

1 **Lowland gorillas (*Gorilla gorilla gorilla*) failed to respond to others' yawn: experimental and**  
2 **naturalistic evidence**

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17 **ABSTRACT**

18 Yawn contagion, possibly a form of emotional contagion, occurs when a subject yawns in response  
19 to others' yawns. Yawn contagion has been reported in humans, chimpanzees, bonobos, geladas,  
20 wolves and dogs. In these species, individuals form strong, long-term relationships and yawn  
21 contagion is highest between closely bonded individuals. This study focuses on the possible  
22 expression of yawn contagion in western lowland gorillas (*Gorilla gorilla gorilla*). Gorillas share  
23 with geladas a similar basic social structure (one dominant male and several adult females with  
24 offspring) and differ from bonobos and chimpanzees, which live in multimale-multifemale  
25 societies. Gorillas stand out because they are spatially aggregated but show especially low levels of  
26 social affiliation. If the expression of yawn contagion is linked to the investment of animals in  
27 establishing long-term social relationships, the phenomenon should not be detected in gorillas  
28 (*Social relationship hypothesis*). For the first time, we applied to the same subjects the naturalistic  
29 approach typically used in ethology (all occurrences behavioural sampling) and the experimental  
30 approach typically used in psychology (response to video stimuli). During the video demonstration  
31 (avatar yawn/control; unfamiliar gorilla yawn/control), we checked for the attentional state of the  
32 subjects. Anxiety related self-directed behaviours were recorded in all conditions and settings. We  
33 failed to detect yawn contagion in both naturalistic and experimental settings, with yawning being  
34 possibly associated with anxiety during video shows (revealed by the increased frequency of self-  
35 directed behaviours). In conclusion, yawn contagion may be a socially modulated phenomenon that  
36 remains largely unexpressed when individuals share weak social affiliation.

37

38 Keywords: Contagion; *Gorilla gorilla gorilla*; Anxiety; Weak social engagement

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## 41 INTRODUCTION

42 Yawn contagion occurs when a subject yawns in response to a triggering yawn emitted by  
43 another subject (Campbell, Carter, Proctor, Eisenberg & de Waal, 2009; Provine, 1986, 2005). As a  
44 form of involuntary mimicry (Thomson & Richer, 2015), yawn contagion may be a form of  
45 emotional contagion, possibly involving the mirror neuron system (Brown, Kim, Sanders,  
46 Bachmann, Thompson, Ropar, Jackson & Jackson, 2017; Haker, Kawohl, Herwig & Rössler, 2013;  
47 Nahab, Hattori, Saad & Hallett, 2009). Through the activation of this system, two individuals can  
48 non-consciously share physiological and related affective states based on perceived motor patterns  
49 (Gallese, Keysers & Rizzolatti, 2004). This perception-action mechanism (de Waal & Preston 2017)  
50 can facilitate behavioural matching and social living because it allows individuals to synchronize  
51 their emotional states through the replication of the actions or facial expressions of other individuals  
52 (Christov-Moore, Simpson, Coudé, Grigaityte, Iacoboni & Ferrari, 2014). However, contextual  
53 factors, such as environmental visual and auditory information, can affect the rates of involuntary  
54 mimicry (Wieser & Brosch 2012).

55 So far, there is strong evidence for yawn contagion in one cercopithecoid monkey species  
56 (geladas, *Theropithecus gelada*; Palagi, Leone, Mancini & Ferrari, 2009). In the stump-tailed  
57 macaques (*Macaca arctoides*) a yawn video elicited significantly more yawns than a control video,  
58 but also more self-directed behaviours like scratching. Therefore, the mechanism in these macaques  
59 might have been due to increasing tension or arousal, and not necessarily to social identification as  
60 required by the perception-action mechanism (Paukner & Anderson, 2006). Yawn contagion has  
61 been found in two hominid species, chimpanzees (*Pan troglodytes*: Anderson, Myowa-Yamakoshi  
62 & Matsuzawa, 2004; Campbell & de Waal, 2011) and humans (*Homo sapiens*: Provine, 1986;  
63 1989), and in both species there was a developmental effect from infancy, childhood to adulthood  
64 (Bartholomew & Cirulli, 2014; Madsen, Persson, Sayehli, Lenninger & Sonesson, 2013). One  
65 report failed to detect yawn contagion in two other hominid species, bonobos (*Pan paniscus*) and  
66 gorillas (*Gorilla gorilla*), but the sample size (4-5 animals) was too small to be conclusive (Amici,

67 Aureli & Call, 2014). Two other studies using larger samples found that yawn contagion is indeed  
68 present in bonobos (Demuru & Palagi, 2012; Tan, Ariely & Hare, 2017). No other investigation has  
69 been carried out on *Gorilla gorilla*, thus leaving the yawn contagion issue open in this species.

70 In humans, studies typically report a yawn contagion rate of around 50%, although the incidence  
71 of this phenomenon can be affected by psychological/neurological disorders such as autism and  
72 schizophrenia (Chan & Tseng, 2017; Helt et al., 2010). Additionally, there is strong evidence that  
73 this phenomenon is socially modulated in both human and non-human primates. In geladas, Palagi  
74 et al. (2009) found that the frequency of yawn contagion correlated with the level of grooming  
75 between individuals but not with their level of spatial proximity. Therefore, the strength of social  
76 bonds appears to modulate yawn contagion in this species. Social modulation may have limited or  
77 no influence on yawn contagion rates in young chimpanzees (Madsen et al., 2013), but adults were  
78 found to be more susceptible to yawns performed by in-group than by out-group members  
79 (Campbell & de Waal, 2011). In humans and bonobos yawn contagion was found to be more  
80 frequent between strongly bonded than between weakly bonded individuals (Demuru & Palagi,  
81 2012), even though both species also responded to strangers' yawns (humans, Norscia & Palagi,  
82 2011; Norscia & Palagi, 2016; bonobos, Tan et al., 2017; both humans and bonobos: Palagi,  
83 Norscia & Demuru, 2014).

84 We investigated the possible expression of yawn contagion in lowland gorillas (*Gorilla gorilla*  
85 *gorilla*). To explore the phenomenon in a comprehensive way, for the first time, we combined both  
86 a naturalistic and an experimental approach in a single study. Gorillas are phylogenetically distant  
87 from geladas but very close to the other African hominids (Sally, Dutheil, Hillier, Jordan,  
88 Goodhead et al., 2012; Stevens, Seiffert, O'Connor, Roberts, Schmitz et al., 2013). The  
89 socioecology of gorillas contains some traits that are similar to geladas at least in the mating  
90 patterns. In both species, the basic social unit includes one dominant male and several adult females  
91 with offspring. Although geladas have a multi-level structure where the different basic social units

92 gather together in larger aggregations (e.g., herds) with the members of the different basic social  
93 units are always in sight (Kummer, 1971; Palagi et al., 2018).

