Yawn contagion in humans and bonobos: emotional affinity more than species matters

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was higher in humans than in bonobos when involving kin and friends but was

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1 YAWN CONTAGION IN HUMANS AND BONOBOS: EMOTIONAL AFFINITY MORE

2 THAN SPECIES MATTERS

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9 **ABSTRACT**

10 In humans and apes, yawn contagion echoes emotional contagion, the basal layer of empathy.

11 Hence, yawn contagion is a unique tool to compare empathy across species. If humans are the

12 most empathic animal species, they should show the highest empathic response also at the level

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18 bonded subjects. Between species, sensitivity to others' yawns was higher in humans than in

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20 subjects. Thus, emotional contagion is not always highest in humans. The cognitive components

21 concur in awakening and nourishing emotional affinity between individuals. Yet, when they are

22 not in play, humans climb down from the empathic podium to return to the "understory", which

23 our species shares with apes.

25 **KEYWORDS**: *Homo sapiens*; *Pan paniscus*; emotional contagion; affective empathy; cognitive

26 empathy; cross-species comparison

INTRODUCTION

28 Most behavioral and cognitive studies have used the most sophisticated human abilities (e.g.

29 theory of mind and language) as the main ground to make comparative arguments. Yet, this top-

30 down approach has contributed to drawing the line between human and other animals' skills.

31 Indeed, selecting the emotional and cognitive pinnacles of the human brain (*sensu* de Waal &

32 Ferrari, 2010) can shed light on unique human traits but not on the common basic mechanisms

33 underlying the more complex ones (de Waal & Ferrari, 2010; Hecht et al., 2012). While the

34 hominin fossil record cannot give us any clues on the social and emotional abilities that may have

35 paved the way for the emergence of human empathy, studying synchronous behaviours and body

36 resonance (e.g. laughing, rapid facial mimicry, yawning; Provine, 2012; Davila-Ross et al., 2008;

37 Mancini et al., 2013a) in our closest living relatives may provide valuable information about how

38 empathy evolved.

39 Empathy is a multilayered phenomenon, whose shared basal forms represent the pre-existing

40 framework in which more complex emotional and cognitive processes are nestled (Preston & de

41 Waal, 2002; de Waal, 2008). Perceiving and sharing others' emotions, the so called

42 "affective empathy", is a phylogenetically old capacity. Affective empathy is

43 an automatic process and may come about through emotional contagion (de

44 Waal, 2008). At a higher layer of the empathic sphere, we find "cognitive

45 empathy" which requires self-other differentiation, perspective-taking and

46 mental state attribution, basic capacities to infer others' emotional states.

47 Affective and cognitive empathy dissociate in humans with the former

48 preceding the latter both ontogenetically and phylogenetically (Decety,

49 2010). Humans show the most complex form of empathy and, therefore, are commonly deemed

50 as the most empathic species (Preston & de Waal, 2002; Decety, 2004; Decety & Cowell, 2014).

51 However, no quantitative, direct inter-specific comparison has ever been made to actually

52 demonstrate that this assumption is true at each floor of the empathic building. Recent findings

53 endorse that other animals show affective empathy (Palagi et al., 2009; de Waal, 2012a; Panksepp

54 & Panksepp, 2013). In this view, cross-species research is needed to explore empathy capacities

55 as a bottom-up, emotional and developmental process of the brain (de Waal, 2012b). According

56 to several neurobiological (Cooper et al., 2012; Haker et al., 2013), psychological (Lehmann,

57 1979; Platek et al., 2003) and ethological findings (Palagi et al., 2009; Campbell & de Waal,

58 2011, 2014; Romero et al., 2013) yawn contagion is an empathy-related phenomenon.

59 Specifically, yawn contagion is a form of emotional contagion, which represents the most basal

60 layer of the empathic sphere (Preston & de Waal, 2002; Hatfield et al., 2009). Several good

61 reasons make the yawn and its contagion excellent phenomena to explore the evolutionary roots

62 of empathy.

63 Due to its evolutionary antiquity, a yawn can be easily detected and quantified, appearing

64 morphologically identical across many different vertebrate taxa and, consequently, withdrawing

65 the risk of any subjective interpretation (Provine, 2005). Therefore, the plesiomorphic nature of

66 yawning enables cross-species research (Baenninger 1987, 1997; Deputte, 1994; Guggisberg et

67 al., 2010). Yawning is automatic, unstoppable and easily recognisable also when people try to

68 hide or inhibit it due to cultural constraints (Lehmann, 1979). These features make this behaviour

69 an honest signal and, therefore, highly reliable (Provine, 1986).

70 Yawn contagion is obvious in human beings - about 50 percent respond to video stimuli of

71 yawning faces (Provine, 1986) - and seems to be based on a perception-action mechanism

72 (Preston & de Waal, 2002; de Waal, 2012c), which consists in the involuntary re-enactment of an

73 observed facial expression and creates shared representations. Neurophysiological evidence of

74 this coupling has derived from the discovery of mirror neurons (di Pellegrino et al., 1992),

75 recently associated with yawn contagion (Cooper et al., 2012; Haker et al., 2013). Therefore,

76   yawn contagion provides a "low-tech" but significant evidence of mirror-like phenomena. Mirror

77   neurons, firstly described in the pre-frontal cortex of the rhesus macaque, fires when the subject

78   either performs a motor action or observes the same action performed by another subject (Gallese

79   et al., 1996; Ferrari et al., 2003). A mirror system, homologous to that of macaques, has been later

80   discovered in humans (Rizzolatti & Craighero, 2004). The mirror mechanism (or motor

81   mimicry), not requiring any kind of conscious awareness, creates an emotional bridge and, thanks

82   to it, two individuals can synchronize their affective states (Hatfield et al., 2009). This emotional

83   bridge, in turn, fosters mirroring and triggers a positive feedback which constitutes the core of

84   social affinity. Such feedback is more easily activated when subjects sharing a strong empathic

85   bonding are involved. While a positive attachment enhances body and emotional resonance (e.g.

