 that continuously and unexpectedly change (for an extensive review see Palagi et al. 2016). During
110 playful interactions (particularly play fighting) motor patterns typical of single or diverse
111 behavioural systems are recruited and re-arranged (Pellis et al. 2019; Llamazares-Martín & Palagi
112 2021); in some species, it has been even hypothesized that play can represent a harmless
113 replacement for aggression (South American sea lions, Llamazares-Martín et al. 2017; domestic
114 pigs, Cordoni et al. 2021a; wild spotted hyenas, Nolfo et al. 2021). In this "fluid" context, playmates
115 need to correctly perceive, process and respond to visual and auditory signals emitted by the partner
116 (Palagi et al. 2016). Within primates, the most common playful signal is the play face that is
117 homologous to human laughter and that can be performed with two variants: Play face (PF) and Full
118 Play Face (FPF) (Palagi, 2006; Davila-Ross & Dezechache 2021). In both types of facial displays,
119 the mouth is opened with the lower (PF) or both lower and upper teeth (FPF) exposed (van Hooff &
120 Preuschoft 2003; Cordoni & Palagi 2013).

121 To our knowledge, all the studies on RFM have been focussed on playful interactions
122 involving both immature and adult subjects thus not allowing to draw any conclusion on the
123 ontogenetic trajectories of the phenomenon. Here, we aimed at demonstrating the occurrence of
124 facial mimicry in infant bonobos, one of the most playful primate species (Palagi 2008, 2011,
125 2018).

126 Since the first days of life, human and non-human primates are sensitive to eye-contact with
127 their caregivers and it has been demonstrated that direct gazing can improve social skills in the long
128 term (Simpson et al. 2019). Experimental data indicate that human neonates show a preference for

129 faces with open eyes (Batki et al. 2000) and that engage in direct gazing (Farroni et al. 2002).
130 Similar findings have been obtained in infants of great apes. Chimpanzees of 10-32 weeks of age
131 clearly prefer looking at the direct gazing face of human experimenter (Myowa-Yamakoshi et al.
132 2003). According to the ‘eye-contact effect’ phenomenon, in human infants starting from 4 months
133 of age direct gazing promotes the ability to process concurrent or subsequent others’ facial actions
134 (Senju & Johnson 2009). Moreover, de Klerk et al. (2018) demonstrated that 4-month-old babies
135 are able to mimic others’ facial expressions (i.e. tongue protrusion, mouth opening) only after
136 engaging in direct gazing. Accordingly, if in human and non-human primates the direct gazing is
137 one of the proximate factors for the occurrence of mimicry phenomena just starting from the first
138 months of life, we expect that also in infant bonobos, during their playful activities, the eye-contact
139 engagement (i.e. face-to-face interaction) may increase the likelihood for playmates to mimic each
140 other (“Prediction 1”).

141 In several primate and non-primate species the fast replication of playful facial expressions,
142 rather than their mere emission, positively affects the session by prolonging its duration and,
143 consequently, the immediate and delayed benefits linked to a successful interaction (meerkats,
144 Palagi et al. 2019a; domestic dogs, Palagi et al. 2015; macaques, Scopa & Palagi 2016; geladas,
145 Mancini et al. 2013b; chimpanzees and lowland gorillas, Palagi et al. 2019b). In this view, if facial
146 mimicry occurs during play between infant bonobos, we expect that the fast replication of the play
147 face (PF/FPF) can prolong the duration of the session (“Prediction 2”).

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METHODS

The study colony

151 This research was carried out on the bonobo colony housed in the Wilhelma Zoo (Stuttgart,
152 Germany) and made by 16 individuals including five infants and one early juvenile (Table S1 in
153 Supplemental Data; Hashimoto 1997). In order to simulate the fission-fusion dynamic typical of the
154 species the colony was separated into two sub-groups that were defined as “Right group” (Rg) and

155 “Left group” (Lg), respectively. The composition of Rg and Lg changed once per month, thus we
156 were able to follow six different sub-groups (Rg₁, Rg₂, Rg₃, Lg₁, Lg₂, Lg₃). The enclosure of each
157 sub-group was composed by an indoor (350 m²) and an outdoor facility enriched with platforms,
158 hammocks, trunks, ropes, straw and cognitive tasks. The sub-groups received food (i.e. vegetables,
159 fruit and yogurt) 3 times per day while water was available ad libitum.

