

1 **SHARING PLAYFUL MOOD: RAPID FACIAL MIMICRY IN *SURICATA SURICATA***

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27 **Abstract**

28 One of the most productive behavioural domains to study visual communication in mammals is social  
29 play. The ability to manage play-fighting interactions can favour the development of communicative  
30 modules and their correct decoding. Due to their high levels of social cohesion and cooperation,  
31 slender-tailed meerkats (*Suricata suricatta*) are a very good model to test some hypotheses on the  
32 role of facial communication in synchronizing playful motor actions. We found that the relaxed open  
33 mouth (ROM), a playful facial expression conveying a positive mood in several social mammals, is  
34 also present in meerkats. ROM was mainly perceived during dyadic playful sessions compared to  
35 polyadic ones. We also found that meerkats mimic in a very rapid and automatic way the ROM  
36 emitted by playmates (Rapid Facial Mimicry, RFM). RFM was positively correlated with the  
37 relationship quality shared by subjects thus suggesting that the mimicry phenomenon is socially  
38 modulated. Moreover, more than the mere presence of isolated ROMs, the presence of at RFM  
39 prolonged the duration of the play session. Through RFM animals can share the emotional mood they  
40 are experiencing and this appears to be particularly adaptive in those species whose relationships are  
41 not inhibited by rank rules and when animals build and maintain their bonds through social affiliation.  
42 The meerkat society is cohesive and cooperative. Such features could have therefore favoured the  
43 evolution of facial mimicry, a phenomenon linked to emotional contagion, one of the most basic  
44 forms of empathy.

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46 **Key Words:** visual communication, relaxed open mouth, emotional contagion, prosocial behaviour,  
47 meerkats.

## 48 **Introduction**

49 Sociality relies on complex forms of communication with individuals searching for signals which  
50 provide useful information to make adaptive behavioural decisions (Freeberg 2012; Megan et al.  
51 2017). Communication is based on signals which are produced by a display/action of one subject (the  
52 sender) to affect the behaviour of another subject (the receiver) in a way that is adaptive either to one  
53 or both parties (Markl 1983; Bradbury and Vehrencamp 1998). Among interacting subjects, an  
54 optimal signal transmission can be reached by selecting different sensory modalities as a function of  
55 the distance between the sender and the receiver and the possible visual/acoustic barriers present in  
56 the environment. For example, acoustic signals can be recruited when the subjects cannot see each  
57 other due to the presence of visual barriers or when the distance separating the animals is too long to  
58 preclude the possibility to perceive subtle visual cues, such as facial expressions (Bradbury and  
59 Vehrencamp 1998).

60 One of the most productive behavioural domains to study visual communication and facial  
61 expressions in social mammals is play because this activity involves a close proximity between the  
62 interacting subjects (Palagi et al. 2016). Social play and, especially, play fighting, can be favoured  
63 through an accurate exchange of visual communicative signals (Pellis and Pellis 1997; van Hooff and  
64 Preuschoft 2003; Palagi 2008; Waller and Cherry 2012; Palagi et al. 2014; Weigel and Berman 2018).  
65 Although play fighting can be distinguished from real fighting on the basis of a variety of features,  
66 such as the emphasis of the movements, the lack of inhibition, the random sequence of the motor  
67 patterns and the self-handicapping tactics (Burghardt 2005; Pellis et al. 2010), in some cases  
68 ambiguity can arise and the prompt use of specific signals can avoid misunderstanding between  
69 players (Palagi et al. 2018). The playfulness of a potentially dangerous pattern can be highlighted by  
70 specific gestures, gaits, vocalizations and facial expressions (Fagen 1981; Bekoff 2001; Panksepp  
71 and Burgdorf 2003; Palagi 2006; Yanagi and Berman 2014; Palagi et al. 2015; Špinka et al. 2016).  
72 In a sort of positive feedback, therefore, the opportunity to manage playful interactions can favour

73 the development of communicative modules and their decoding, two skills that are beneficial in many  
74 different contexts other than play itself (Burghardt 2005; Palagi and Cordoni 2012).

75 Here, we focus on playful facial communication in a species, *Suricata suricatta*, which has been  
76 extensively studied for its complex vocal repertoire and communication (Manser et al. 2014) but that  
77 has been relatively neglected for its facial communication. Even though the functions of play fighting  
78 in this species have not yet been identified (Sharpe and Cherry 2003; Sharpe 2005a,b,c), meerkats  
79 are a very good model to test some hypotheses on the potential role of playful facial communication  
80 in fine tuning the playful session. Play fighting is present at every stage of life and the frequency of  
81 play increases when animals are food provisioned (Sharpe et al. 2002), as it occurs in captivity.

82 Meerkats show high levels of social cohesion, prosocial behaviour and cooperation (Clutton-Brock  
83 et al. 2001; Madden and Clutton-Brock 2011; Clutton-Brock and Manser 2016). Adults provide care  
84 to both related and unrelated pups by babysitting (Clutton-Brock et al. 1998), feeding (Brotherton et  
85 al. 2001) and teaching them foraging tactics (Thornton and McAuliffe 2006). Adults also contribute  
86 to other communal behaviours such as guarding (Clutton-Brock et al. 1999), mobbing (Graw and  
87 Manser 2007) and digging burrows (Manser and Bell 2004). In meerkats such prosocial behaviours  
88 are mediated by oxytocin (Madden and Clutton-Brock 2011), a peptide hormone that, in many  
89 mammalian species, is implicated in social bonding (Bales and Carter 2003), generosity (Korb et al.  
90 2016), emotional sharing (Burkett et al. 2016) and facial mimicry (Korb et al. 2016; Somppi et al.  
91 2017).

92 The large communicative repertoire of meerkats seems to provide the basis for their behavioural  
93 synchronization and cooperation during group activities (Gall et al. 2017). We hypothesize that, as it  
94 occurs in other highly cohesive species (wolves, Cordoni 2009, Cafazzo et al. 2018; dogs, Palagi et  
95 al. 2015, Byosiere et al. 2016; spotted hyena, Drea et al. 1996; Tonkean macaques, Scopa and Palagi  
96 2016; bonobos, Palagi 2008), in meerkats the capacity to manage play fighting can be achieved by  
97 the use of specific communicative signals of both auditory and visual nature.

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100 **Prediction 1 - *Relaxed open mouth (ROM) as a directed signal***

101 The specific facial expression punctuating play fighting is the relaxed open-mouth display (ROM)  
102 which is commonly observed in several mammals (coyotes, wolves, dogs, Bekoff 1974; dogs, Palagi  
103 et al. 2015; polecats, Poole 1978; otters, Pellis 1984; American black bears, Henry and Herrero, 1974;  
104 sun-bears, Taylor et al. 2019; South American sea lions, Llamazares-Martin et al. 2017; lemurs, Pellis  
105 and Pellis 2007, Palagi et al. 2014; macaques, van Hooff and Preuschoft 2003; orang-utans, Davila  
106 Ross et al., 2008; bonobos, Palagi 2008; gorillas, Waller and Cherry 2012; chimpanzees, Palagi et al.  
107 2018). The *Ritualization Hypothesis* (Tinbergen 1952) predicts that some behavioural patterns can be  
108 separated from their original function to fulfil new functions. The ROM is considered a ritualized  
109 signal that copies the intention of biting during a play session (Poole 1978; van Hooff and Preuschoft  
110 2003; Palagi 2006; Palagi et al. 2014). To evaluate whether a pattern actually derives from the  
111 ritualization process it should be demonstrated that it is detached from the presence of the original  
112 behaviour which the ritualized pattern is supposed to originate from. After the ritualization process,  
113 the original behaviour no longer results in the original outcome, but it can assume different meanings.  
114 Hence, if in *Suricata suricatta* ROM is a playful signal, it should occur significantly more frequently  
115 without the presence of play biting (Prediction 1a). Moreover, since ROM can be potentially  
116 perceived by all the subjects involved in a play session, we expect that the signal is optimized during  
117 polyadic (more than one playmate) than dyadic sessions (one playmate) simply because there is a  
118 higher number of potential receivers (Prediction 1b).