94 Similar to bonobos and chimpanzees, gorillas possess a long ontogenetic trajectory (with the  
95 weaning period lasting up to 4-6 years) and highly developed cognitive abilities (de Lathouwers &  
96 van Elsacker, 2006; Watts & Pusey, 1993). On the other hand, gorillas differ from both African  
97 great apes and geladas in the levels of social affiliation between individuals (Cordoni, Norscia,  
98 Bobbio & Palagi, 2018). Chimpanzees and bonobos live in fission-fusion groups in which group-  
99 mates form strong and enduring social bonds, e.g. via grooming exchange and agonistic support  
100 (Foerster, Franz, Murray, Gilby, Feldblum, Walker & Pusey, 2016; Gruber & Clay, 2016;  
101 Langergrabe, Mitani & Vigilant, 2009; Muller & Mitani, 2005; Slocombe, Kaller, Turman,  
102 Tawnsend, Papworth, Squibbs & Zuberbühler, 2010). In gelada social basic units, females engage  
103 in high levels of affiliative contact and establish long-term social relationships between them  
104 (Dunbar & Dunbar, 1975). In lowland gorilla one-male groups, females show extremely low levels  
105 of social affiliation because they spatially aggregate around one adult male, the silverback, mainly  
106 for protection reasons (Harcourt & Stewart, 2007). The death of the silverback leads to group  
107 disruption and females disaggregate moving to other groups (Harcourt & Stewart, 2007). In the  
108 wild, Stokes (2004) observed only eight affiliative interactions during 802 hrs of observation; six of  
109 them were between silverback and reproductive females and involved sexual behavior and physical  
110 contact. Grooming between adults was never observed and females engaged in almost no affiliative  
111 behavior with each other. These findings led the authors to consider lowland gorilla as a species  
112 characterized by low levels of affiliation (Cordoni et al. 2018; Masi, Cipolletta & Robbins, 2009;  
113 Stokes, 2004). In gorillas, the migrating males can join together and form bachelor groups (Robbins  
114 1996; Stoinski et al., 2004). It has been found that these males share a certain amount of affiliation  
115 and social cohesiveness that strongly decrease when females join the group (Harcourt & Stewart,  
116 2007).

117 Based on the above framework, we formulated two alternative hypotheses on yawn contagion.  
118 *Social relationship hypothesis* – If the expression of yawn contagion co-varies with the level of  
119 affiliative contacts that animals engage in to form strong social inter-individual relationships, we  
120 expect that yawn contagion is not expressed in gorillas, owing to their especially low investment in  
121 social affiliative exchange (Prediction 1). *Alternative hypothesis* - If the expression of yawn  
122 contagion does not depend on the quality of the inter-individual social relationships but depends on  
123 shared biological and cognitive features (common to all African great apes), we expect that yawn  
124 contagion is expressed in gorillas, as it is expressed in other African hominids (Prediction 2).

125

## 126 **METHODS**

### 127 *The colonies*

128 The study was carried out on two colonies of lowland gorillas hosted at the ZooParc de Beauval  
129 (St. Aignan sur Cher, France): a family group composed of 12 individuals and a bachelor group  
130 composed of 5 individuals (Table 1). Each colony had indoor (~200 m<sup>2</sup>) and outdoor facilities  
131 (~2000 m<sup>2</sup>). The indoor facilities were equipped with tree trunks, lianas, ropes, and platforms so  
132 that the gorillas could move freely in all three dimensions. The outdoor enclosures (islands) were  
133 delimited by an artificial moat. From 05:30 p.m. to 10:00 a.m. both groups stayed in the night cages  
134 not visible to the visitors but accessible to the researchers during the experiments. Animals received  
135 food (vegetables, seeds and grains, branches with green leaves) five times per day; water was  
136 always available. No stereotypic or aberrant behaviours were observed in the two groups.

137

### 138 *Data collection in the naturalistic setting*

139 Data were collected in October 2014 and October-December 2015, outside the peak visiting  
140 season, to reduce the impact of visitors on animal behaviour. Data were always collected by two  
141 observers, on a daily basis over a 6-h period that spanned morning and afternoon (including feeding  
142 times), both indoors and outdoors. Before starting systematic data collection, the two observers

143 underwent a 10-hr training period to become skilled in animal identification and behavioural pattern  
144 distinction under the guide of two expert coders (EP and GC). For training purposes only, the same  
145 focal animal was followed by the observers simultaneously, and the data were then compared and  
146 discussed. Cohen's  $\kappa$ , calculated for each behaviour considered in this study (yawning, self-  
147 scratching, self-grooming, nose wiping, head shaking and agonistic behaviours listed in Table 2),  
148 was never below 0.85 (Kaufman & Rosenthal, 2009).

149 Through scan animal sampling performed every 10 minutes, we collected data on grooming,  
150 contact sitting and spatial proximity (family group=65 hours with the exception of Maisha=6 hours;  
151 bachelor group=41 hours). Two subjects were in spatial proximity when they were within an arm-  
152 length distance. For each behavioural category we calculated the hourly frequency and divided it on  
153 the number of individuals available in both familiar (n=11) and bachelor groups (n=4).

154 By all occurrences sampling (family group=85 hours; bachelor group=44 hours) we collected  
155 yawns performed by gorillas during their everyday activity in their natural social setting. A yawning  
156 event is characterized by gaping of the mouth, until the acme is reached, followed by a passive  
157 closure of the jaws, with all phases accompanied by respiratory components. In some cases, the  
158 eyes can be closed and the neck and shoulders can be hunched (Provine, 1986).

159 For each yawning event we recorded i) yawner identity (hereafter, trigger), ii) exact time of the  
160 yawn, iii) individual/s who could detect the yawn (hereafter, receiver), and iv) individual/s who  
161 could not detect the yawn. The distance between the observers and gorillas ranged from 1 meter  
162 (experimental setting) to 5-10 meters (naturalistic setting). The recorded yawns were silent (no  
163 auditory cue), so the possible detection of the trigger's yawn was based on the visual cue. In  
164 particular, we considered the yawn as non-visually detectable when the head of the potential  
165 receiver was rotated by 180° with respect to the trigger (Baseline condition). All the yawns  
166 performed by subjects without the detection of the yawn emitted by the trigger were considered to  
167 be spontaneous. The yawn was considered to be detected when the receiver was positioned to see  
168 the head of the trigger (within 3 meters) and the receiver had its eyes open (Yawn condition). All

169 the yawns performed by the receiver after the yawning stimulus were considered to be infected  
170 yawns (yawn contagion).

171 Based on previous ethological works on contagious yawning, we recorded yawn responses on a 3-  
172 min time window (Palagi et al., 2014). The probability of miscoding a yawning response (coding a  
173 spontaneous yawn as contagious) is lower in the first three minutes after the yawning stimulus than  
174 later, when autocorrelation is more likely (the presence of a yawn performed by a subject at  $t_0$   
175 increases the probability to have another yawn by the same subject at  $t_{(0+X)}$  where X is the  
176 increasing unit of time; Kapitány & Nielsen, 2017). We also took note of whether each yawning  
177 event was accompanied by self-scratching and self-grooming or not.