160 *Data collection, operational definition and statistics*

161 The observations were carried out for 4 months (November 2017-March 2018) on a daily
162 basis, from 8:00 am until 5:00 pm including feeding times. E. Palagi trained M. Bertini and G.
163 Annicchiarico for about 30 hr. At the end of the training period the agreement between observers in
164 animal and behavioural domain identification (e.g., play, sex) reached a Cohen’s K of 0.85 (almost
165 perfect agreement).

166 The data were collected by using Digital Videocamera Panasonic HC V-180EG-K Full-HD
167 optical zoom 90 ×. We applied the all occurrences behavioural sampling (Altmann 1974) to record
168 all playful interactions between infants and we extracted from the videos the following information:
169 (i) the playmate identities (sex, age and sub-group), (ii) the types of behavioural pattern performed
170 and their exact chronological order (see Table S2 in Supplemental Data), (iii) the duration of the
171 playful expressions (in csec), (iv) the perception condition of the playmates and (v) the duration of
172 the entire session (in sec). With this method we collected 435 play sessions between immature
173 individuals.

174 A play session started when a subject directed any playful pattern towards the fellow and
175 finished when playmates stopped the interaction (e.g. one of two players moves away or a third
176 individual disturbs the session; Palagi 2008). If the interaction between two players was interrupted
177 for more than 10 sec the subsequent play session was considered as new one (Cordoni et al. 2016,
178 2018).

179 We calculated the Play Asymmetry Index (PAI; Cordoni et al. 2016, 2018; Llamazares-
180 Martín et al. 2017; Nolfo et al. 2021) to evaluate the level of asymmetry for each session as follows:

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$$PAI = \frac{(\text{offensiveA} + \text{defensiveB}) - (\text{offensiveB} + \text{defensiveA})}{(\text{offensiveA} + \text{defensiveB}) + (\text{offensiveB} + \text{defensiveA}) + (\text{neutral behaviour})}$$

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184 In this formula “offensive” represents the number of unidirectional patterns of attack
185 directed by one player towards the partner, while “defensive” represents the number of patterns of
186 body protection and contact avoidance performed by one player in response to the attack by the
187 partner. “Neutral” refers to the number of play patterns not classified as offensive or defensive (see
188 Table S2 in Supplemental Data). As a whole, PAI evaluates the proportion of wins by player A
189 (offensiveA + defensiveB) by subtracting the proportion of wins by player B (offensiveB +
190 defensiveA) and its values range between – 1 and + 1 (0 value = perfect symmetry).

191 We recorded the two variants of playful expressions that is Play Face (PF) and Full Play
192 Face (FPF). To determine the duration of each expression, we made a frame-by-frame video-
193 analysis by employing the program VideoLAN Client 2.2.1 and Jump-to-Time (VLC extension).
194 The duration of facial display was measured starting from the first frame in which the inferior and
195 superior lips were separated until the first frame in which the mouth was closed again (Palagi et al.
196 2019b).

197 We determined two perception conditions of playmates: perception and no-perception. In
198 the perception condition the first playful expression (PF or FPF) emitted by one of the players (the
199 trigger) is visually detected by the partner (the observer). On the other hand, in the no-perception
200 condition the first playful expression emitted by the trigger is not visually detected by the partner.
201 When the trigger is in direct visual contact with the partner, within the range of his/her stereoscopic
202 view, we considered the facial display as detected (face-to-face interaction–perception condition);
203 whereas, when the observer is facing away from the trigger without direct visual contact, the facial
204 display is considered as not detected (no-perception condition). We excluded from the analyses all
205 cases in which playmate views were lateral or playmates’ faces were not clearly visible by the

206 experimenters. The RFM (always < 1 sec) and DFM (1-5 sec) latencies were calculated starting
207 from the perception of the trigger PF/FPF and ending with the onset of the receiver's PF/FPF (2-
208 csec accuracy).