119

120 **Prediction 2 – *Presence of Rapid facial mimicry (RFM) and relationship quality***

121 Facial expressions convey information about the motivational and emotional state of the sender  
122 (Palagi and Scopa 2017; Russell and Fernandez-Dols 2017). In this view, the correspondence between  
123 facial signals emitted and elicited could be a valuable criterion to evaluate not only the ability to  
124 decode and interpret the signal of the playmates (Schmidt and Cohn 2001) but also the emotional  
125 sharing of the two interacting subjects (e.g., emotional contagion) (kea parrots, Schwing et al. 2017;

126 dogs, Palagi et al. 2015, Huber et al. 2017; humans, Bryant et al. 2016; Prochazkova and Kret, 2017).

127 Play is a rewarding behaviour for the player because it induces a positive emotional state that can be

128 shared with the playmate through a specific form of motor resonance defined rapid facial mimicry

129 (RFM). RFM is an automatic, congruent and fast response (less than 1 s) in which individuals

130 involuntary mimic others' expressions (Davila-Ross et al. 2008; Palagi et al. 2015; Scopa and Palagi

131 2016; Taylor et al. 2019). Recent studies have highlighted a covariance between the presence of motor

132 resonance phenomena (e.g., rapid mimicry) and the level of tolerance, affiliation and familiarity

133 shared by the interacting subjects (the so-called *empathic-gradient hypothesis*, de Waal and Preston,

134 2017; Clay et al., 2018). These social features influence play modality as demonstrated by the studies

135 on macaques. Highly cohesive macaque species tend to show highly symmetric and cooperative play

136 (Reinhart et al. 2010) and a frequent use of facial expressions which are often mimicked in a rapid

137 and automatic way (Scopa and Palagi 2016). Even in those species having largely solitary lifestyle,

138 rapid mimicry can emerge when subjects grow up in a social environment and have the opportunity

139 to develop social bonds and high familiarity levels with conspecifics (orang-utans, Davila-Ross et

140 al.2008; sun bears, Taylor et al. 2019). The cohesive nature of *Suricata suricatta* is highlighted by

141 the presence of behaviours that seem to be independent from the subjects' rank (Gall et al. 2017). For

142 example, during foraging activity some individuals can initiate group movements using 'lead' calls,

143 and groups can move to different foraging patches using 'move' calls in a collective response

144 (Bousquet et al. 2011). In this communicative exchange, dominant and subordinate individuals do

145 not show strong differences and engage in both "move" and "lead" calls at similar rates. Moreover,

146 the time spent to forage depends on the foraging success of all subordinates more than by the foraging

147 success of the dominant individuals. This suggests that the decision to return to sleeping sites is

148 shared among high- and low-ranking subjects rather than controlled by dominants (Gall et al. 2017).

149 Due to the cooperative and cohesive nature of this species we predict that meerkats are able to express

150 Rapid Facial Mimicry (RFM) by mirroring facial expressions of others, such as the relaxed open

151 mouth (ROM) (Prediction 2a). In case Prediction 2a is confirmed, if RFM is a phenomenon

152 modulated by emotional contagion, we also expect that RFM is affected by the quality of relationship  
153 shared by the players (calculated via the following affiliative patterns: grooming, body contact,  
154 embracing/huddle) and not affected by their rank difference (Prediction 2b).

155

156 **Prediction 3 – RFM, relationship quality and the duration of play session**

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158 If RFM and the relationship quality are good predictors of emotional contagion, we expect that they  
159 favour the playful mood shared between the players. In this view, we expect that both RFM and good  
160 relationships can positively affect the duration of play sessions (Prediction 3).

161

## 162 **METHODS**

### 163 **Ethics Statement**

164 Because the study was purely observational the committee of the University of Pisa (Animal Care  
165 and Use Board) waived the need for a permit.

166

### 167 **Subjects and Data Collection**

168 The colony of *Suricata suricatta* (Table 1) under study was hosted at the Zoological Gardens of  
169 Pistoia. During the data collection (April-June 2016) the colony was composed by nine adult males,  
170 three adult females, and three immature subjects (Table 1). The animals were housed in an open-top  
171 naturalistic enclosure of 90 m<sup>2</sup> connected with two indoor facilities (5 m<sup>2</sup>; inaccessible to the human  
172 observer). The indoor and outdoor enclosures were connected through two guillotine doors and the  
173 animals could freely move between them. The external area was provided with a substrate in soil and  
174 sand (suitable for the formation of underground tunnels) and was enriched by boulders, trunks and  
175 climbing structures. There was herbaceous, shrubby and arboreal vegetation, as well as a pool with  
176 running water, so water was always available. Observations were carried out exclusively outdoor.

177 Data collection occurred twice a week and behavioural data were video-recorded (about 150 hours)  
178 by one observer (EM). In the period before the data collection and concomitantly with the routine  
179 veterinary checking, adult individuals were weighed (mean 944.50 grams  $\pm$ 15.73 SE) and marked by  
180 colouring the fur in different body parts with a black hair dye (Table 1). Adults were individually  
181 identified by the marking and their physical characteristics. Immature individuals were recognized  
182 exclusively through their morphological features (e.g., size, fur colour, tail shapes, etc.).

183 The animals were fed in the indoor area twice a day at 10.00 a.m. (fruit, vegetables, dog pellet) and  
184 04:30 p.m. (chicks or quails). In addition, they were randomly provided with a feeding enrichment to  
185 stimulate foraging behaviour. The enrichment consisted of card-board boxes containing mealworms,  
186 chopped fruits and vegetables mixed with straw or dry leaves. The boxes were always placed outdoor.

187 Video recording was *in continuum*. The animals were videotaped daily from 08:30 a.m. until 06:30  
188 p.m. when visible. Data collection was carried out with the aid of three camera devices (SONY DCR-  
189 SX15E, SONY DCR-SX33, SONY ILCE-5000L).

190 Scan sampling was performed every 30 seconds on all the videos collected (150 hours; 18000 scan  
191 samplings). Via scan sampling we recorded the following affiliative patterns: directional grooming,  
192 mutual grooming, body contact, embracing/huddle (Table 2).

193 All occurrences sampling was used i) to collect data on dismiss/avoidance interactions on all the  
194 videos collected (150 hours) and ii) to gather data on social play (play fighting). We video-analysed  
195 play sessions for a total of 38 hours of videos. We employed a frame-by-frame method using VLC  
196 media player 2.2.6 and Jump to time, with an accuracy of 0.01 seconds.

197 Before commencing systematic analysis of the videotaped sequences, the observer (EM) and the  
198 trainer (EP) tested their inter-observer reliability in behavioural coding, until reaching a Cohen's  $\kappa$   
199 value  $> 0.85$  (Kaufman and Rosenthal 2009). During the video-analysis, this procedure was repeated  
200 every 3 hours of video analysed, with both observers scoring the same 15 minutes of video, to ensure  
201 consistent inter-observer reliability for each behavioural item scored Table 2. For each of the  
202 behavioural items, Cohen's  $\kappa$  value was never less than 0.85.