178 In order to calculate the dominance relationships of the subjects, via all occurrences sampling we  
179 collected data on dyadic agonistic encounters that were identified according to the behavioural  
180 items described in Table 2. We recorded the identity of the opponents involved in decided conflicts.

181 Decided conflicts involved a clear winner, with an animal directing an aggressive behaviour  
182 toward another individual (the loser), which fled or moved away either vocalizing or not. As  
183 regards intervention during an ongoing conflict (i.e. agonistic support) we defined as supporter the  
184 individual who attacked the victim (in case of agonistic support in favor of the aggressor) or the  
185 aggressor (in case of agonistic support in favor of the victim).

186 The decided dyadic conflicts were entered in a winner-loser sociomatrix to determine dominance  
187 relationships based on Normalized David's Scores (NDS scalar values). NDS values were obtained  
188 via the R supported package Steepness 2.2. The values were calculated on the basis of a dyadic  
189 dominance index ( $D_{ij}$ ) in which the observed proportion of wins ( $P_{ij}$ ) is corrected for the chance  
190 occurrence of the observed outcome. The chance occurrence of the observed outcome is calculated  
191 on the basis of a binomial distribution with each animal having an equal chance of winning or  
192 losing in every dominance encounter (de Vries, Stevens & Vervaecke, 2006). We determined the  
193 dominance level of each individual based on their NDSs scalar values. The NDS scalar values were  
194 included as a fixed factor in the GLMM analysis (Table 3).



195

196 *Experimental setting*

197 **Trial video assemblage**

198 Four mute videos were used for the experimental trials showing the facial movements (yawn  
199 condition and control condition showing mouth movements) of an unfamiliar gorilla and of a virtual  
200 ape-like face (hereafter, avatar). The two avatar videos were created as a three-dimensional  
201 computer animation via LIGHTWAVE 3D (see Campbell et al., 2009). The two gorilla videos  
202 included models of all sex and age classes (immatures and adults, males and females). The models  
203 were unknown to the experimental subjects. We selected clips of gorillas from youtube  
204 ([www.youtube.com](http://www.youtube.com)) and used them as yawn and control videos.

205 Avatar yawn video - The video randomly showed three different ape-like yawning faces in one  
206 of three directions (lateral, frontal, and three quarter profile) and each animation clip lasted 9 s. The  
207 video was shown to the subject for 10 min.

208 Avatar control video - This video was built exactly as the Yawn video. The video randomly  
209 showed three different ape-like heads and included mouth opening and closing movements, lip  
210 protrusion, and relaxed open-mouth associated with head bobbing. Each movement was shown with  
211 the animation facing in one of three directions: lateral, frontal, and three quarter profile. Each  
212 animation clip lasted 9 s. The video was shown to the subject for 10 min. Clip samples of both  
213 yawn and control avatar videos are available in Campbell et al. (2009)  
214 (<http://rspb.royalsocietypublishing.org/content/276/1676/4255.figures-only>).

215 Gorilla yawn video - From each video, we extracted only the clip showing the yawning pattern  
216 (5-10 sec per pattern), leaving out any other mouth movement that preceded or followed the yawn  
217 itself. The facial expressions were presented in three different positions: lateral, frontal, and three  
218 quarter profile. We randomly combined the clips of eight different subjects into a 24-clip video.  
219 Each video lasted 3 min and 20 s and was repeated until reaching about 10 min of show duration.

220

221 Gorilla control video - From the same clips used to build the yawn video we extracted frames of  
222 5-10 s showing the mouth movements right before and after the yawning (lip/tongue protrusion,  
223 chewing, mouth opening and closing). In this way, the control clips matched the yawn clips in terms  
224 of background, shown individual, head direction, and body posture. The facial expressions were  
225 presented in three different positions: lateral, frontal, and three quarter profile. The control clips  
226 were virtually identical to the yawn clips, except for the expression itself. The video was composed  
227 of 24 clips showing eight different subjects in random order. The video lasted 3 min and 20 s and  
228 was repeated until reaching about 10 min of show duration.

### 229 **Experimental procedure**

230 The authors carried out all the experiments during early morning (08:00-10:30) in the night  
231 facilities where animals were housed alone or in small sub-groups (in the latter case using adjoining  
232 rooms). No one, except keepers and researchers, was allowed in indoor facilities. No physical  
233 contact between the experimenters and the gorillas was permitted.

234 Before the beginning of each trial session, the researchers waited 15 minutes to habituate the  
235 animals to their presence. The tested gorillas never showed any aggressive behaviour toward the  
236 researchers. Each gorilla was tested individually when alone. If another subject entered the room  
237 during the trial, the trial was considered valid and included in the analysis only in absence of  
238 detectable yawns from other gorillas. During each experimental trial, one experimenter showed a  
239 video on a tablet (*EeePad Transformer TF101*, Screen dimension 10.1 inches; [L\*H\*S][mm], 271 x  
240 12.98 x 171) while a second experimenter recorded the session with a camera (Sony HDR-PJ240).  
241 The trial began when the animal spontaneously started watching the video and ended when the  
242 animal went away and was not visible anymore (time spent by the subjects in a trial = mean 6.31  
243  $\pm 0.326$ SE minutes). All 12 subjects were recorded for at least five consecutive minutes while  
244 carrying out the trial. The animals who were motivated to perform the task stayed close to the  
245 device and watched the video (Video S1) whereas the others did not (Video S2). The gorillas could  
246 easily watch the video from behind the bars of the cage at a minimum distance of 15 cm. The

247 environmental light conditions ensured video perception. During the video show, it was clear when  
248 the animals looked or did not look at the source of the video (Video S1). We checked for the  
249 attentional state of individuals (mean 167.33 s  $\pm$ 17.35SE) by verifying whether the animal directed  
250 their gaze at the screen (the animal fixed their eyes steadily towards the screen). Considering the  
251 screen and the frame size, the facial display shown on the video fell within the visual stereoscopic  
252 range of the animals when they looked straight at the screen. We calculated the time (seconds)  
253 during which the subjects were looking at the screen and this time was used to evaluate whether the  
254 attentional time differed across conditions.

255 The experimental and control videos (for both avatar and gorilla tasks) were shown to the  
256 subjects in a random order. Each subject underwent one trial per day (e.g., day<sub>1</sub>= gorilla control  
257 video; day<sub>2</sub>=avatar yawn video; day<sub>3</sub>= avatar control video; day<sub>4</sub>= gorilla yawn video). Twelve  
258 individuals out of 17 completed testing (Table 1).

259

### 260 **Post-recording video analyses**

261 The video analyses were carried out using VLC media player 2.2.6 (extension: Jump to time).  
262 Timing and frequency were extrapolated from the videos for the following behavioural patterns:  
263 yawning, self-scratching, self-grooming, nose wiping, and head shaking. To ensure unequivocal  
264 coding, data extrapolation from videos was carried out by two observers concurrently (first and last  
265 author) after separate training over 10% of the total videos (Cohen's  $k \geq 0.85$  for the considered  
266 behavioural patterns; Kaufman & Rosenthal, 2009).