86   emotional reactions, unconscious mimicry, self-other overlap and shared representations), a

87   negative attachment or a prejudice can inhibit or suppress it (Xu et al., 2009; Avenanti et al.,

88   2010). In humans, when the attachment is profoundly negative (as in case of defectors, enemies,

89   competitors) empathy can even turn into *Schadenfreude* that is feeling pleasure from the

90   sufferings of others (de Waal, 2008; Decety & Cowell, 2014). This emotional circuitry, in its

91   positive and negative form, has been found not only in humans (Singer et al., 2006; Pfeifer et al.,

92   2008) but also in monkeys (Masserman et al., 1964; Palagi et al., 2009; Mancini et al., 2013a,b;

93   Ferrari et al., 2009; Paukner et al., 2009) and apes (Anderson et al., 2004; Davila-Ross et al.,

94   2008; Campbell & de Waal, 2011, 2014).

95   In humans (*Homo sapiens*) and one of its closest living phylogenetic relatives, the bonobo (*Pan*

96   *paniscus*), yawn contagion is present and significantly affected by the emotional closeness

97   linking the responder to the first yawner (the trigger). In the two species, the yawn response is

98   most likely when the yawning stimulus comes from kin or friends (Norscia & Palagi, 2011;

99   Demuru & Palagi, 2012). Since both in humans and bonobos yawn contagion is a socially

100   modulated phenomenon, these species are good models to test some hypotheses on the

101   evolutionary origins of the linkage between yawn contagion and empathy. The opportunity

102   provided by yawn contagion to apply the same unit of measurement and identical operational

103   definitions permits to directly compare human empathy with that of other species. Indeed, most

104   of the studies on empathic capacities in *Homo sapiens* have been carried out through

105   questionnaires used to measure self-reported scores of empathy. This approach bears the risk of

106   overestimating the human empathic potential and leads to the unfeasibility of comparing it to that

107   of other species (Lawrence et al., 2004).

108   As a whole, the possibility to employ a highly straightforward behaviour, such as yawning, to

109   explore a highly complex phenomenon, such as empathy, represents a unique opportunity to

110   investigate and compare empathy in human and non-human species (de Waal, 2012b).

111   Theoretically, humans could appear as the most empathic species not because they experience

112   greater emotional contagion (affective empathy) but because they can better understand others'

113   perspective and simulate others' emotional experiences (cognitive empathy). Indeed, empathy is a

114   construct comprising dissociable components interacting and operating in parallel (Decety &

115   Cowell, 2014). Cognitive empathy can be impaired in autistic subjects (Dziobek et al., 2008;

116   Usui et al., 2013) whereas emotional empathy can be dramatically impaired in narcissistic

117   individuals (Ritter et al. 2011), criminal psychopaths (Woodworth & Porter, 2002), rapists

118   (Englander, 2007), and child molesters (Marshall et al., 2001). Yet, both emotional and cognitive

119   empathy contribute to physiological human empathy (Cox et al., 2011; Decety & Cowell, 2014).

120   Therefore, if humans are actually the most empathic species, they should possess the highest

121   empathic response starting with emotional contagion, the ground level of affective empathy.

122   We tested this hypothesis by comparing our species with bonobos, which diverged from the

123   human line about 5-7 mya (Fleagle, 2013). We expect that the frequency of yawn response is

124   always higher in humans than in bonobos, whatever the relationship quality linking the responder

125   to the trigger. Since the time elapsing from the yawn stimulus to the response can be reduced

126 when the social bond is strong (Norscia & Palagi, 2011), we also expect that the emotional

127 affinity linking the subjects affects, more in humans than in bonobos, the promptness of the yawn

128 response.

129

130 **METHODS**

131 **(a) Ethics statement**

132 This study was purely observational, with no manipulation whatsoever. For humans, information

133 was entered in an anonymous form. Thus, the ethics committee of the University of Pisa waived

134 the need for a permit.

135 **(b) Data collection**

136 We gathered data on yawn contagion in both species in their daily life environment, by applying

137 the same observational paradigm based on identical operational definitions. The naturalistic

138 approach has been selected because it permits to collect reliable data thanks to the absence of

139 invasive, artificial management practices (social isolation, spatial limitation, interaction with

140 novel objects and persons) which can produce different psychological and behavioural biases in

141 the two species, and differential attention to artificial stimuli. For example, previous research on

142 humans has demonstrated that the awareness of being observed can inhibit yawns (Provine, 2005)

143 whereas simply reading about yawning is sufficient to trigger yawns (Provine, 1986) and possibly

144 inflate yawn response in the experimental subjects (Bartholomew & Cirulli, 2014).