203

## 204 **Operational definitions**

### 205 *The play session*

206 A play session began when one partner directed a playful pattern toward a conspecific who responded  
207 with another playful pattern (Table 2). A session ended when playmates ceased their activities, one  
208 of them moved away, or when a third individual interfered, thus interrupting the interaction. If another  
209 play session began after a delay of 10 seconds, that session was counted as new. For each play session  
210 we recorded: (a) identities of the subjects (i.e., name, sex, age), (b) playful bodily motor patterns and  
211 facial expressions in their exact sequence, (c) exact time in which each pattern occurred (with an  
212 accuracy of 0.01 seconds), (d) number of players and (e) duration of the interaction (in seconds). We  
213 recorded and analysed 1035 play sessions via all occurrences sampling method.

214

### 215 *Polyadic and dyadic sessions*

216 As for the definition of polyadic sessions, we used the following criteria. If the individuals A and B  
217 were playing and C joined in, the session shifted from dyadic to polyadic and the two sessions were  
218 considered as distinct. Similarly, if one of the three meerkats dropped out, the session shifted into a  
219 dyadic session and it was considered as a new session. When at least one of the players changed  
220 during a polyadic/dyadic playful interaction, that session was considered as a new session.

221 To compare the ROM frequency between dyadic and polyadic play sessions, we calculated at the  
222 individual level the number of ROMs emitted by each subject when engaging in dyadic and polyadic  
223 sessions.

224 For the LMM analysis, we calculated the duration of each play session at the dyadic level. In case of  
225 polyadic play, we calculated the duration of the session involving each dyad as follows a-b-c = a-b;  
226 a-c; b-c.

227

### 228 *Play Asymmetry Index, PAI*

229 To calculate the *Play Asymmetry Index* (PAI), we classified the playful patterns as offensive and  
230 defensive (Bauer and Smuts 2007; Ward et al. 2008; Cordoni et al. 2016; Llamazares-Martín et al.  
231 2017) (Table 2). We calculated the PAI for each session as follows: the number of “play wins” for  
232 animal A in a dyad equalled the number of offensive play patterns by A directed at B plus the number  
233 of defensive play patterns by B directed toward A. B’s “play wins” were calculated in the same way  
234 (Table 2). Next, we calculated the proportion of “play wins” for A as the number of “play wins” for  
235 A divided by the number of “play wins” for both A and B. We calculated the number of “play wins”  
236 for B in the same way. We subtracted the “A play win ratio” from the “B play win ratio” thus  
237 obtaining a value that represented the measure of the degree of asymmetry (Ward et al. 2008; Palagi  
238 et al. 2014; Cordoni et al. 2016). The neutral patterns (defined and listed in Table 2) are not  
239 directional, for this reason they cannot attributed to a specific player. The PAI ranges from -1 to 1.

240

$$241 \frac{(\text{OFF play patterns A} + \text{DEF play patterns B}) - (\text{OFF play patterns B} + \text{DEF play patterns A})}{(\text{OFF play patterns A} + \text{DEF play patterns B}) + (\text{OFF play patterns B} + \text{DEF play patterns A}) + \text{NEUTRAL patterns}}$$

242

243 We calculated the PAI value of each session in which the animals A and B were involved. Then, we  
244 calculated the mean value of the PAI distribution of the A-B dyad. In case of polyadic play, we  
245 calculated the PAI of each dyad involved in the session as follows a-b-c = a-b; a-c; b-c.

246

#### 247 *Rapid Facial Mimicry (RFM)*

248 To examine the presence of RFM, defined as the mirror facial response given by the receiver within  
249 1 second from the perception of the stimulus (Mancini et al. 2013), we focused on the specific playful  
250 signal, the ROM (operational definition: an individual opens and closes its mouth while moving  
251 towards a playmate; upper and lower teeth may be exposed and visible; the degree of opening has to  
252 reach at least the 50% of the mouth's maximum opening). 1584 ROMs were included in the analysis.

253 We focused on the facial expression of one individual (the receiver) to see whether it varied as a  
254 function of the facial signal displayed by the individual (the sender) within a 1 second time window.  
255 The sender was defined as the first playmate who emitted the stimulus (ROM). To reliably assess that  
256 the ROM produced by the receiver was actually elicited by the ROM emitted by the sender, we  
257 considered only those interactions in which the receiver looked at the sender and did not show ROM  
258 in the 1 second prior to the emission of the facial stimulus (ROM) by the sender.

259 The RFM latencies were measured frame-by-frame starting from the onset of the sender stimulus (the  
260 first frame showing the separation of the inferior from the superior jaw) and ending with the onset of  
261 the receiver's facial response (the first frame showing the separation of the inferior from the superior  
262 jaw) with 1 cs accuracy.

263 We measured the attentional state of the receiver by considering its head orientation in relation to the  
264 head orientation of the sender (Figure 1). When the sender was in front of the receiver (i.e., within  
265 the range of its stereoscopic view, direct visual contact condition), we considered the facial expression  
266 as perceived. When the receiver was facing away from the sender (without direct visual contact  
267 condition), we considered facial expressions as not perceived.

268 All the doubtful cases linked to lateral views were discarded from the analyses (Figure 1) and RFM  
269 was calculated after all the coding was finished.

270

271 *Calculation of the dominance relationships* - We evaluated hierarchical relationships of the subjects  
272 on the basis of the dyadic dismiss/avoidance interactions. For each interaction, data were entered into  
273 a socio-matrix used to assess the rank by Normalized David's Scores (Table 1). Normalized David's  
274 scores (NDS) were calculated on the basis of a dyadic dominance index ( $D_{ij}$ ) in which the observed  
275 proportion of displacements ( $P_{ij}$ ) is corrected for the chance occurrence of the observed outcome.  
276 The chance occurrence of the observed outcome was calculated on the basis of a binomial distribution  
277 with each animal having an equal chance of winning or losing in every dominance encounter

278 (Vervaecke et al. 2007). The correction is necessary when, as in the case of our study group, the  
279 interaction numbers was different between the dyads.

280

281 *Relationship quality* - The quality of the relationship between the subjects forming each dyad (A-B)  
282 was determined by calculating the ratio between the number of affiliative patterns (directional  
283 grooming, mutual grooming, body contact, embracing/huddle) and the total number of scans in which  
284 at least one of the subject of the dyad was present.

285

## 286 **Statistics**

287 Due to the non-normal distribution of the data (Kolmogorov-Smirnov  $>0.05$ ), we used non-  
288 parametric statistics to perform the analyses. The Exact Wilcoxon's paired sample T test was used to  
289 compare the frequency of i) ROM followed/not followed by play bites (*Prediction 1a*), ii) ROM  
290 perceived during dyadic/polyadic sessions (*Prediction 1b*) and iii) the congruent response  
291 (ROMreceiver/ROMsender) between "direct visual contact" and "without visual contact" conditions  
292 (*Prediction 2a*).

293 To check for a possible correlation between RFM and the absolute difference in NDS values between  
294 the individuals forming a dyad, we applied the randomization test for correlation. The same test was  
295 also applied to check for the presence of a correlation between RFM and the relationship quality  
296 shared (measured by affiliative patterns) by the subjects forming a dyad (*Prediction 2b*). This kind of  
297 procedure is used to avoid pseudo-replication due to non-independence of data (the same individual  
298 is included in more than one dyad; therefore, dyads are not independent data-points). The correlation  
299 via randomization test was employed with a number of 10,000 permutations using resampling  
300 procedures (via Resampling Procedures 1.3 package by David C.Howell).