### 267 *Statistical analyses*

268 Parametric tests were applied when the data distribution was normal (Kolmogorov-Smirnov, ns),  
269 as they were for attentional time and yawning frequency (Y/min) in both experimental and  
270 naturalistic settings. The ANOVA Two-Way repeated measures test was used to check for  
271 attentional time and yawning response frequency (Y/min) across the following conditions: avatarY;  
272 avatarC; gorillaY; gorillaC. The paired-t test was applied to check for yawning frequency variation

273 between conditions (naturalistic setting: yawning after the detection of a yawn event vs yawning  
274 without the detection of a yawn event). Non-parametric tests were applied in case of non-normal  
275 data distribution (Kolmogorov-Smirnov  $p < 0.05$ ), as they were for yawning frequency (Y/hour) and  
276 self-directed behaviours under naturalistic setting (SDB/hour). The Mann-Whitney U test was used  
277 for  $k=2$  independent variables, i.e. to check for possible differences in the baseline levels of  
278 spontaneous yawning (Y/hour) between the bachelor and family gorilla groups and their response to  
279 the different videos (Y/min). The Wilcoxon Signed-Rank test was used for  $k=2$  dependent  
280 variables, i.e. to check for the possible difference in the frequency of yawning in presence and  
281 absence of self-directed behaviours in the naturalistic setting. Exact probability values (which are  
282 adjusted for the small sample size) were selected following Mundry & Fischer (1998). The above  
283 mentioned tests were carried out at the individual level. When the test involved dyads, data were  
284 considered as pseudo-replicated because the same individual can be present in different dyads.  
285 Hence, we used randomized procedures via freeware Resampling Procedures 1.3 package by David  
286 C. Howell.

287 We applied the GLMM to test which fixed factors (Table 3) explained the distribution of  
288 yawning frequency (Y/min), which was introduced as a dependent variable. The fixed factors  
289 included: sex, age, rank (calculated via Normalized David's Score values), experimental condition  
290 (yawn vs control), type of stimulus (avatar vs unfamiliar gorilla), self-directed behaviour (see Table  
291 3 for details). The individual and group identities were introduced as random factors (Table 3). Via  
292 the Anderson–Darling test (EasyFit 5.5 Professional software), we found that the distribution which  
293 best fit the dependent variable was the gamma distribution. For this reason, we selected the gamma  
294 log-link function to run the GLMM. We tested models for each combination of variables of interest,  
295 spanning from the null model to the model including all the fixed factors (full model). We also  
296 tested all the interactions between the different variables related to either yawner characteristics or  
297 contextual characteristics (Table 3). To select the best model, we used the Akaike's Corrected  
298 Information Criterion (AICc), a measure for comparing mixed models based on the  $-2$  (Restricted)

299 log likelihood. The model with a lower value of AICc was considered to be the best model. To  
300 measure the extent of improvement of the best model compared to the next best models, we  
301 calculated the difference ( $\Delta\text{AICc}_i$ ) between the AICc value of the best model and the AICc value  
302 for each of the other models. We considered as competing the models showing a  $\Delta\text{AICc} < 6$   
303 (Symonds & Moussalli, 2011). To assess the relative strength of each candidate model, we  
304 employed  $\Delta\text{AICc}_i$  to calculate the Akaike weight ( $w_i$ ). The  $w_i$  (ranging from 0 to 1) is the weight of  
305 evidence or probability that a given model is the best model, taking into account the data and set of  
306 candidate models (Symonds & Moussalli, 2011).

## 307 **RESULTS**

### 308 *Grooming, contact sitting, spatial proximity and agonistic support*

309 We evaluated the levels of affiliative interactions (grooming, contact sitting and spatial proximity)  
310 and agonistic support in both family and bachelor group. In the family group, the mean individual  
311 rates (= hourly frequency/number of individuals available in the group) of grooming, contact sitting  
312 and spatial proximity were  $0.001 \pm 0.001$  SE,  $0.030 \pm 0.011$  SE and  $0.077 \pm 0.011$  SE, respectively.  
313 In the bachelor group, the mean individual rates (= hourly frequency/number of individuals  
314 available in the group) of grooming, contact sitting and spatial proximity were  $0.000 \pm 0.000$  SE,  
315  $0.030 \pm 0.018$  SE and  $0.051 \pm 0.012$  SE, respectively. In particular, throughout the study period we  
316 recorded only four grooming sessions between a single related dyad in the family group (i.e. Sheila  
317 and Sawa). Five individuals of both groups never stayed in body contact with fellows (i.e. contact  
318 sitting).

319 The mean individual level of agonistic support (number of support/number of witnessed aggression)  
320 was  $0.005 \pm 0.003$  SE for the family group and  $0.007 \pm 0.005$  SE for the bachelor group. In the  
321 family group, we recorded six cases of support (only between related dyads, i.e. mother-offspring  
322 and siblings) on 136 agonistic encounters recorded; in the bachelor group, we recorded only two  
323 cases of agonistic support on 106 aggressive contacts.

324

325 *Experimental trials using videos*

326 Eleven subjects were tested for all the four trials (avatarY; avatarC; gorillaY; gorillaC), only one  
327 subject was tested for two trials (gorillaY; gorillaC). The ANOVA two-way repeated measures test  
328 revealed that the attentional time of the tested subjects was not affected by any of the following  
329 factors: Avatar/Gorilla stimuli ( $F_{(1,10)}=0.769$ ,  $df=10$ ,  $p=0.401$ ; Effect size partial eta-squared:  
330 0.003), Y/C condition ( $F_{(1,10)}=0.025$ ,  $df=10$ ,  $p=0.877$ ; Effect size partial eta-squared: 0.071) and  
331 Avatar/Gorilla\*Y/C ( $F_{(1,10)}=1.818$ ,  $df=10$ ,  $p=0.207$ ; Effect size partial eta-squared: 1.154).

332 The ANOVA two-way repeated measures test revealed that the yawning response of the tested  
333 subjects was not affected by any of the following factors: Avatar/Gorilla stimuli ( $F_{(1,10)}=1.468$ ,  
334  $df=10$ ,  $p=0.254$ ; Effect size partial eta-squared: 0.128), Y/C condition ( $F_{(1,10)}=0.005$ ,  $df=10$ ,  
335  $p=0.945$ ; Effect size partial eta-squared: 0.001) and Avatar/Gorilla\*Y/C ( $F_{(1,10)}=1.700$ ,  $df=10$ ,  
336  $p=0.222$ ; Effect size partial eta-squared: 0.145) (Figure 1).

337 We also carried out the Anova two-way repeated measures excluding immature individuals. The  
338 ANOVA revealed that the yawning response was not affected by any of the following factors:  
339 Avatar/Gorilla stimuli ( $F_{(1,7)}=0.140$ ,  $df=7$ ,  $p=0.720$ ; Effect size partial eta-squared: 0.020), Y/C  
340 condition ( $F_{(1,7)}=1.199$ ,  $df=7$ ,  $p=0.310$ ; Effect size partial eta-squared: 0.146) and  
341 Avatar/Gorilla\*Y/C ( $F_{(1,7)}= 2.426$ ,  $df=7$ ,  $p=0.163$ ; Effect size partial eta-squared: 0.257).