145 *Humans* - Naturalistic observations on humans were performed over a total of 380 hours (in

146 2010, 2011 and 2013) and involved 33 adults, 19 females and 14 males. The study subjects were

147 observed during their everyday activity, in their natural social setting (at work, in restaurants,

148 waiting rooms, during social meals, etc.). In public spaces, the authors sat down close to the study

149 subjects and observed. Subjects included people known to the authors, such as friends, family

150 members, coworkers, and students. The study also included individuals that the authors did not

151 know but whose personal information (e.g., country of origin and social bond with other study

152 subjects) was stated by the observed subjects during conversations. Data were typed and stored in

153 mobile phones (e.g., during dinners), entered in the laptop (when possible, e.g., on the train), or

154 noted down on paper (e.g., in public spaces where this practice could easily go unnoticed). Data

155 collection occurred only when at least five subjects were present to make observations on humans

156 comparable with the observations on bonobos (see below). During each observation bout

157 (spanning 1-4 hours), yawns were collected via the all occurrences sampling method (Altmann,

158 1974). Dyads of strangers were excluded. We collected a total of 1375 yawn events. The

159 observed subjects were not aware of being under investigation and the data collected were

160 entered in an anonymous form with an alphanumerical code uniquely assigned to each subject.

161 *Bonobos* - Naturalistic observations on bonobos were daily performed on the colonies hosted at

162 the Apenhuel Primate Park (Apeldoorn, The Netherlands) and at the Wilhelma Zoo (Stuttgart,

163 Germany) for a total of 502 and 323 hours, respectively (2009/2010). The all occurrences

164 sampling observations involved 16 adults, 12 females and 4 males in different contexts (foraging,

165 resting, feeding both indoor and outdoor). At least five bonobos were always present in the same

166 enclosure. During each observation bout (spanning 2-5 hours), yawns were collected via the all

167 occurrences sampling (Altmann, 1974). We collected a total of 1125 yawn events for the

168 Apenheul group and 998 for the Stuttgart group.

169 Both for humans and bonobos when a subject spontaneously yawned, we recorded 1) time; 2) the

170 encoded identity of the yawner (hereafter, the "trigger") and of each potential responder

171 (hereafter, the "observer"), that is every individual that could visually and/or auditorily perceive

172 the triggering yawn; 3) presence/absence of contagion within 3-min following the last triggering

173 yawn; 4) time latency in the yawn response; 5) trigger's and observer's sex. Before starting

174 systematic data collection, the three observers (the authors) underwent a training period during

175 which they simultaneously followed the same group of subjects. The training procedures were

176 identical for the two species. Each yawning event and the possibility to perceive it by other

177 observed subject were the items we considered for the calculation of the Cohen's kappa. Training

178 ended when the observations produced a Cohen's kappa >0.80. Every 50 hours of data collection

179 we checked observational reliability (Cohen's kappa never <0.80).

180 **(c) Operational definitions**

181 In humans we defined strongly and weakly bonded dyads on the basis of previous literature

182 (Norscia & Palagi, 2011). Friends, regular partners, and kin were labeled as strongly bonded

183 dyads. Friends were defined as non related individuals sharing a direct relationship, frequenting

184 each other voluntarily. Regular partners were defined as couples living together from at least one

185 year. Those dyads having a coefficient of relatedness $r \geq 0.25$ were defined as kin (7 dyads, r=0.5;

186 1 dyad=0.25). Weakly bonded dyads involved acquaintances, that is people who exclusively

187 shared an indirect relationship based on a third external reference, for example work duty

188 (colleagues) or friends in common (friends of friends). The relationship between people was

189 known to the authors. Ambiguous cases were excluded from the dataset (e.g. kin with r<0.25,

190 colleagues frequenting each other outside work).

191 In bonobos we also categorized strongly and weakly bonded dyads on the basis of previous

192 literature (Demuru & Palagi, 2012; Palagi & Norscia, 2013). By focal animal sampling (Altmann,

193 1974 - 25 hours of observation per subject), we were able to record all the contact sitting,

194 grooming, and food sharing sessions performed by each focal animal with any other group

195 member. Each subject was followed every day (each focal lasted 30 minutes) and at different

196 times to obtain data covering the entire day in balanced proportions as much as possible. Friends

197 and kin were clustered into the strongly bonded category. Friend dyads were categorized using a

198 combined measure of the three behaviors collected during focal observations and calculating the

199 quartile points of dyadic scores for each focal individual. Only dyads with scores falling into the

200 top quartile were considered as friends. Kinship was based on maternal lineages only, as paternity

201 was unknown. Our kin sample consisted in 7 dyads (r=0.5), all showing top frequencies of

202 affinitive contact exchange (strong bond). All the dyads not included in the previous categories

203 (non-kin dyads' scores falling outside the top quartile) were labeled as weakly bonded.

204 **(d) Statistics**

205 Due to the normality of data (Kruskall-Wallis, p>0.05), we made use of parametric statistics.

206 Independent sample t-test was used to compare the frequency and the latency of yawn contagion

207 between the two species.