209 During video analysis, E. Palagi, G. Annicchiarico and M. Bertini every 15 days re-assessed
210 the inter-observer reliability to check for the agreement between observers in distinguishing playful
211 patterns and expressions and in determining perception/no-perception condition and latency in
212 facial expression replication (< 1/1-5 sec). For each of the behavioural categories, conditions and
213 time latency the Cohen's k was never below 0.80.

214 To evaluate the factors possibly affecting the occurrence of Rapid Facial Mimicry (RFM)
215 we ran a General Linear Mixed Model (GLMM). We considered as dependent variable the
216 presence/absence of PF/FPF performed by one player within 1 sec after the emission of the first
217 PF/FPF by the trigger (0 = absence, 1 = presence; binomial distribution). The fixed factors included
218 in the analysis were (i) sex-combinations of the trigger and the observer (factorial variable: 1 =
219 female-male, 2 = male-male, 3 = male-female) and (ii) the perception condition (factorial variable:
220 0 = no-perception by the observer, 1 = perception by the observer). Dyads and sub-groups were
221 entered as random factors. The dataset used for this analysis was $N_{\text{trigger stimuli}} = 381$, $N_{\text{dyads}} = 14$ and
222 $N_{\text{sub-groups}} = 4$.

223 The same fixed and random factors were entered in the GLMM analysis carried out to test
224 for factors possibly predicting the occurrence of Delayed Facial Mimicry (DFM). In this case the
225 dependent variable was the presence/absence of PF/FPF performed by one player between 1 and 5
226 sec after the perception of the first PF/FPF emitted by the trigger (0 = absence, 1 = presence;
227 binomial distribution). The dataset used for this analysis was $N_{\text{trigger stimuli}} = 344$, $N_{\text{dyads}} = 14$ and
228 $N_{\text{sub-groups}} = 4$. Finally, we ran a Linear Mixed Model (LMM) for evaluating which factors could
229 affect the duration (in sec) of the playful session (\log_{10} -transformed play duration, normal
230 distribution). The fixed factors were (i) presence/absence of mimicry (factorial variable: 0 =
231 presence of RFM, 1 = presence of DFM, 2 = absence of both RFM and DFM), (ii) sex-

232 combinations of the trigger and the observer (factorial variable: 1 = female-male, 2 = male-male, 3
233 = male-female) and (iii) absolute values of PAI (scale variable). Dyads and sub-groups were entered
234 as random factors. If in a single play session were present both RFM and DFM events, this case was
235 classified as 0 = presence of RFM. The dataset used for this analysis was $N_{\text{play sessions}} = 435$, $N_{\text{dyads}} =$
236 14 and $N_{\text{sub-groups}} = 4$.

237 The GLMM/LMM were fitted in R (R Core Team 2019, version 3.6.1) by using the *lme4*
238 package (Bates et al. 2015). The significance of full model was contrasted with the significance of
239 the null model (i.e. model including only random factors) by employing a likelihood ratio test
240 (Anova with argument test "Chisq"; Dobson 2002). The *P*-values for the individual predictors were
241 calculated by using the R-function "*drop1*" (Barr et al. 2013).

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RESULTS

244 *Prediction 1*

245 The first model was built to test the variables possibly affecting the occurrence of RFM
246 (binomial distribution: absence = 0, presence = 1). The full model significantly differed from the
247 null model ($\chi^2 = 123.25$, $df = 3$, $P < 0.001$). The only variable with a significant effect on the
248 presence/absence of RFM was the perception condition (Table 1), with higher probabilities of
249 occurrence of RFM when the PF/FPF of the trigger was visually detected by the observer compared
250 to when it was not visually perceived (Fig. 1). No collinearity was found between the predictors
251 (Min vif = 1.00; Max vif = 1.00). Moreover, no overdispersion was found (residual deviance =
252 293.99, $df = 375$, ratio = 0.784).

253 The second model aimed at evaluating the factors possibly predicting the occurrence of
254 DFM (binomial distribution: absence = 0, presence = 1). The full model was significantly different
255 from the null model ($\chi^2 = 82.047$, $df = 3$, $P < 0.001$). As for RFM, the only variable with a
256 significant effect on the presence/absence of DFM was the perception condition (Table 2), with
257 higher probabilities of occurrence of DFM when the PF/FPF of the trigger was visually detected by

258 the observer compared to when it was not perceived (Fig. 2). No collinearity was found among the
259 predictors (Min vif = 1.00; Max vif = 1.00). Moreover, no overdispersion was found (residual
260 deviance = 208.167, df = 338, ratio = 0.616).