342 There was no difference in the frequency of yawning between the family and the bachelor group  
343 in response to the four videos (avatarY: Mann-Whitney  $U=10.00$ ,  $N_{family}=8$ ,  $N_{bachelor}=3$ ,  $p=0.745$ ,  
344 Effect size z-score =-0.157; avatarC: Mann-Whitney  $U=4.50$ ,  $N_{family}=8$ ,  $N_{bachelor}=3$ ,  $p=0.170$ , Effect  
345 size z-score =-0.503; gorillaY: Mann-Whitney  $U=6.00$ ,  $N_{family}=8$ ,  $N_{bachelor}=3$ ,  $p=0.321$ , Effect size z-  
346 score=-0.428; gorillaC: Mann-Whitney  $U=6.00$ ,  $N_{family}=8$ ,  $N_{bachelor}=3$ ,  $p=0.321$ , Effect size z-score  
347 =-0.428).

348 Via GLMM, we explored which variables explained the frequency of yawn response. We found  
349 five competing models ( $AIC_{c_{min}}=41.964$ ;  $AIC_{c_{max}}=42.925$ ; Table 4) with the random factor  
350 variance ranging from 0.002 to 0.038 ( $0.745 \leq p \leq 0.983$ ). Each of the five models contained the

351 variable SELFDIRECTED which was the only one that had a significant effect and remained in all  
352 models (Table 4). The model including the intercept only had an AICc of 49.324 and the full model  
353 was the worst one (AICc=50.381). The analysis of correlation via randomization revealed a  
354 significant positive relation between yawn response and self-directed behaviours ( $r=0.467$ ;  
355  $N_{\text{trials}}=46$ ;  $p=0.001$ ; Figure 2). In the video setting, the frequency of SELFDIRECTED behaviours  
356 (SDB/min) did not differ between the yawn (Y) and control condition (C) (paired-sample  
357 randomization test  $t=0.725$ ,  $N=23$ ,  $p=0.472$ , Effect size z-score = 0.151).

### 358 *Naturalistic observation*

359 We recorded a total of 365 yawns. The baseline yawn activity (number of yawns/hours of  
360 observation) between the family (mean  $0.279 \pm 0.085\text{SE}$ ) and the bachelor group (mean  $0.478$   
361  $\pm 0.148\text{SE}$ ) was not significantly different (Mann-Whitney  $U=16.0$ ;  $N_{\text{family}}=11$ ;  $N_{\text{bachelor}}=5$ ;  $p=0.221$ ;  
362 Effect size z-score = -0.326).

363 The frequency of yawns performed in absence of direct visual contact with the trigger (no  
364 perception of the yawn emitted by the trigger, spontaneous yawn) was comparable to the frequency  
365 of yawns performed after the perception of the yawn emitted by the trigger (direct visual contact  
366 with the yawning trigger, contagious yawn) (individual mean yawn/stimulus undetectable =  $0.098$   
367  $\pm 0.021\text{SE}$ ; individual mean yawn/stimulus detectable =  $0.082 \pm 0.025\text{SE}$ ; paired t test;  $t=-0.509$ ,  
368  $df=14$ ,  $p=0.619$ ; Effect size z-score = -0.131; Figure 3). One subject that received only one stimulus  
369 was excluded from the analysis (Kajolu); all the other subjects were exposed to at least 3 detectable  
370 stimuli. In the family group, adult females were not infected by the yawns emitted by the silverback  
371 (Asato). One female (Kabinda) yawned only once after Asato's yawns.

372 The frequency of yawning associated with self-directed behaviours (scratching/self-grooming  
373 performed during a yawn) was significantly lower than the frequency of yawning not associated  
374 with self-directed behaviours (no self-scratching/self-grooming associated with a yawn) (Wilcoxon  
375  $T=7.50$ ; ties=1;  $N=16$ ;  $p=0.001$ ; Effect size z-score = -0.746; Figure 4).

376

377 **DISCUSSION**

378 The results show that, in our study groups of gorillas, yawn contagion was not found in either the  
379 naturalistic (Figure 3) or video setting (Figure 1) (*Social relationship hypothesis* supported). In both  
380 settings the frequency of yawns following the yawning stimulus (yawn condition) did not  
381 significantly differ from the control condition (mouth opening and closing in the video setting and  
382 no detectable yawn in the naturalistic setting). In the video setting, yawns were released from  
383 unknown gorilla individuals (and avatar) whereas in the naturalistic setting yawns came from  
384 familiar subjects (group-mates). Therefore, the absence of yawn contagion in our study groups  
385 cannot be related to the unfamiliarity between subjects. Moreover, the inability to find yawn  
386 contagion in our gorilla groups cannot be ascribed to their low rates of spontaneous yawns because  
387 our results show that the frequency of spontaneous yawning recorded in gorillas  
388 (yawn/hour/individual: mean  $0.341 \pm 0.075$  SE) tends to be higher than the frequency recorded in  
389 geladas (yawn/minute/individual: mean  $0.085 \pm 0.035$  SE calculated from Leone, Ferrari & Palagi,  
390 2014) and in the other African great apes (bonobo yawn/minute/individual: mean  $0.143 \pm 0.043$  SE,  
391 Demuru & Palagi, 2012; chimpanzee yawn/minute/individual: mean  $0.130 \pm 0.025$  SE, calculated  
392 from Campbell & de Waal, 2011), all species in which yawn contagion was found.

393 In the experimental condition (video setting), self-directed behaviours partly influenced the  
394 distribution of yawning frequencies (Table 4 and Figure 2) but the levels of self-directed behaviour  
395 did not significantly differ between yawn and control condition, which suggests that anxiety may  
396 have affected yawning in a similar way in the two conditions.

397 There is behavioural and pharmacological evidence that self-directed behaviours, including self-  
398 scratching and self-grooming, are good indicators of anxiety in primates, from lemurs to apes and  
399 humans (Maestripieri, Schino, Aureli & Troisi, 1992; Norscia & Palagi, 2016; Palagi & Norscia,  
400 2011; Schino, Perretta, Taglioni, Monaco & Troisi, 1996; Troisi, 2002). Yawning itself has been  
401 found to be linked to anxiety in strepsirhine and haplorhine primates (Maestripieri et al., 1992;  
402 Troisi, 2002; Zannella, Norscia, Stanyon & Palagi, 2015). Moreover, “tension yawns” related to



403 conflict situations and possible arousal were described in geladas (Leone et al., 2014), Tonkean  
404 macaques (Zannella, Stanyon & Palagi, 2017), and chimpanzees (Vick & Paukner, 2010). Even  
405 though yawning in our groups may have been also related to anxiety, it is not possible to conclude  
406 that anxiety is the main factor responsible in suppressing yawn contagion when animals are in their  
407 social context. As a matter of fact, under the naturalistic condition, yawning was not temporally  
408 associated with self-directed behaviours (Figure 4). Moreover, the increase of scratching observed  
409 in the experimental setting does not necessarily imply a negative effect on contagious yawning. In  
410 humans, for example, the increase of cortisol following the administration of a stressful stimulus  
411 has been hypothesized to increase all yawning (Thompson, 2014). However, the relationship  
412 between yawn contagion and anxiety in human and non-human primates deserves further  
413 investigations.