208 To explore the effect of the different variables on the frequency of yawn contagion we analyzed

209 data via Linear Mixed Model (LMM). The dependent scale variable was the relative frequency of

210 yawn contagion of each observer; that is, the number of yawns the observer performed after

211 perceiving a given trigger's yawn normalized on the number of occasions (number of a given

212 trigger's yawns perceived by the observer). In the analysis, triggers and observers' identities were

213 entered as random factors (nominal variables). We tested models for each combination involving

214 the variables of interest, spanning from a single-variable model to a model including all the fixed

215 factors (full model). To select the best model, we used the Akaike's Corrected Information

216 Criterion (AICc), a measure for comparing mixed models based on the -2 (Restricted) log

217 likelihood. The AICc corrects the Akaike's Information Criterion (AIC) for small sample sizes.

218 As the sample size increases, the AICc converges to AIC. The model with a lower value of AIC

219 was considered to be the best model. To avoid the increase of type II errors, factors were

220 excluded from a model only if this improved the model fit by >2 AICc units. The value of

221 degrees of freedom is given by the effective sample size (N) minus the rank design matrix of

222 fixed effects (X). The denominator degree of freedom is estimated by SPSS via Satterthwaite's

223 approximation.

224 To check for the inter-specific differences in the frequency of yawn contagion between weakly

225 and strongly bonded dyads we applied the randomization test for two independent samples. This

226 kind of procedure is used to avoid pseudo-replication due to non-independence of data (the same

227 individual is included in more than one dyad; therefore, dyads are not independent data-points).

228 Specifically, randomization tests were employed with a number of 10,000 permutations using

229 resampling procedures (via Resampling Procedures 1.3 package by David C. Howell).

230 To test for the individual differences in the latency of yawn contagion as a function of

231 relationship quality shared by subjects, we used the paired sample t-test.

232

233 **RESULTS**

234 The individual yawn response did not differ between the two species (mean yawn response ±SE:

235 *Homo*=0.296 ±0.042; *Pan*=0.210 ±0.029; Independent sample test: t=1.348; df=47; p=0.184).

236 Both humans (Norscia & Palagi, 2011) and bonobos (Demuru & Palagi, 2012) (Supplementary

237 Video 1) preferentially responded within the first minute after perceiving a yawn. However, our

238 direct comparison between the two species showed that, within the first minute, humans'

239 responses were more frequent than bonobos' (first minute: Independent sample test: t=3.854;

240 df=37; p<0.0001), who showed a longer tail-effect in their contagion response compared to

241 humans (second minute: t=-0.737; df=37; p=0.466; third minute: t=-7.555; df=37; p<0.0001)

242 (Fig. 1). Since this analysis considered three different minutes in which yawn contagion may

243 occur, only the subjects showing at least three contagion events were included in the test.

244 We employed Linear Mixed Models (LMM) to verify which variables could explain the variation

245 in the frequency of yawn contagion (dependent variable). Data distribution was normal. Species

246 (*Homo sapiens*/*Pan paniscus*), trigger and observer's sex, and social bonding (weak/strong) were

247 entered as fixed factors. Trigger and observer's identities were entered as random factors. This

248 analysis was restricted to those dyads in which each contagion event could be univocally

249 assigned to a specific trigger and when the opportunities were at least 3 per dyad. For these

250   reasons, the LMM dataset included 44 human and 56 bonobo dyads with 375 and 484 contagion

251   events, respectively.

252   Both species and social bonding remained in the best model (best model AICc =-3.312; worst

253   model $_{\text{intercept only}}$ AICc=6.828) and significantly affected the frequency of yawn contagion (Table

254   1).

255   In both humans and bonobos, yawn contagion was higher between individuals sharing strong

256   relationships (randomization test for two independent samples: bonobos, t=-2.772, N_{strong}=28

257   dyads, N_{weak}=28 dyads p=0.0061; humans, t=-3.646, N_{strong}=28 dyads, N_{weak}=16 dyads, p=0.0007).

258   At the inter-specific level, the frequency of yawn contagion in humans and bonobos significantly

259   differed only when strongly bonded dyads (N_{Pan}=28; N_{Homo}=28) were involved (randomization

260   test for two independent samples t=-3.916, p=0.0001). On the contrary, weakly bonded dyads

261   (N_{Pan}=28; N_{Homo}=16) of the two species did not differ in the frequency of yawn contagion

262   (randomization test for two independent samples t=-0.799, p=0.455) (Fig. 2).

263   In order to understand if the response latency was affected by the relationship quality shared by

264   the trigger and the responder in the two species, we analyzed the minute distribution of the

265   response as a function of weak and strong bonds. In bonobos, the analysis showed that the

266   response latency did not change as a function of the relationship quality (Paired sample test: t_{1min}

267   =-0.233, df=12, p=0.820; t_{2min} =0.196, df=12, p=0.848; t_{3min} =0.199, df=12, p=0.846; Fig. 3a). On

268   the contrary, in humans, the response latency was sensitive to the relationship quality. The human

269   subjects concentrated their response within the first minute only when the yawn stimulus came

270   from a strongly bonded subject (Paired sample test: t_{1min} =4.760, df=12, p=0.0001). On the other

271   hand, the human subjects responded more frequently in the second and third minute after

272   perceiving the yawn stimulus from a weakly bonded trigger (t_{2min} =-3.774, df=12, p=0.003; t_{3min}

273   =-2.670, df=12, p=0.020; Fig. 3b). All these analyses included only subjects showing at least

274   three contagion response per each bonding category (weak and strong).