301 *Statistical Model Analysis* - We ran a multi-model comparison of Linear Mixed Models (LMM) to  
302 determine what variables affected the duration of the play session (Play Duration, PD) (*Prediction*  
303 *3*). In the model, the dependent variable was the logarithmic values of PD (Normal distribution,

304 Anderson-Darling, ns, EasyFit 5.5 Professional). The fixed and random factors are listed and defined  
305 in Table 3.

306 We tested 23 models involving the nine fixed factors of interest (Table 3), spanning a single-factor  
307 model and a model including all the fixed factors (full model). To select the best model, we used the  
308 Akaike's corrected information criterion (AICc), which corrects the Akaike's information criterion  
309 (AIC) for small sample sizes. As the sample size increases, the AICc converges to AIC. To measure  
310 how much better the best model is compared to the next best models, we calculated the difference  
311 ( $\Delta AICc$ ) between the AICc value of the best model and the AICc value for each of the other models.  
312 As a coarse guide, models with  $\Delta AICc$  values less than 2 are considered to be essentially as good as  
313 the best model (also defined as "substantial", Burnham and Anderson 2002) and models with  $\Delta AICc$   
314 up to 6 should probably not be discounted (also defined as "considerably less", Burnham and  
315 Anderson 2002). Moreover, to assess the relative strength of each candidate model, we employed  
316  $\Delta AICc$  to calculate the evidence ratio and the Akaike weight ( $w_i$ ). The  $w_i$  (ranging from 0 to 1) is the  
317 weight of evidence or probability that a given model is the best model, taking into account the data  
318 and set of candidate models (Symonds and Moussalli 2011).

319

## 320 **RESULTS**

### 321 **Prediction 1**

322 The percentage of ROM not followed by a bite was  $75.00\% \pm 27.49$  SE. The number of ROMs  
323 (ROM/second) not followed by bites were more frequent than those followed by bites (Exact  
324 Wilcoxon  $T=0.00$ ; ties=0;  $N=12$ ;  $p=0.0001$ ; Figure 2) (Prediction 1a supported). The ROMs  
325 perceived during dyadic sessions were significantly more frequent than those perceived during  
326 polyadic sessions (Exact Wilcoxon  $T=0.00$ ; ties=0;  $N=12$ ;  $P=0.0001$ ; Figure 3) (Prediction 1b not  
327 supported).

328

### 329 **Prediction 2**

330 The frequency of ROMs performed when the stimulus was emitted in presence of direct visual contact  
331 with the playmate was significantly higher compared to the frequency of ROMs performed when the  
332 stimulus emitted by the sender was not visually perceived by the receiver (Wilcoxon Signed Rank  
333 test  $T=0.00$ ;  $N=9$ ;  $P=0.004$ ; Figure 4) (Prediction 2a supported). The mean group frequency of RFM  
334 was  $0.273 \pm 0.023SE$ . The RFM time latency was mean  $19.63 \text{ cs} \pm 2.01SE$ . The total RFM performed  
335 by the players correlated with their levels of relationship quality (correlation via randomization  
336  $r=0.639$ ;  $N_{\text{dyads}}=22$ ;  $p=0.009$ ; Figure 5) but not with their rank distances measured via the absolute  
337 difference in their NDS scores (correlation via randomization  $r=0.123$ ;  $N_{\text{dyads}}=22$ ;  $p=0.540$ )  
338 (Prediction 2b supported).

339

### 340 **Prediction 3**

341 To verify which factors affected the duration of each play session, we ran a LMM. The best model  
342 ( $AICc=1399.026$ ) contained the variables "RFM" and "relationship quality" and explained about  
343 50.50% of the distribution. The  $AICc$  of intercept only was 1478.874 and that of the full model was  
344 1418.818. Four 'considerably less' models ( $2 < \Delta AICc < 6$ ; Burnham and Anderson 2002; Table 4)  
345 cannot be discounted as potential models explaining the distribution of the Play Duration. However,  
346 these four models contained as fixed factors "RFM" and "relationship quality" and among all the  
347 added variables only "sex of player1" was a significant predictor with none of the additional variables  
348 improving the model. For details of the results see Table 5. In the best model the variables "RFM"  
349 (Figure 6) and "relationship quality" (Figure 7) were both statistically significant, this means that both  
350 variables produce a general effect in prolonging the session.

351

### 352 **Discussion**

353 As a whole, our findings support the hypothesis that visual communication has an important role in  
354 managing playful interactions in *Suricata suricatta*. In particular, meerkats perform the relaxed open  
355 mouth (ROM) during their playful contacts. Since ROM occurred more frequently without the

356 presence of play biting (Figure 2), it possibly underwent a ritualization process so that this specific  
357 facial expression should be considered as a signal. It is possible that also acoustic stimuli (not  
358 collected during this study) can have a concomitant role in fine-tuning the play session and it could  
359 be extremely interesting to evaluate if some vocalizations can accompany the ROM performance.  
360 Surprisingly, the perception of the ROMs emitted by the sender did not increase with the number of  
361 players involved in the session. Indeed, during dyadic play the perception of the signal was higher  
362 than during polyadic play (Figure 3, Prediction 1b not supported). This finding suggests a certain  
363 degree of social sensitivity because the animals seem to be able to place the facial expressions in the  
364 appropriate social context (e.g., receiver attention). This is in agreement with the evidence obtained  
365 in several primate and non-primate species. In a very recent paper, Taylor et al. (2019) demonstrated  
366 that sun-bears (*Helarctos malayanus*) produce open-mouth faces mainly when the sender has got the  
367 attention of the receiver. Ring-tailed lemurs (*Lemur catta*) that, as meerkats, are characterized by  
368 well-developed olfactory and acoustic communicative systems (Jolly 1966), engage in ROM to  
369 modulate their play fighting interactions which can be extremely risky due to the high levels of  
370 despotism shown by the species. In lemurs, ROM was particularly frequent during dyadic playful  
371 sessions and when play fighting was strongly unbalanced (Palagi et al. 2014). ROM has also been  
372 demonstrated in the South American sea lion (*Otaria flavescens*, Llamazares-Martín et al. 2017) and  
373 in dogs (*Canis lupus familiaris*, Palagi et al. 2015). In these species, ROM is expressed through a  
374 similar motor action (the mouth is kept open in a relaxed way without any retraction of the lip  
375 corners), it is context specific (play), it can be adjusted to maximize the probability to be perceived  
376 and it has a role in prolonging the duration of the playful interaction. Data coming from literature  
377 strongly suggest that ROM is a highly conserved trait that is shared among mammals (Preuschoft and  
378 van Hooff 1995). In this perspective, the presence of ROM in meerkats is not surprising due to the  
379 social affiliation typical of the species. The high levels of social cohesiveness, well demonstrated in  
380 meerkats (Manser et al. 2014; Clutton-Brock and Manser 2016), require sophisticated communicative  
381 skills often based on different sensory modalities (Freeberg 2012). In some cases, visual signals can

382 be preferred to acoustic signals by players to reduce the probability to be detected by predators,  
383 especially when the attentional level of the subject is focussed on the playmate and not on the  
384 surrounding environment as it occurs during play fighting. This hypothesis, however, deserves further  
385 studies based on a multi-modal approach and conducted on a larger number of social groups both in  
386 captivity and in the wild.