261 *Prediction 2*

262 The third model (LMM) aimed at evaluating the presence of RFM or DFM potentially
263 affected the duration of the playful session. The full model only approached statistical significance
264 when compared to the null model ($\chi^2 = 9.36$, df = 5, $P = 0.09$).

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DISCUSSION

267 In the present study we demonstrated the occurrence of both rapid (RFM) and delayed facial
268 mimicry (DFM) during playful interactions between infant bonobos (“Prediction 1 confirmed”).
269 Moreover, contrary to our expectation we found that neither RFM nor DFM prolonged the duration
270 of play session (“Prediction 2 not confirmed”).

271 Eye-contact can facilitate the non-verbal communicative exchange between individuals. By
272 creating a context in which the interactants are mutually attentive, eye-contact can enhance the
273 mimic response that may convey the message “I am like you” to the partner (Bavelas et al. 1986;
274 Bavelas 2007; Bavelas & Gerwing 2007; Iki & Hasegawa 2020). In human infants, mimicry
275 behaviour can be favoured when the subject acts in a communicative domain that is when they
276 interact with conspecifics which directly gaze at them (Kaye & Fogel 1980; Yale et al. 2003).

277 In bonobos, eye fixation seems to be a well-automated action. In an experiment, bonobos
278 looked at eyes of both familiar and unfamiliar subjects more rapidly and for longer period compared
279 to chimpanzees (Kano et al. 2015). Moreover, eye-to-eye contact may promote the establishment of
280 social relationships between unfamiliar adult females by producing a positive effect in prolonging
281 their socio-sexual contacts (ventro-ventral genito-genital rubbing; Annicchiarico et al. 2020). Our
282 findings provide further support to the hypothesis that eye-contact can enhance mimicry response in
283 bonobos. Although having access to the precise gaze direction of the players was not always

284 possible, our video analysis easily allowed to evaluate the relative positions of the subjects' faces.
285 In infant play, the occurrence of both RFM and DFM was promoted by the detection of the player's
286 facial expression during face-to-face interactions. Thus, the access to the face of conspecifics seems
287 to be particularly important during contact play because it allows observer to easier perceive visual
288 signals and promptly replicate to them thus establishing a mutual intersubjective engagement with
289 the playmate (Palagi et al. 2016; Heesen et al. 2017).

290 It is worth noting that, in our study, infants were observed in their environmental setting,
291 during their ordinary playful activities, in absence of any forms of physical limitation and under
292 natural stimuli emitted by conspecifics. In other words, the subjects were studied in the social
293 context under which the facial expression and possible motor resonance response are naturally and
294 spontaneously performed (Bos et al. 2016). This approach may give insights in delineating potential
295 ontogenetic trajectories of the development of mimicry phenomena both in human and non-human
296 primates (Cordoni et al. 2021b).

297 In adult bonobos RFM during sexual interactions was positively affected by the sex of the
298 subjects with female sexual contacts being punctuated by a higher presence of mimicry (Palagi et al.
299 2020b). This evidence fits with the structure of bonobo society in which the core of the group is
300 represented by adult females. Among females, alliances and close social relationships are developed
301 and maintained through affiliation and homosexual contacts (Moscovice et al. 2017, 2019;
302 Hohmann & Fruth 2000). Our data show that the sex of the infants did not affect the occurrence of
303 mimicry phenomena during play. During infancy the role of subjects according to their sex within
304 the group is not yet established and the communicative exchange between players can simply have
305 the immediate function of sharing and clarifying the mood of subjects (Palagi & Cordoni 2012;
306 Genty et al. 2015).