275

DISCUSSION

The inter-specific analysis of the overall frequency of yawn contagion did not reveal any difference between human and bonobo response susceptibility. The inter-species comparison revealed a higher promptness in humans than in bonobos, who showed a longer tail-effect in their response latency. However, both species concentrated their responses within the first minute after perceiving the stimulus yawn (Figure 1). Being yawn contagion the expression of a mirror-like phenomenon (Cooper et al., 2012; Haker et al., 2013), our findings suggest not only that yawn contagion is well-rooted in the biology of bonobos and humans but also that the neural processes underlying and modulating yawn contagion might have been already present in the most recent common ancestor of the two species (5-7 mya, Fleagle, 2013). The similar sensitivity to others' yawns shown by the two species is probably due to similar selective pressures. In fact, both species are characterized by obligate gregariousness based on one of the most complex forms of social structure: the fission-fusion system (Aureli et al., 2008). Behavioural (Couzin, 2007) and emotional synchronization (Špinka, 2012) has been playing a pivotal role in favouring and shaping the evolutionary pathways leading to social living (Supplementary Video 1). Synchronizing with others requires the ability to mirror their motor actions, to experience their emotional states and, consequently, to act in the appropriate manner. In this process familiarity makes the difference. Our intra-specific analysis demonstrated that yawn contagion is a socially modulated phenomenon, with strongly bonded subjects showing a higher susceptibility than weakly bonded subjects, thus confirming previous results (humans, Norscia & Palagi, 2011; bonobos, Demuru & Palagi, 2012). In this respect, the degree of contagion of around 50% reported by previous studies using videos of strangers' yawns as stimuli (Provine 2005) may be a conservative estimate.

299   The social modulation of yawn contagion has been proven also in the congeneric species of

300   bonobos, the chimpanzee (*Pan troglodytes*). Chimpanzees are more susceptible to respond to

301   videos showing yawns performed by in-group than by out-group members (Campbell & de Waal,

302   2011). This result is in line with a great body of research on human in-group/out-group bias that

303   affects numerous empathy-driven behavioural and emotional reactions (Bourgeois & Hess, 2008;

304   Xu et al., 2009; Avenanti et al., 2010). Recently, Campbell and de Waal (2014) also found that the

305   rate of chimpanzee response to others' yawns was similar when the stimulus came from an in-

306   group chimpanzee and from a human subject, thus demonstrating that the chimpanzee

307   involuntary empathic response goes beyond the species boundary, as it occurs in humans

308   (Phillips, 2009). Yet, no evidence of a social modulation in chimpanzee yawn contagion emerged

309   as a function of the relationship quality shared between the responder and the in-group, familiar

310   trigger (Massen et al., 2012). Both neuroanatomical (Rilling et al., 2012) and behavioral features

311   (Hare et al., 2012) can account for the different effect of the relationship quality on chimpanzee

312   and bonobo yawn contagion. Compared to chimpanzees, bonobos seem to show a different

313   emotional and affective sensitivity (Furuichi, 2011; de Waal & Lanting, 1997; Hare et al., 2007)

314   and a milder competitive propensity (Kano, 1992; Tan & Hare, 2013). Moreover, genetic findings

315   revealed that a DNA segment regulating the responses to a hormone involved in social bonding

316   (vasopressin) is present in humans and bonobos, but can lack in chimpanzees (Hammock &

317   Young, 2005). However, the different effects of the relationship quality on yawn contagion in the

318   two *Pan* species has to be taken cautiously due to the different methodological approaches used

319   to verify and quantify the phenomenon (video stimulus - Massen et al., 2012; living stimulus -

320   Demuru & Palagi, 2012).

321   At the inter-specific level, striking differences emerged in the social modulation of human and

322   bonobo yawn contagion. While strong and weak relationships between individuals had to be

323   assessed according to species-specific criteria (see Methods section), the previous works on

324   bonobos (Demuru & Palagi, 2012) and humans (Norscia & Palagi, 2011) indicate that the strong-

325   weak categorization produces a similar effect on yawn contagion in either species, with yawn

326   contagion being highest between individuals sharing strong relationships. This result is confirmed

327   in this study. Compared to bonobos, the human susceptibility (Figure 2) and promptness (Figure

328   3) to others' yawns were significantly more potentiated when kin and friends were involved.

329   Humans' responses were more frequent and faster when the trigger and the responder shared a

330   strong emotional bond. On the other hand, susceptibility and promptness incredibly overlapped

331   between the two species when a strong emotional involvement between subjects was lacking,

332   thus indicating that emotional contagion is not always highest in humans. It is worth remarking

333   that these findings would have been impossible to detect if limiting the analysis to the intra-

334   specific level.