387 Even though our study has been conducted on a single group of captive meerkats, it demonstrates the  
388 presence of rapid facial mimicry (RFM) in this species (Figure 4; Prediction 2a supported). In  
389 primates, RFM was not found in all the species tested. According to the *Covariance Hypothesis*  
390 (Thierry 2000), it seems that this behavioural trait covaries with the level of tolerance and affiliation  
391 characterizing each species (see Palagi and Scopa 2017 for an extensive review). Primates living in  
392 cooperative and egalitarian societies clearly show the phenomenon of emotional mimicry (Tonkean  
393 macaques, Scopa and Palagi 2016; geladas, Mancini et al. 2013) which is inhibited when the social  
394 relationship between animals are built upon strict dominance more than affiliative interactions  
395 (despotic societies) (Japanese macaques, Scopa and Palagi 2016). Rapid mimicry can also be found  
396 under particular conditions. When subjects belonging to solitarily species grow up in a social  
397 environment and have the opportunity to spend together a large amount of time, motor resonance  
398 phenomena can emerge (orang-utans, Davila-Ross et al.2008; sun bears, Taylor et al. 2019). The  
399 meerkat society is extremely cohesive and this could have favoured the evolution of facial mimicry,  
400 which is linked to the basic form of emotional contagion (Prochazkova and Kret, 2017). The linkage  
401 between RFM and emotional contagion in meerkats seems to be supported by our finding showing a  
402 strong positive correlation between the relationship quality shared by subjects and their levels of RFM  
403 (Figure 5) (Prediction 2b supported). Moreover, some forms of prosociality have been reported in  
404 meerkats (Madden and Clutton-Brock 2011). Oxytocin, a neuropeptide hormone, has been  
405 demonstrated to play a role in shaping prosocial behaviours in this species (Madden and Clutton-  
406 Brock 2011). The nasal oxytocin administration has been demonstrated to increase facial mimicry  
407 and emotional contagion in humans (Korb et al. 2016) and dogs (Somppi et al. 2017) thus suggesting



408 that oxytocin has a role in modulating fundamental emotional processing through a mechanism that  
409 may facilitate communication between subjects. Further studies would clarify the role of oxytocin in  
410 modulating rapid facial mimicry in meerkats to verify if the phenomenon of emotional contagion can  
411 be one of the engines of helping behaviour in this species.

412 It is now widely accepted that mammals express and perceive emotions and that this capacity has an  
413 adaptive value because it allows animals to respond to various situations quickly (e.g., fear) and  
414 appropriately (e.g., play) thus facilitating survival and increasing fitness (Mendl et al. 2010;  
415 Watanabe and Kuczaj 2013). Through spontaneous facial mimicry animals can share their emotional  
416 mood and this appears to be particularly adaptive when the relationships are not inhibited by rank  
417 rules and when animals build and maintain their bonds through cooperation and social affiliation  
418 (Nakahashi and Ohtsuki 2015). During play animals experience a positive mood that is often unveiled  
419 through facial expressions (e.g., ROM). The automatic and rapid replication of the playmate's facial  
420 expression is informative about reciprocal attentiveness, social sensitivity (*sensu* Taylor et al. 2019)  
421 and strong bonding (Palagi et al., 2015). Through the reflexive facial mimicry animals inform  
422 playmates that the signal has been perceived and interpreted (i.e., fast mirroring response) thus  
423 making the interactions more successful. This process seems to be sustained by the quality of  
424 relationship shared by subjects (Palagi and Scopa, 2017). Accordingly, in meerkats the presence of  
425 RFM during play fighting (Figure 6) and the quality of relationship shared by the players significantly  
426 prolonged the interaction (Figure 7). In absence of RFM, the mere perception of the relaxed open  
427 mouth did not produce the same effect on the duration of play (Figure 6). It seems, therefore, that in  
428 meerkats the facial motor mirroring and the relationship quality can inform emotional sharing (see  
429 Prochazkova and Kret, 2017 for an extensive review).

430 In conclusion, even though meerkats rely on olfactory and acoustic cues to manage most of their  
431 maintenance activities, it seems that during their playful, self-rewarding interactions they can make  
432 large use of visual cues as well. They not only perform the typical playful facial expression emitted  
433 by many other mammals (the Relaxed Open Mouth), but they are also able to engage in rapid facial

434 mimicry, a motor resonance process sustained by social bonding, which in human and non-human  
435 primates is considered to be linked to the phenomenon of emotional contagion. A multi-modal  
436 approach to the study of rapid mimicry would clarify if and how the integration of different sensory  
437 modalities (e.g., visual and acoustic) can modulate motor resonance phenomena.

438

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443

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644 **Compliance with ethical standards**

645 **Conflict of interest** The authors declare that they have no conflict of interest.

646 **Ethical approval** As the present study was exclusively observational without any manipulation of  
647 animals, all applicable international, national, and/or institutional guidelines for the care and use of  
648 animals were followed. Also, all procedures were in accordance with the ethical standards of the  
649 University of Pisa.

650 **Informed consent** No need for an informed consent for this study

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**Table 1** – Group of *Suricata suricatta* hosted by Zoological Gardens of Pistoia.

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| Name    | Sex | Date of Birth | Age      | Mark            | NDS   |
|---------|-----|---------------|----------|-----------------|-------|
| M_alpha | ♂   | 02/2008       | adult    | -               | 8.027 |
| B_alpha | ♂   | 06/2009       | adult    | tail            | 7.261 |
| F       | ♀   | 05/2013       | adult    | side            | 5.449 |
| ZAS     | ♂   | 05/2014       | adult    | left frontlimb  | 5.716 |
| S       | ♂   | 05/2015       | adult    | shoulder        | 5.115 |
| SPEL    | ♂   | 05/2015       | adult    | tail basis      | 6.395 |
| ZDD     | ♂   | 05/2015       | adult    | right hindlimb  | 6.242 |
| ZDS     | ♂   | 05/2015       | adult    | left hindlimb   | 6.151 |
| T       | ♂   | 07/2015       | adult    | head            | 6.265 |
| ZAD     | ♂   | 07/2015       | adult    | right frontlimb | 5.499 |
| MAX     | ♂   | 03/2016       | immature | -               | 4.448 |
| MIN     | ♂   | 03/2016       | immature | -               | 5.432 |
| PULCE   | ♂   | 06/2016       | immature | -               | 6.000 |

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**Table 2.** Behavioral items recorded during the study. Ethogram based on Wemmer and Fleming (1974) and integrated by preliminary observations on the colony under study.