307 As it occurs in chimpanzees (Palagi et al. 2019b), the presence of DFM indicates that also in
308 bonobos such phenomenon is already present starting from the infant stages. Even though up to
309 know no studies are available on neural and cognitive basis of DFM, it has been hypothesized that

310 rapid and delayed mimicry can recruit different neuro-anatomical systems linked to diverse levels
311 of automaticity (see Palagi et al. 2020a for an extensive review). Probably, the less automaticity
312 characterizing DFM compared to RFM may be linked to the engagement of more complex and
313 time-demanding cognitive processes that lead to the expression of a "more intentional"
314 communication (Davila-Ross et al. 2011).

315 Contrary to our expectation, neither RFM nor DFM prolonged the duration of play
316 interactions. In previous studies, the mimicry effect in prolonging play has been demonstrated
317 within playmate dyads belonging to all age-class combinations. For example, in lowland gorillas
318 and chimpanzees, RFM increased the duration of play bouts that involved infants, juveniles and
319 adults (Palagi et al. 2019b). In geladas, Mancini et al. (2013b) found that RFM significantly
320 prolonged the duration of play sessions involving both infant and juvenile subjects. In domestic
321 dogs, the occurrence of RFM prolonged the playful sessions among adult individuals (Palagi et al.
322 2015). We could argue that during the first phases of individual development, the mimicry
323 phenomena in bonobos are not necessarily recruited to manipulate the session at an immediate
324 level. Actually, the playful sessions of infant bonobos under study were highly symmetric and well-
325 balanced (mean PAI \pm SE = 0.065 \pm 0.015) if compared with the playful sessions recorded in
326 chimpanzees (0.164 \pm 0.081) and gorillas of the same age (0.187 \pm 0.045) (data extracted from
327 Cordoni et al. 2018; Palagi et al. 2019b). In chimpanzees and lowland gorillas, mimicry seems to
328 have an impact in the modulation of the play sessions that last longer when they are punctuated by
329 RFM events (Palagi et al. 2019b). In bonobos the mimicry phenomenon does not seem to be crucial
330 in the management of the session that appears to be highly fair and well balanced. Mimicking infant
331 peers could simply booster the sharing of the mood between players thus increasing familiarity and
332 affiliation. In *Macaca mulatta*, newborns that were able to imitate caregivers' mouth movements
333 (i.e., lip smacking) showed greater social competence and higher levels of play at 1 year of age
334 compared to the non-imitators (Kaburu et al. 2016). Probably, facial mimicry in infant bonobos can

335 have a "broad effect" such as promoting affinitive interactions between group companions and, in
336 the long term, endorsing the acquisition of social competence (Lakin et al. 2003).

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ACKNOWLEDGMENTS

339 We wish to thank Elisa Demuru and Cristina Giacomina for inviting us to contribute to the
340 special issue. We are grateful to the Wilhelma Zoo (Germany) and specifically the mammal curator
341 Marianne Holtkötter and bonobo keepers for allowing and facilitating this work.

342

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DISCLOSURE STATEMENT

344 The authors declare no competing interests.

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FUNDING

347 This research did not receive any grant from funding agencies in the public, commercial, or
348 not-for-profit sectors.

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ETHICAL STANDARD

351 The present study was purely observational, and animals were not manipulated. The
352 University of Pisa (OPBA committee) waived the need for ethical approval according to the Italian
353 and European guidelines and regulations. The authors had the permission of the Wilhelma Zoo
354 (Stuttgart, Germany) to make videos on bonobos.

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AUTHOR CONTRIBUTION

357 E. Palagi and G. Cordoni conceived and designed the experiment; M. Bertini, G.
358 Annicchiarico and C. Bresciani collected data; E. Palagi trained M. Bertini and G. Annicchiarico for
359 the data analysis and checked for reliability; M. Bertini and G. Annicchiarico performed the video-
360 analysis; E. Palagi and C. Bresciani carried out the statistical analyses. E. Palagi and G. Cordoni

361 wrote the manuscript. All authors reviewed the manuscript. E. Palagi and G. Cordoni share the
362 senior authorship.

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364 SUPPLEMENTAL DATA

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366 ORCID

367 *Elisabetta Palagi* 0000-0002-2038-4596

368 *Giada Cordoni* 0000-0001-7093-0025

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370 DATA ACCESSIBILITY

371 All data (.csv) analysed in this study are provided as Supplementary Information files.

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Figure legends

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575 Fig. 1. — Percentage of the presence (grey bars) and absence (black bars) of Rapid Facial Mimicry
576 (RFM) in relation to perception and no-perception conditions. See Table 1 for the statistical results.