335   What explains the difference in yawn contagion between species is the deepness of the emotional

336   affinity linking the subjects. Compared to bonobos, humans show a different degree of

337   sensitiveness at the most basal layer of empathy, but only when they are strongly emotionally

338   involved. Moreover, the latency of yawn contagion is socially modulated in humans (the stronger

339   the emotional involvement, the faster the response) but not in bonobos. Therefore, the positive

340   feedback linking emotional affinity and the mirroring process is more easily and rapidly activated

341   in humans than in bonobos. Such over-activation explains not only the human potentiated

342   yawning response, but also other kinds of unconscious mimicry response, such as happy, pain or

343   angry facial expressions (Chiao et al., 2008). Minagawa-Kawai and coworkers (2009)

344   investigated the response latency of smiles in mother-infant pairs and found neurobiological

345   support for the "over-activation" hypothesis. The faster response was associated with an increased

346   activation in the regions around the orbitofrontal cortex in mothers while viewing their own

347   infant's smile compared to an unfamiliar infant's smile. In these mothers, specific neuronal

348   regions involved in positive emotional regulation were activated by both viewing familiar and

349 unfamiliar infants but the magnitude of activation was greater when affective attachment was

350 involved. A similar neuro-ethological approach has never been applied to quantify the extent of

351 the neural activation at the basis of the difference in yawn contagion latency as a function of the

352 emotional closeness.

353 The higher human sensitiveness to yawns emitted by friends and kin can be explained by the

354 peculiarity of the emotional attachment characterizing our species (Bowlby, 1969; Maestripieri,

355 2003). Compared to bonobos, the strong relationships established between humans are probably

356 qualitatively different, because they are built upon more complex and sophisticated emotional

357 foundations linked to cognition, memory, and memories. This interpretation is in line with

358 findings endorsing that affective and cognitive empathy cooperate in modulating the phenomenon

359 of yawn contagion in humans as it occurs for other kinds of unconsciously mimicked behaviours

360 (van Baaren et al., 2009). The idea that also the cognitive component of human empathy explains

361 some features of yawn contagion is supported by the ontogenetic co-emergence of yawn

362 contagion and theory of mind capacities in children (Anderson & Meno, 2003; Helt et al., 2010;

363 Millen & Anderson, 2011) and the correlation of these two phenomena in adults (Platek et al.,

364 2003). Therefore, it seems that in humans affective empathy is enhanced by the cognitive

365 components concurring in awakening and nourishing the affective involvement characterizing

366 strong relationships (van Baaren et al., 2009).

367 The most intriguing and original result emerging from our cross-species analysis is the strong

368 similarity between human and bonobo contagion susceptibility when the stimulus comes from a

369 familiar, but weakly bonded subject. This finding indicates that the foundations of the empathic

370 mechanism are alike in the two species. The absence of a strong emotional involvement seems to

371 bring to light the most basic component of yawn contagion by removing the influence of the

372 higher and more complex layers characterizing the cognitive sphere of human empathy (e.g.

373 perspective taking, mental state attribution, theory of mind). As a whole, our cross-species

374 approach supports the shared and multilayered architecture of animal empathy (Preston & de

375 Waal, 2002; de Waal, 2008). Therefore, we cannot state that emotional contagion is always

376 highest in humans, but only that they are able to create a unique and extremely intense form of

377 emotional attachment, thanks to the complexity of the neural circuits linking social experiences

378 and cognitive capacities. When such a pervasive attachment is missing, humans climb down from

379 the highest step of the empathic podium to return to the understory layer which our species shares

380 with other great apes.

381

382 **ACKNOWLEDGMENTS**

383 Thank are due to Frank Rietkerk (Apenheul Primate Park, Apeldoorn, The Netherlands) and

384 Marianne Holtkötter (Wilhelma Zoo, Stuttgart, Germany) and the bonobo keepers for allowing

385 and facilitating this work. We also thank Francesca Coppola and White Palagio for their

386 important clarifying input in discussing results.

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575

576

577 **Figure 1 -** Timing distribution of yawn contagion in the two species. The error bars show the

578 mean (±SE) of the individual frequency as a function of the 3-min time window.

579 **Figure 2** - Error bars showing the dyadic frequency of yawn contagion (number of responses per

580 yawn stimulus perceived) (mean ±SE) in the two species as a function of the relationships quality

581 linking the subjects involved.

582 **Figure 3** - Error bars (mean ±SE) showing the timing distribution of the dyadic yawn contagion

583 in bonobos (a) and humans (b) as a function of the relationship quality shared by the subjects

584 involved.

585

586 **Supplementary Video 1** - Video showing a yawn contagion event between two bonobo females

587 hosted at the Apenheul Primate Park (Apeldoorn, The Netherlands). The two females are laying

588 in proximity and are concurrently nursing their newborns. The female on the right, Zuani, yawns

589 at second 2. The female on the left, Kumbuka, perceives Zuani's yawn and emits a yawn response

590 at second 11.

Figure 1

Timingdistribution of yawn contagion inthe two species.

Timing distribution of yawn contagion in the two species. The error bars show the mean (±SE) of the individual frequency as a function of the 3-min time window.