| <b>PLAY PATTERNS</b>       | <b>DEFINITIONS</b>   |
|----------------------------|--|
|                            | <b>Offensive play patterns</b>   |
| Ambush (o)                 | The player approaches the playmate from behind (when it is turned or distracted in doing another activity) and performs a play pattern   |
| Attempt to bite (o)        | An individual moves its open mouth towards the playmate and quickly closes the mouth touching or not the playmate's skin which, however, is never bitten. Each body part can be the target of the behaviour. While closing the mouth the animal lunges at the playmate trying to catch it. |
| Grasping from behind (o)   | The player supports its forebody on playmate's back while clasping the other's sides, between the ribcage and groin  |
| Body play bite (o)         | Bite directed to the back of the playmate's body, without damage to the receiver   |
| Grasping (o)               | The player grabs the playmate surrounding it with the forelimbs  |
| Knock down (o)             | The player push the playmate to the ground   |
| Muzzle play bite (o)       | Bite directed to the muzzle of the playmate, without damage to the receiver  |
| Nape play bite (o)         | Bite directed to the nape of the playmate, without damage to the receiver  |
| Neck play bite (o)         | Bite directed to the neck of the playmate, without damage to the receiver  |
| Over (o)                   | One animal stands over a playmate who adopts a submissive posture lying on its back  |
| Paw play bite (o)          | Bite directed to the paw of the playmate, without damage to the receiver   |
| Play nose push (o)         | To push away the playmate with the muzzle  |
| Play push (o)              | To push away the playmate  |
| Play retrieve (o)          | The player holds his playmate who tries to escape with his forelimbs   |
| Play run (o)               | To chase the playmate  |
| Play slap (o)              | The individual gently slaps any part of the playmate's body  |
| Pull (o)                   | The individual pulls the playmate with his forelimbs   |
| Push with paws (o)         | The player tries to move away his playmate by pushing him away with his paws (usually the first player is in a supine position)  |
| Shoulder play bite (o)     | Bite directed to the shoulder of the playmate, without damage to the receiver  |
| Side play bite (o)         | Bite directed to the side of the playmate, without damage to the receiver  |
| Tail play bite (o)         | Bite directed to the tail of the playmate, without damage to the receiver  |
| Throat play bite (o)       | Bite directed to the throat of the playmate, without damage to the receiver  |
| Ventral play bite (o)      | Bite directed to the ventral part of the playmate's body, without damage to the receiver   |
|                            | <b>Defensive play patterns</b>   |
| Jump (d)                   | The player performs a jump to get away   |
| Supine play invitation (d) | The player A approaches the player B after a brief play session and lies down on his back in contact with B, looking at him/her.   |
|                            | <b>Neutral play patterns</b>   |
| Grappling (n)              | Both animals stand bipedally, clasping each other with their forelegs and attempting to push one another over  |

|                                  |  |
|----------------------------------|--|
|                                  |  |
| Play grooming (n)                | The players interrupt the play, clean each other and then start playing again  |
| Piroetting (n)                   | The individual performs a somersault   |
| Muzzle rubbing (n)               | The player rubs his muzzle against the playmate  |
| Leave (n)                        | The player moves away and leaves the play session  |
| Licking genitals (n)             | The player licks the genitals of the playmate during play  |
| Nose body contact (n)            | Muzzle-body contact: the individual smells a body area of the playmate, excluding the nose (play nose to nose contact) and the genitals (play sniff genitals)  |
| Play nose-to-nose contact (n)    | Muzzle-muzzle contact: two players approach and touch each other's nose  |
| Play scratching (n)              | The individual scratches himself/herself during a play session   |
|                                  |  |
| Play sniff genitals (n)          | The individual smells the genitals of the playmate   |
| Reciprocal knock down (n)        | The players push each other to the ground  |
| Reciprocal mouth bite (n)        | The player A grasps the inferior jaw of the player B with his/her mouth, while the player B grasps the inferior jaw of the player A with his/her mouth at the same time  |
| Reciprocal muzzle play bite (n)  | The players bite the muzzle each other in a non-harmful way  |
| Reciprocal neck play bite (n)    | The players bite the neck each other in a non-harmful way  |
| Reciprocal nose body contact (n) | Muzzle-body contact: the players smell the body areas each other   |
| Relax open mouth (n)             | An individual opens and closes its mouth while moving towards a playmate. Upper and lower teeth may be exposed and visible. The degree of opening has to reach at least the 50% of the mouth's maximum aperture. |
| Rolling (n)                      | The individual turns its body from side while supine   |
| Rubbing (n)                      | The player rubs his body side against playmate   |
| <b>AFFILIATIVE PATTERNS</b>      | <b>DEFINITION</b>  |
| Body contact                     | The individual is sitting or lying in contact with other individuals   |
| Directional grooming             | One subject cleans different parts of the companion's body, using the mouth or the forepaws  |
| Embracing/huddle                 | The subject A put its forelimbs around the body of the subject B   |
| Mutual grooming                  | The two subjects clean different parts of the their bodies by using the mouth or the forepaws  |

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**Notes:** **o** = **offensive** pattern (those attack/pursuit playful patterns giving to one of the players a distinct and clear physical advantage over the partner); **d** = **defensive** pattern (those patterns by which the player tries to cope with attack/pursuit playful patterns performed by the partner, the subject performing the defensive pattern generally attains or maintains a losing position); **n** = **neutral** pattern (those patterns not showing any attack/pursuit or losing nature).

| NAME   | TYPE   |
|--|--|
| <b>DEPENDENT VARIABLE</b>                                |  |
| Play Duration (seconds)                                  | Continuous   |
| <b>FIXED EXPLANATORY VARIABLES</b>                       |  |
| Play Asymmetry Index                                     | Continuous   |
| Relationship Quality                                     | Continuous (frequency of affiliative patterns)   |
| RFM  | Nominal (0=ROM not present or not perceived;<br>1=at least 2 ROM but no RFM; 2=at least 1 RFM event) |
| N players  | Nominal (0=dyadic; 1=polyadic)   |
| SEX <sub>player1</sub>                                   | Nominal (0=male; 1=female)   |
| SEX <sub>player2</sub>                                   | Nominal (0=male; 1=female)   |
| $\Delta$ NDS (absolute value)                            | Continuous (NDS <sub>PL1</sub> -NDS <sub>PL2</sub> )   |
| AGE <sub>player1</sub>                                   | Nominal (0=immature; 1=adult)  |
| AGE <sub>player2</sub>                                   | Nominal (0=immature; 1=adult)  |
| <b>RANDOM VARIABLES</b>                                  |  |
| Identity <sub>player1</sub> *Identity <sub>player2</sub> | Nominal  |

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**Table 3** – Description of the variables used in LMM analysis. The dependent variable is Play Duration. Player1 initiated the play bout.

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**Table 4** - The AIC values for each of the models tested. The dependent variable=Play Duration. RFM=Rapid Facial Mimicry;  $\Delta$ NDS= differences of the NDS values of the individuals forming the different dyads.

| (n) MODELS   | AIC      | $\Delta$ AIC | Wi    | wi*100 |                         |
|--|----------|--------------|-------|--------|-------------------------|
| 1. RFM_relationship quality  | 1399.026 | 0.000        | 0.505 | 50.505 | best model              |
| 2. RFM_relationship quality_sex <sub>player1</sub> ,sex <sub>player2</sub> | 1401.409 | 2.383        | 0.153 | 15.342 | considerably less model |
| 3. RFM_relationship quality_age <sub>player1</sub> ,age <sub>player2</sub> | 1401.955 | 2.929        | 0.117 | 11.676 | considerably less model |
| 4. RFM_relationship quality_dyadic play,polyadic play                      | 1401.995 | 2.969        | 0.114 | 11.445 | considerably less model |
| 5. RFM_relationship quality_Play Asymmetry Index                           | 1403.830 | 4.804        | 0.046 | 4.573  | considerably less model |
| 6. RFM_relationship quality_ $\Delta$ NDS                                  | 1405.114 | 6.088        | 0.024 | 2.406  | considerably less model |
| 7. RFM   | 1405.824 | 6.798        | 0.017 | 1.687  | discounted model        |
| 8. RFM_age <sub>player1</sub> ,age <sub>player2</sub>                      | 1406.976 | 7.950        | 0.009 | 0.948  | discounted model        |
| 9. RFM_dyadic play,polyadic play   | 1407.869 | 8.843        | 0.006 | 0.607  | discounted model        |
| 10. RFM_sex <sub>player1</sub> ,sex <sub>player2</sub>                     | 1407.991 | 8.965        | 0.006 | 0.571  | discounted model        |
| 11. RFM_Play Asymmetry Index   | 1410.513 | 11.487       | 0.002 | 0.162  | discounted model        |
| 12. RFM_ $\Delta$ NDS  | 1411.533 | 12.507       | 0.001 | 0.097  | discounted model        |
| 13. Full model   | 1418.818 | 19.792       | 0.000 | 0.003  | discounted model        |
| 14. RFM* relationship quality  | 1433.782 | 34.756       | 0.000 | 0.000  | discounted model        |
| 15. dyadic play,polyadic play  | 1471.126 | 72.100       | 0.000 | 0.000  | discounted model        |
| 16. relationship quality   | 1472.657 | 73.631       | 0.000 | 0.000  | discounted model        |
| 17. relationship quality_sex <sub>player1</sub> ,sex <sub>player2</sub>    | 1476.546 | 77.520       | 0.000 | 0.000  | discounted model        |
| 18. Play Asymmetry Index   | 1478.600 | 79.574       | 0.000 | 0.000  | discounted model        |
| 19. relationship quality_ $\Delta$ NDS                                     | 1478.695 | 79.669       | 0.000 | 0.000  | discounted model        |
| 20. age <sub>player1</sub> , age <sub>player2</sub>                        | 1478.780 | 79.754       | 0.000 | 0.000  | discounted model        |
| 21. Intercept (null model)   | 1478.874 | 79.848       | 0.000 | 0.000  | discounted model        |
| 22. sex <sub>player1</sub> , sex <sub>player2</sub>                        | 1481.562 | 82.536       | 0.000 | 0.000  | discounted model        |
| 23. $\Delta$ NDS   | 1484.819 | 85.793       | 0.000 | 0.000  | discounted model        |