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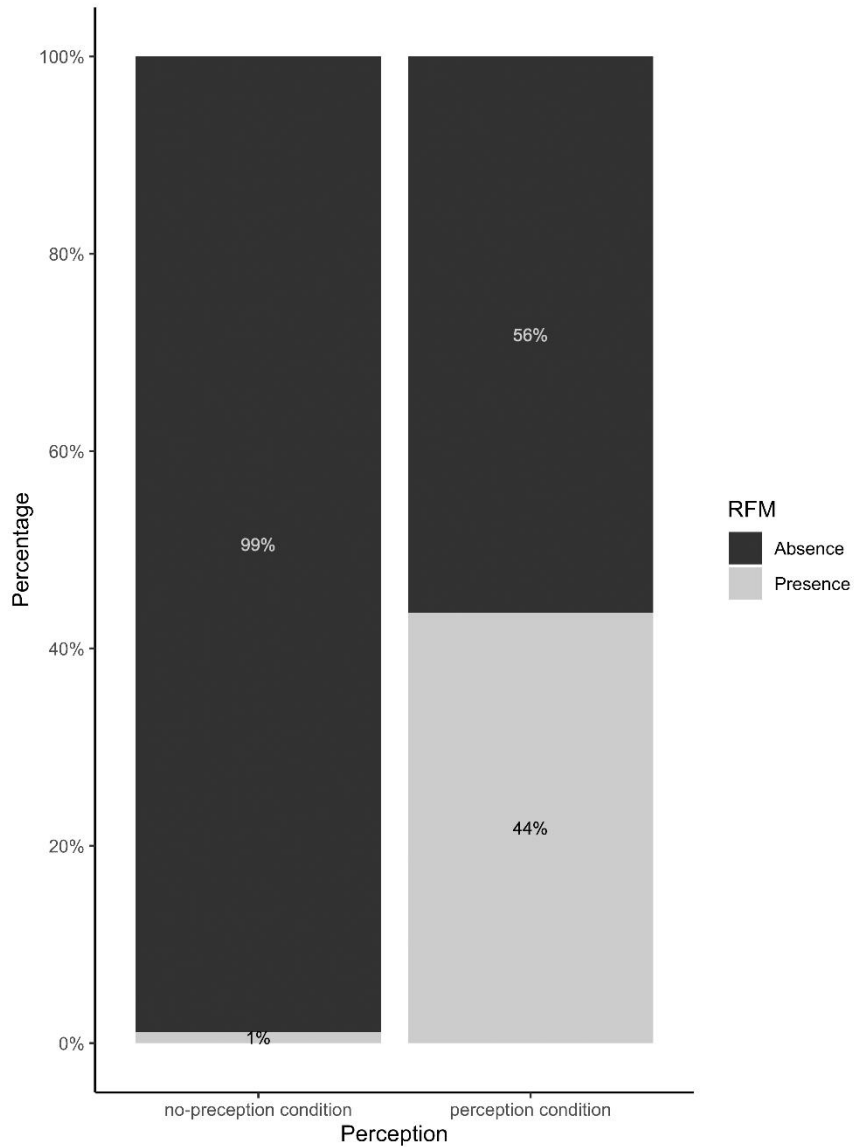
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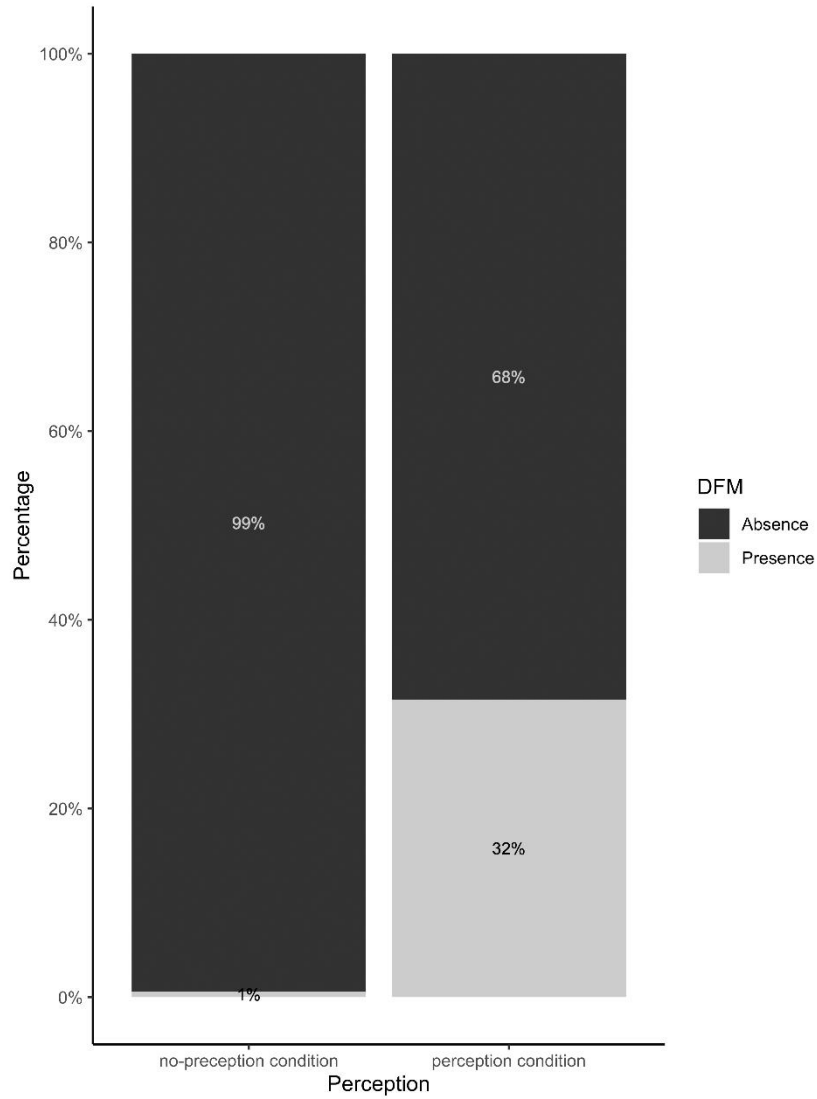
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599 Fig. 2. — Percentage of the presence (grey bars) and absence (black bars) of Delayed Facial
600 Mimicry (RFM) in relation to perception and no-perception conditions. See Table 2 for the
601 statistical results.