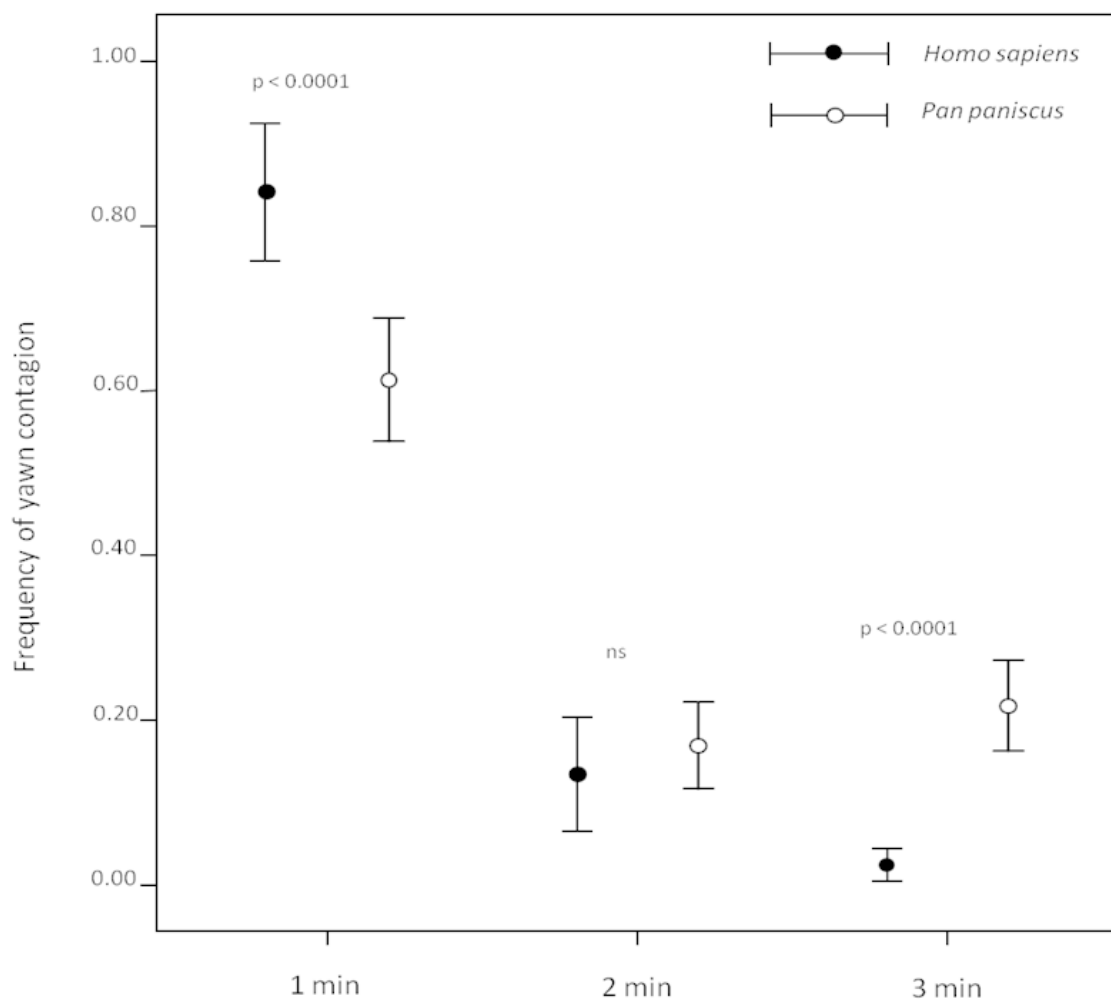



Figure 2

Yawn contagion and relationship quality in the two species.

Error bars showing the dyadic frequency of yawn contagion (number of responses per yawn stimulus perceived) (mean ±SE) in the two species as a function of the relationships quality linking the subjects involved.