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715 **Table 5** – Results of the best model (RFM and Relationship Quality) and the four 'considerably less'  
 716 models explaining the distribution of Play Duration (PD) in meerkats. AICc=Akaike's Corrected  
 717 Information Criterion. RFM= Rapid Facial Mimicry; DIA=dyadic play; POLI=polyadic play.  
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| <b>MODELS (dependent variable = Play Duration)</b>       |          |            |            |               |
|--|----------|------------|------------|---------------|
| <b>Fixed Variables (AICc = 1399.026)</b>                 | <b>F</b> | <b>df1</b> | <b>df2</b> | <b>P</b>      |
| RFM  | 43.597   | 2          | 1.031      | <b>0.0001</b> |
| Relationship Quality                                     | 8.473    | 1          | 1.031      | <b>0.0040</b> |
| <b>Random variables</b>                                  | <b>Z</b> |            |            | <b>P</b>      |
| Identity <sub>player1</sub> *Identity <sub>player2</sub> | 1.128    |            |            | 0.259         |
| <b>Fixed Variables (AICc = 1401.409)</b>                 | <b>F</b> | <b>df1</b> | <b>df2</b> | <b>P</b>      |
| RFM  | 44.406   | 2          | 1.029      | <b>0.0001</b> |
| Relationship Quality                                     | 7.243    | 1          | 1.029      | <b>0.0070</b> |
| SEX <sub>player1</sub>                                   | 4.839    | 1          | 1.029      | <b>0.0280</b> |
| SEX <sub>player2</sub>                                   | 0.212    | 1          | 1.029      | 0.6450        |
| <b>Random variables</b>                                  | <b>Z</b> |            |            | <b>P</b>      |
| Identity <sub>player1</sub> *Identity <sub>player2</sub> | 1.589    |            |            | 0.112         |
| <b>Fixed Variables (AICc = 1401.955)</b>                 | <b>F</b> | <b>df1</b> | <b>df2</b> | <b>P</b>      |
| RFM  | 43.074   | 2          | 1.029      | <b>0.0001</b> |
| Relationship Quality                                     | 4.431    | 1          | 1.029      | <b>0.0360</b> |
| AGE <sub>player1</sub>                                   | 3.546    | 1          | 1.029      | 0.0600        |
| AGE <sub>player2</sub>                                   | 0.839    | 1          | 1.029      | 0.3600        |
| <b>Random variables</b>                                  | <b>Z</b> |            |            | <b>P</b>      |
| Identity <sub>player1</sub> *Identity <sub>player2</sub> | 1.786    |            |            | 0.074         |
| <b>Fixed Variables (AICc = 1401.995)</b>                 | <b>F</b> | <b>df1</b> | <b>df2</b> | <b>P</b>      |
| RFM  | 38.876   | 2          | 1.030      | <b>0.0001</b> |
| Relationship Quality                                     | 7.325    | 1          | 1.030      | <b>0.0070</b> |
| DIA_POLI   | 2.232    | 1          | 1.030      | 0.1350        |
| <b>Random variables</b>                                  | <b>Z</b> |            |            | <b>P</b>      |
| Identity <sub>player1</sub> *Identity <sub>player2</sub> | 1.047    |            |            | 0.295         |
| <b>Fixed Variables (AICc = 1403.830)</b>                 | <b>F</b> | <b>df1</b> | <b>df2</b> | <b>P</b>      |
| RFM  | 32.573   | 2          | 1.030      | <b>0.0001</b> |
| Relationship Quality                                     | 8.130    | 1          | 1.030      | <b>0.0040</b> |
| Play Asymmetry Index                                     | 2.338    | 1          | 1.030      | 0.1270        |
| <b>Random variables</b>                                  | <b>Z</b> |            |            | <b>P</b>      |
| Identity <sub>player1</sub> *Identity <sub>player2</sub> | 1.113    |            |            | 0.266         |

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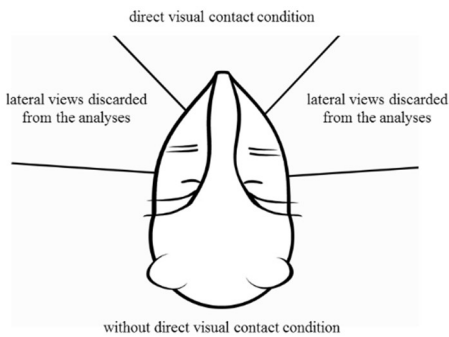
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724 **Legends**

725 **Figure 1** - Scheme illustrating the criteria used to evaluate the perception and no-perception  
726 conditions. We considered the head orientation of the receiver in relation to the head orientation of  
727 the sender. When the sender was in front of the receiver (i.e., within the range of its stereoscopic  
728 view, direct visual contact condition), we considered the facial expression as perceived. A ROM was  
729 considered not visually perceived when the potential receiver had his/her head rotated by 180° with  
730 respect to the sender (without direct visual contact condition). All the doubtful cases linked to lateral  
731 views were discarded from the analyses.

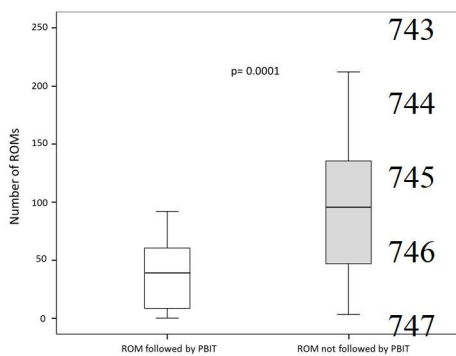


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739 **Figure 2** – Number of ROMs followed by a bite compared to the number of ROMs not followed by  
740 a bite. The box plots show the median and 25<sup>th</sup> and 75<sup>th</sup> percentiles; the whiskers indicate the values  
741 within 1.5 times the inter-quartile range, IQR.