414 Failing to find yawn contagion in lowland gorillas might at first sound counter-intuitive due to  
415 the high levels of cognition of this species and the close phylogenetic relationship with other great  
416 apes and humans (Scally et al., 2012; de Lathouwers & van Elsacker, 2006). However, following  
417 the bottom-up approach proposed by de Waal & Ferrari (2010) and the Russian doll model of  
418 empathy (de Waal & Preston, 2017), the expression of basic empathy via emotional contagion does  
419 not necessarily require complex cognitive abilities and can be the outcome of a pre-conscious  
420 mechanism. High cognition is not sufficient *per se* to assume that emotional contagion is present  
421 because this phenomenon is also strictly related to the activity of subcortical areas (e.g. amygdala,  
422 insula, hippocampus) in mice and humans (Choi & Yeung, 2017; Sturm, Yokoyama, Seeley,  
423 Kramer, Miller & Rankin, 2013).

424 On the other hand, emotional contagion, including yawn contagion, is affected by the  
425 relationship quality between individuals and social closeness (de Waal & Preston, 2017). This is  
426 expected considering that the adaptive role of empathy is to favour prosocial behaviour and  
427 cooperation leading to the increase of direct and indirect fitness (Decety, Bartal, Uzefovsky &  
428 Knafo-Noam, 2016). Indeed, the inability to find yawn contagion in our groups of gorillas seems to

429 support the hypothesis that inter-individual social affiliation more than social structure or shared  
430 biological features (e.g. neural complexity related to shared phylogeny) is crucial to yawn contagion  
431 (*Social relationship hypothesis supported*). In this study, we found that the level of social affiliation  
432 (measured via spatial proximity, grooming, contact sitting and agonistic support) was virtually close  
433 to zero in both the family and the bachelor group. This result is consistent with the findings of a  
434 comparative study carried out by Cordoni et al. (2018) including the same gorilla family group as  
435 the present study, in which the authors demonstrated that social affiliation was strikingly lower in  
436 gorillas than in chimpanzees. Although in the gorilla society the silverback plays the central role in  
437 protecting and maintaining the integrity of the social group (Harcourt & Stewart, 2007), the  
438 yawning stimuli emitted by the silverback did not elicit any response in the females of our family  
439 group.

440 Two previous studies have shown that social cohesion between individuals can become the  
441 factor that is most important in eliciting yawn contagion, even more than inter-specific differences  
442 (Campbell & de Waal, 2014; Palagi et al., 2014). In a direct comparison between bonobos and  
443 humans, Palagi et al. (2014) found that yawn contagion rates were not affected by the species the  
444 individuals belonged to when the individuals shared weak social bonds. Campbell & de Waal  
445 (2014) also found that the rate of chimpanzee response to triggering yawns was similar when the  
446 stimulus came from an in-group chimpanzee and from a human subject, thus demonstrating that the  
447 response can go beyond the species boundary. Silva and coworkers (2012) not only showed that  
448 dogs were able to respond to human yawns, but also found that dogs yawned more at yawns  
449 released by familiar than unfamiliar human subjects. Recently, Tan et al. (2017) found that bonobos  
450 are infected by yawns of strangers and familiar subjects at similar rates. However, in humans,  
451 chimpanzees, bonobos and wolves closely bonded individuals showed higher levels of yawn  
452 contagion compared to weakly bonded individuals (Campbell & de Waal, 2011; Demuru & Palagi,  
453 2012; Norscia & Palagi, 2011; Palagi et al., 2014; Romero, Ito, Saito & Hasegawa, 2014). The  
454 inability to find yawn contagion in these gorillas may be linked to their lower levels of social

455 affiliation compared to other species. This view is reinforced by the fact that yawn contagion is  
456 expressed in geladas (Palagi et al., 2009), which share with gorillas a similar basic social structure  
457 but possess higher levels of social affiliation compared to gorillas (Dunbar & Dunbar, 1975;  
458 Kummer, 1971). It seems therefore that inter-individual spatial association does not equate with  
459 social closeness.

460 Emotional contagion through facial mimicry can enhance affective and behavioural  
461 synchronization with others (de Waal & Preston, 2017; Couzin, 2007) and, for this reason,  
462 contagion might have acquired an important adaptive value in social groups that are built upon solid  
463 inter-individual relationships. When the factor keeping a group together is mainly spatial proximity  
464 (as it is the case of adult gorilla females aggregated around the silverback) the selective pressure  
465 over the mechanisms promoting behavioural and emotional matching, including yawn contagion,  
466 may have weakened.

467 Some scholars have pointed out that low frequencies of yawn contagion might reflect low  
468 attention to the stimulus, which can vary depending on the stimulus source (e.g. familiar vs  
469 unfamiliar subject; for a review see Massen & Gallup 2017). It could be therefore argued that the  
470 low attention that individuals pay to each other in the group makes it difficult for gorillas to express  
471 yawn contagion. It is indeed true that the response to a stimulus can be elicited only if the source of  
472 the stimulus is detected. In this study, we made sure that the yawning stimulus fell into the  
473 stereoscopic visual range of the potential gorilla responders, and in the experimental setting we also  
474 controlled for the time that the subject actually looked at the video (Video S1). Despite this control,  
475 yawning did not transfer from one gorilla to another. Usui and colleagues (2013) found that children  
476 with autism spectrum disorder showed yawn contagion as typically developing children when  
477 specific measures were taken to ensure that the subjects could detect the video stimulus. In the only  
478 study published so far on the influence of selective attention on yawn contagion in nonclinical  
479 human subjects, Chan & Tseng (2017) found that the perceptual detection sensitivity to yawning  
480 expression (the ability to detect a yawn as such) was related to the duration of gaze to the eyes of

481 the stimulus releasing face, but the authors failed to find evidence that eye-gaze patterns modulated  
482 contagious yawning behaviour. Previous studies in humans also found that yawn contagion seems  
483 not to be sensitive to the number of triggering yawns (Norscia & Palagi, 2011), the sensory  
484 modality (auditory, visual or audio-visual) (Arnott, Singhal & Goodale, 2009; Norscia & Palagi,  
485 2011) or the visual perspective of the triggering stimulus (yawns in orientations of 90°, 180°, and  
486 270° were as potent or nearly as potent as normal, upright, 0° yawns; Provine, 1989, 1996).  
487 Campbell & de Waal (2011) found that chimpanzees yawned more frequently in response to in-  
488 group mate yawns compared to out-group chimpanzee yawns, even though they looked longer at  
489 out-group chimpanzee videos.