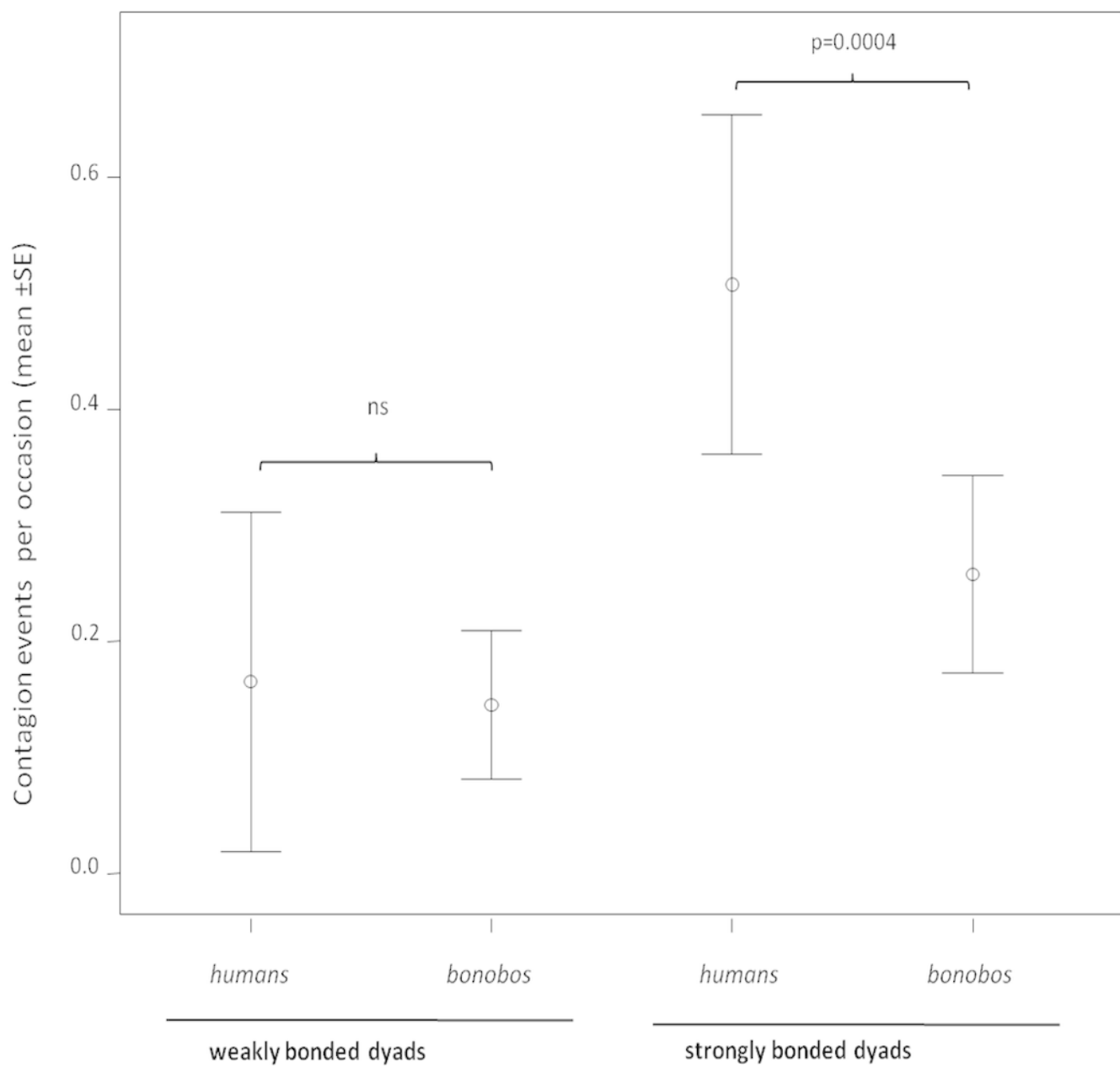
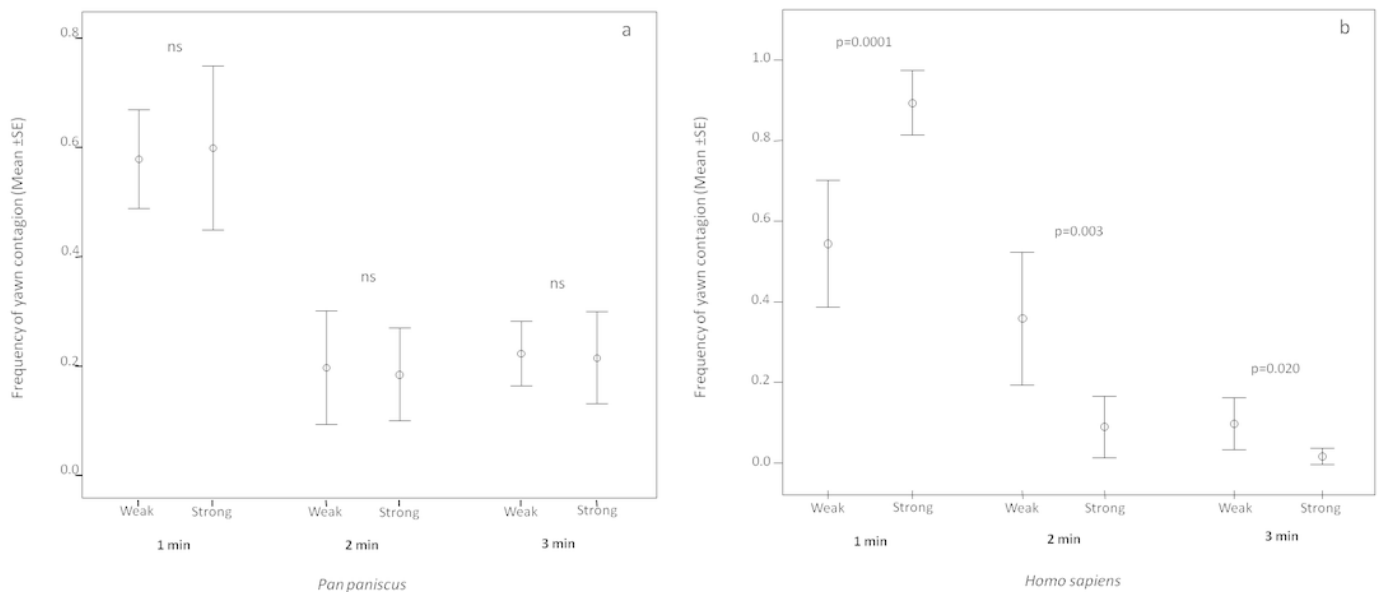



Figure 3

Latency of yawn contagion as a function of relationship quality.

Error bars (mean ±SE) showing the timing distribution of the dyadic yawn contagion in bonobos (a) and humans (b) as a function of the relationship quality shared by the subjects involved.

LMM results.

Best LMM explaining the occurrence of yawn contagion (AICc =-3.312).

Table 1. Best LMM explaining the occurrence of yawn contagion (AICc =-3.312).

	Numerator df	**Denominator df**	**F**	**Significance level**
Intercept	1	17.771	52.037	0.000
FIXED FACTORS				
Social bonding**	1	72.536	10.610	0.002
Species*	1	17.380	7.621	0.013
RANDOM FACTORS	**Variance**	**SE**		
Trigger's identity	0.0333	0.017		
Observer's identity	0.0038	0.004		

df: degrees of freedom; SE: standard error