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Table 1.

Estimated parameters, Standard Error (SE), and results of the Likelihood Ratio Tests (LRT) of the Generalized Linear Mixed Model (RFM presence/absence, binomial error distribution). $N_{\text{trigger_stimuli}} = 381$; $N_{\text{dyads}} = 14$; $N_{\text{groups}} = 4$. Variance for the random factor DYAD = $0.674 \pm 2.596e-05$ SD; GROUP = 0.021 ± 0.1434 SD.

Fixed Effects	Estimate	SE	df	LRT	<i>P</i>
Intercept	- 5.078	0.771	a	a	a
Sex			2	5.058	0.08
Sex (male-male) ^{b,c}	0.703	0.349			
Sex (male-female) ^{b,c}	- 0.228	0.222			
Perception (yes) ^b	4.280	0.731	1	118.430	< 0.0001

^aNot shown as not having a meaningful interpretation.

^bEstimate \pm SE refer to the difference of the response between the reported level of this categorical predictor and the reference category of the same predictor.

^cThese predictors were dummy coded, with the “Sex (female-male)” being the reference category.

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Table 2.

Estimated parameters, Standard Error (SE), and results of the Likelihood Ratio Tests (LRT) of the Generalized Linear Mixed Model (DFM presence/absence, binomial error distribution). $N_{\text{trigger_stimuli}} = 381$; $N_{\text{dyads}} = 14$; $N_{\text{groups}} = 4$. Variance for the random factor DYAD = 0.191 ± 0.437 SD; GROUP = 0.142 ± 0.377 SD

Fixed Effects	Estimate	SE	df	LRT	<i>P</i>
Intercept	- 5.640	1.069	a	a	a
Sex			2	4.272	0.118
Sex (male-male) ^{b,c}	0.285	0.467			
Sex (male-female) ^{b,c}	1.035	0.487			
Perception (yes) ^b	4.485	1.019	1	78.086	< 0.0001

^aNot shown as not having a meaningful interpretation.