490 In sum, the existing evidence suggests that attention is important in eliciting the yawning  
491 response in so far as it ensures stimulus detection. In this respect, non-conscious processing and  
492 bottom-up (stimulus driven) attention and not top-down, selective attention (*sensu* Bachman, 2011;  
493 Katsuki & Constantinidis, 2014; Kaya & Elhilali, 2011) is likely to be involved in yawn contagion.  
494 Moreover, the level of the yawning response seems not to be sensitive to the level of attentiveness  
495 or overstimulation (more than a stimulus). Further studies on larger sample sizes are necessary to  
496 understand whether the inability to find yawn contagion in our gorilla groups reflects the actual lack  
497 of the phenomenon. If this is the case, it will remain to be clarified whether the absence of yawn  
498 contagion is linked to gorillas' scarce baseline attention to conspecifics or to their scarce  
499 responsiveness to others' stimuli in a society that is characterized by loose social relationships.

500

501 **Ethical approval** - This article does not contain any studies with human participants performed by  
502 any of the authors. This study was approved by University of Pisa (Animal Care and Use Board).  
503 Since the study was purely observational the committee waived the need for a permit. The study  
504 was conducted with no manipulation of animals. Gorillas were observed in their home enclosures,  
505 including the video presentation. Data were collected on the animals that spontaneously approached  
506 the tablet. The animals were never deprived of water and food at any stage and were never isolated

507 from their social group. All animal experiments were carried out in accordance with the U.K.  
508 Animals (Scientific Procedures) Act, 1986 and associated guidelines, EU Directive 2010/63/EU for  
509 animal experiments.

510

511 **Data accessibility** - The data used for this study are provided as electronic supplementary material.  
512 The statistical tools EASYFIT, and SPSS used in this study are proprietary software. However,  
513 trials (limited time/limited functionality) can be found online on the producer's websites  
514 (EASYFIT: [www.mathwave.com](http://www.mathwave.com); SPSS: <https://www-01.ibm.com>). The freeware Resampling  
515 Procedures 1.3 package by David C. Howell  
516 (<https://www.uvm.edu/~dhowell/StatPages/ResamplingWithR/ResamplingR.html>).

517

518 **Authors' contributions** - E.P. conceived the study. E.P. and G.C. designed the study. E.P., I.N. and  
519 G.C. performed the video experiments. E.P., I.N. and G.C. analysed videos and data. E.P., I.N.,  
520 G.C. wrote the paper.

521

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709 **Table 1** - The gorilla colonies under study hosted at the ZooParc de Beauval

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SUBJECT	SEX	AGE CLASS	YEAR OF BIRTH	KINSHIP	TESTED SUBJECT
<b>FAMILY GROUP</b>					
<b>Asato (AS)</b>	M	Adult	1991	KH, MY, MS, MP, KU, SA, MA's father	YES
<b>Inge (IN)</b>	F	Adult	1980		YES
<b>Kabinda (KA)</b>	F	Adult	1982	MA, MP, MY, KH's mother	YES
<b>Tamarilla (TA)</b>	F	Adult	1986	Ku's mother	YES
<b>Sheila (SH)</b>	F	Adult	1991	SA, MS's mother	NO
<b>Khala (KH)</b>	F	Adult	2007		YES
<b>Mayombè (MY)</b>	F	Adult	2007		YES
<b>Maïsha (MS)</b>	F	Subadult	2008		YES
<b>Mapenzi (MP)</b>	M	Juvenile	2010		YES
<b>Kwimba (KU)</b>	F	Juvenile	2010		YES*
<b>Sawa (SA)</b>	F	Juvenile	2011		NO
<b>Mayelè (MA)</b>	F	Infant	2013		NO
<b>BACHELOR GROUP</b>					
<b>Yangu (YA)</b>	M	Adult	1983		YES
<b>Kumi (KU)</b>	M	Adult	2004		YES
<b>Banjoko (BA)</b>	M	Subadult	2006		NO
<b>Sadiki (SA)</b>	M	Subadult	2006	KA's brother	NO
<b>Kajolu (KA)</b>	M	Juvenile	2010	SA's brother	YES

711 \*Kwimba carried out only two out of four trials (gorilla yawn and gorilla control videos).

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**Aggressive and submissive behavioural items**

<b>Avoiding</b>	An individual moves out of the path when another individual approaches or takes a less direct route around the other
<b>Biting</b>	One individual closes its mouth on another's body
<b>Brusque rushing</b>	One individual jumps forcefully with its four limbs on another
<b>Chasing-Fleeing</b>	One individual runs in pursuit of another who is rapidly withdrawing
<b>Crouching</b>	An individual bends all four limbs, presses its ventrum to the ground, and may try to travel while in this position, or an individual may crouch while sitting by lowering the head, hunching the shoulders, and often covering the head with an arm
<b>Dismissing</b>	One individual performs a brusque movement to keep another away
<b>Pulling</b>	One individual grasps another and forcefully brings it closer
<b>Pushing</b>	One individual uses arms or legs forcefully to move another away
<b>Screaming</b>	Frightened vocalization mainly performer during conflicts
<b>Slapping</b>	Rapidly charging toward fellows individual slaps it with an open hand
<b>Stamping</b>	Jumping forcefully on another individual or on an object

**Table 2** - Aggressive and submissive behavioural patterns used to classify the agonistic contacts in this study (Palagi et al., 2008). The agonistic contacts were used to create a socio-matrix for the calculation of the individual Normalized David's Score to be included as fixed variable in the GLMM.

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**Table 3** - Description of the variables used in GLMM analyses of yawn response.

NAME	TYPE
<b>DEPENDENT VARIABLES</b>	
Yawn frequency (in minutes)	Scale
<b>FIXED EXPLANATORY VARIABLES</b>	
<b>Yawner characteristics</b>	
Sex of the subjects	Nominal (0=Male; 1=Female)
Age of the subjects (in months)	Scale
Rank (Normalized David's Score values)	Scale
<b>Contextual characteristics</b>	
Experimental condition	Nominal (0=Control; 1=Yawn)
Type of stimulus	Nominal (1=Avatar; 2=Unfamiliar gorilla)
Self-directed behaviour frequency (in minutes)	Scale
<b>RANDOM FACTORS</b>	
Group identity*Yawner Identity	Nominal (1=family group; 2=bachelor group)*Initials