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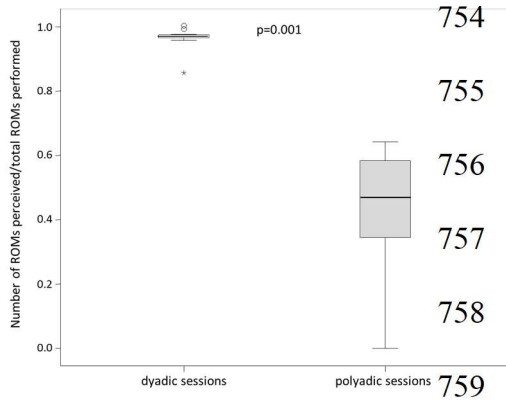


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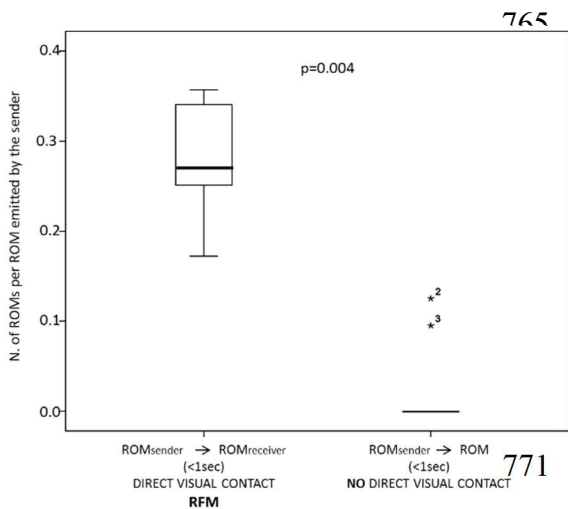
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751 **Figure 3** – Number of ROMs perceived on the total number of ROMs performed during dyadic and  
752 polyadic playful interactions. The box plots show the median and 25<sup>th</sup> and 75<sup>th</sup> percentiles; the  
753 whiskers indicate the values within 1.5 times the inter-quartile range, IQR.



760 **Figure 4** – ROM emitted by the receiver after the perception of the ROM emitted by the sender (direct  
761 visual contact within 1 s) compared with ROM performed when the stimulus emitted by the sender  
762 was not visually perceived by the receiver (no direct visual contact, within 1 sec). The box plots show  
763 the median and 25<sup>th</sup> and 75<sup>th</sup> percentiles; the whiskers indicate the values within 1.5 times the inter-  
764 quartile range, IQR.



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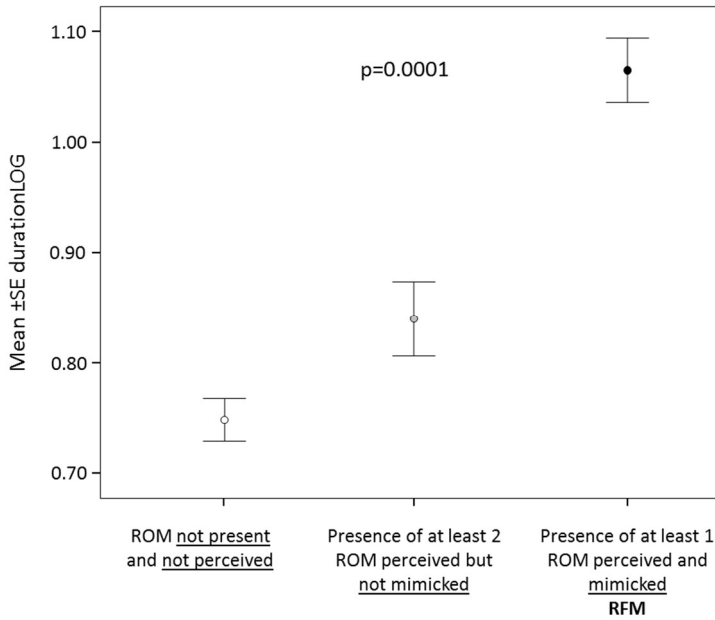
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793 **Figure 6** – Mean  $\pm$ SE of Duration ( $\text{LOG}_{\text{transformed}}$ ) of the play sessions according to the three  
794 conditions defined as follows: no ROM event present or not perceived by the receiver; at least two  
795 ROM events perceived by the receiver but not replicated within 1 sec; at least 1 ROM perceived and  
796 replicated within 1 sec by receiver (Rapid Facial Mimicry, RFM).



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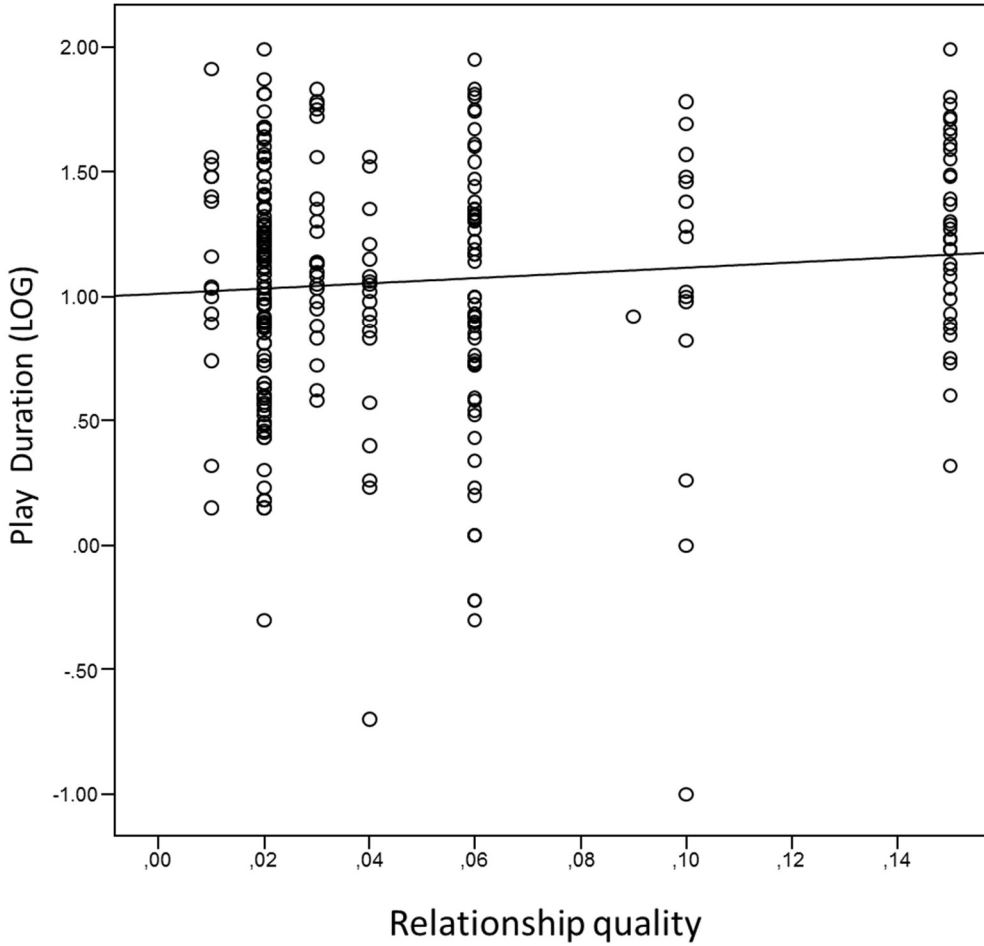
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811 **Figure 7** – Scatterplot showing the relationship between relationship quality (measured via affiliative  
812 patterns) shared by the subjects forming the dyad and play duration ( $\text{LOG}_{\text{transformed}}$ ).

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824 **Supplementary Figure 1** – Pictures showing the two conditions. A – direct visual contact condition.

825 The two animals are within the range of their stereoscopic view. B – without direct visual contact

826 condition. The player 1 performs the play face, but the player 2 is not able to perceive it.



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