^bEstimate \pm SE refer to the difference of the response between the reported level of this categorical predictor and the reference category of the same predictor.

^cThese predictors were dummy coded, with the “Sex (female-male)” being the reference category.

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Table S1.

674 Composition of the colony of bonobos under study including sex and age categories.

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Subject	Sex class	Years/Age class
Banbo	F	14.9/adult
Bobali	M	4.5/infant
Chimba	F	22.1/adult
Chipita	F	16.1/adult
Fimi	F	8.5/adult
Haiba	F	17.2/adult
Huenda	F	10.5/adult
Kasai	M	13.2/adult
Kolela	F	1.9/infant
Kombote	F	51.1/adult
Koju	M	0.3/newborn
Liboso	F	19.1/adult
Lubao	M	4.8/infant
Makasi	M	2.2/infant
Mobikisi	M	37.1/adult
Yanola	F	1.9/infant

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Table S2.

690 Play behavioural patterns recorded in the video-analysis and distinction among “offensive behaviours” (o),
 691 “defensive behaviours” (d) and “neutral behaviours” (n).

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Behavioural patterns	Definitions
Acrobatic play (n)	Solitary or social: the individual swings using a rope as support.
Clinging (n)	Individual A walks together with individual B by keeping the hand over its shoulders/back.
Finger/Hand in mouth (d)	Individual A attempts to put its fingers/hand in the mouth of individual B.
Leapfrog (o)	Individual A jumps over individual B.
Moon walk (n)	Individual looks at the other playmate while walking backward.
Pirouetting (n)	Individual pirouettes on itself on the ground or from a rope.
Play bite (o)	Individual A attempts to bite individual B in a non-aggressive/playful way.
Play brusque rush (o)	Individual A leaps on individual B using its four limbs.
Play climb or stand on another (o)	Individual A climbs or places itself over the body of individual B.
Play drag (o)	Individual A sweeps individual B holding it from the limbs.
Play eye cover (o)	Individual A attempts to cover the eyes of individual B with hands/feet.
Play grab/Grab genitals (o)	Individual A attempts to catch individual B or/and its genitals.
Play jump/jump over someone (n/o)	Individual jumps from one place to another and/or jump over individual B.
Play kick (o)	Individual A kicks individual B in a playful way.
Play manipulation (n)	Individual holds and examines an object without any specific, evident goal.
Play pull (o)	Individual A gently pulls individual B using hands/feet.
Play push (o)	Individual gently pushes individual B using hands/feet.
Play recovering a thing/Play object steal (o)	Individual A pushes individual B away and attempts to steal the object carried by it.
Play retrieve (o)	Individual A restrains individual B preventing him/her escaping.
Play run (o)	Individual A runs after individual B.
Play shaking (o)	Individual A shakes the rope of individual B.
Play slap/Gentle/Hard touch (o)	Individual A slaps any body parts of individual B in a playful way.
Play turn around (n)	Individual A and B run/walk around the same object.
Play walk on someone (o)	Individual A (generally infant) attempt to walk on individual B.
Play wrestling/Rough & Tumble (n)	Individuals A and B fight together by using behavioural patterns such as kick, slap, bite. Similar to real fighting but performed in a playful manner.
Roll (n)	Individual turns its body from side-to-side while it is laying down.
Play Shelter (d)	Individual A puts its arms over the head and attempts to protect itself from individual B bites, slaps, kicks.
Shake over someone (n)	Individual A swings over individual B who tries to catch it.
Somersault (n)	The individual performs somersaults on the ground or using a vertical support, such as ropes, in solitary or even in social context.
Tickling (n)	Individual A tickles any body parts of individual B using hands/feet.
Tug-of-war (n)	Individuals A and B try to catch an object by pulling it towards themselves.
Wriggle (d)	Individual A attempts to wriggle away from individual B.

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