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<b>GLMM<sub>1</sub> (AIC<sub>1</sub>=41.964; <math>\Delta</math>AIC<sub>1-1</sub>=0.000; wi=0.225; wi*100=22.55; Wbest/wi=1.000)</b>				
<b>Fixed variable/s</b>	<b><i>F</i></b>	<b><i>df1</i></b>	<b><i>df2</i></b>	<b><i>P</i></b>
Selfdirected	6.180	1	16	0.024
Y C	2.547	1	16	0.130
<b>GLMM<sub>2</sub> (AIC<sub>2</sub>=41.982; <math>\Delta</math>AIC<sub>2-1</sub>=0.018; wi=0.224; wi*100=22.35; Wbest/wi=1.009)</b>				
<b>Fixed variable/s</b>	<b><i>F</i></b>	<b><i>df1</i></b>	<b><i>df2</i></b>	<b><i>P</i></b>
Selfdirected	7.476	1	17	0.014
<b>GLMM<sub>3</sub> (AIC<sub>3</sub>=42.149; <math>\Delta</math>AIC<sub>3-1</sub>=0.185; wi=0.206; wi*100=20.56; Wbest/wi=1.097)</b>				
<b>Fixed variable/s</b>	<b><i>F</i></b>	<b><i>df1</i></b>	<b><i>df2</i></b>	<b><i>P</i></b>
Selfdirected	5.244	1	16	0.036
Sex	0.01	1	16	0.920
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<b>GLMM<sub>4</sub> (AIC<sub>4</sub>=42.791; <math>\Delta</math>AIC<sub>4-1</sub>=0.827; wi=0.149; wi*100=14.92; Wbest/wi=1.512)</b>				
<b>Fixed variable/s</b>	<b><i>F</i></b>	<b><i>df1</i></b>	<b><i>df2</i></b>	<b><i>P</i></b>
Selfdirected	6.444	1	16	0.022
AVATAR_GORILLA	0.024	1	16	0.879
<b>GLMM<sub>5</sub> (AIC<sub>5</sub>=42.925; <math>\Delta</math>AIC<sub>5-1</sub>=0.961; wi=0.139; wi*100=13.95; Wbest/wi=1.617)</b>				
<b>Fixed variable/s</b>	<b><i>F</i></b>	<b><i>df1</i></b>	<b><i>df2</i></b>	<b><i>P</i></b>
Selfdirected	4.712	1	15	0.046
AVATAR_GORILLA	0.019	1	15	0.891
Sex	0.013	1	15	0.910

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**Table 4** - GLMM results of the 5 best competing models. AIC=Akaike Information Criterion; wi=Akaike weight; Wbest= best value of Akaike weight



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780 **FIGURE AND SUPPLEMENTARY VIDEO LEGENDS**

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782 **Figure 1 (experimental phase)** - Number of yawns per minute (mean  $\pm$ SE) performed in relation  
783 to the different trials proposed to subjects (avatar yawn; avatar control; gorilla yawn; gorilla  
784 control).

785 **Figure 2 (experimental phase)** - Scatterplot showing the correlation between the frequency of self-  
786 directed behaviours (self-scratching, self-grooming, nose wiping, and head shaking) and yawning  
787 calculated on the total of trials performed (avatar yawn video; avatar control video; gorilla yawn  
788 video; gorilla control video).

789 **Figure 3 (naturalistic observation)** - Number of yawns per stimulus (mean  $\pm$ SE) performing in the  
790 3-min time window after the perception of the yawn emitted by the trigger (detectable stimulus =  
791 yawn condition) and in the absence of direct visual contact with the trigger (undetectable stimulus =  
792 baseline condition).

793 **Figure 4 (naturalistic observation)** - Boxplot showing the hourly frequency of yawning associated  
794 with self-directed behaviours (scratching/self-grooming performed during a yawn) and NOT  
795 associated with self-directed behaviours (no self-scratching/self-grooming performed during a

796 yawn). The box plots show the median and 25th and 75th percentiles; the open dots are outliers  
797 more than 1.5x IQR from the rest of the scores.

798 **Video S1** – A juvenile male of lowland gorilla motivated to watch the screen

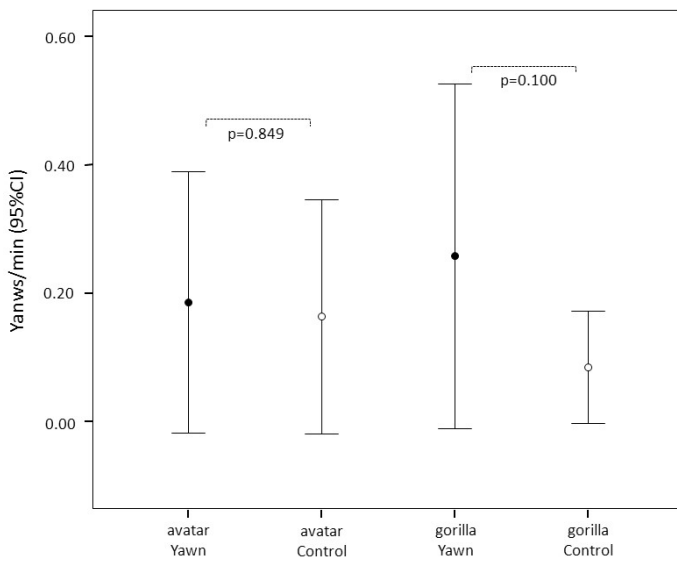
799 **Video S2** – An adult female of lowland gorilla not motivated to watch the screen

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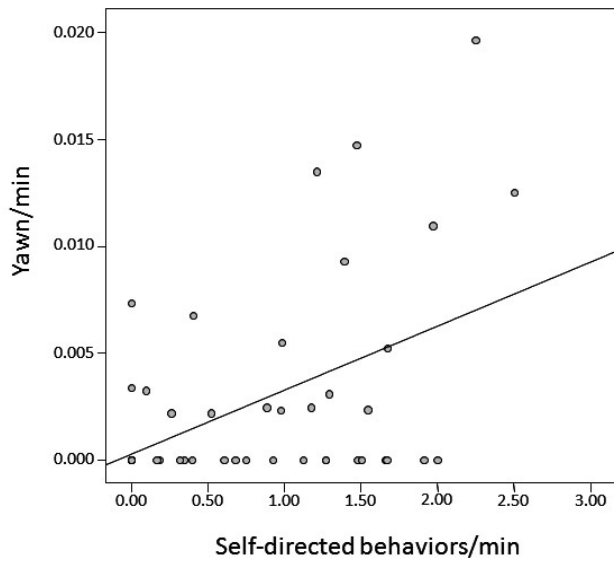


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805 **Figure 1**

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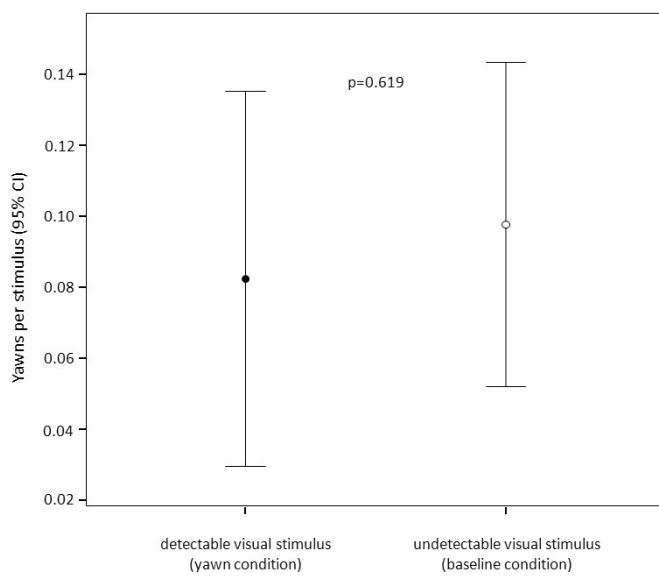
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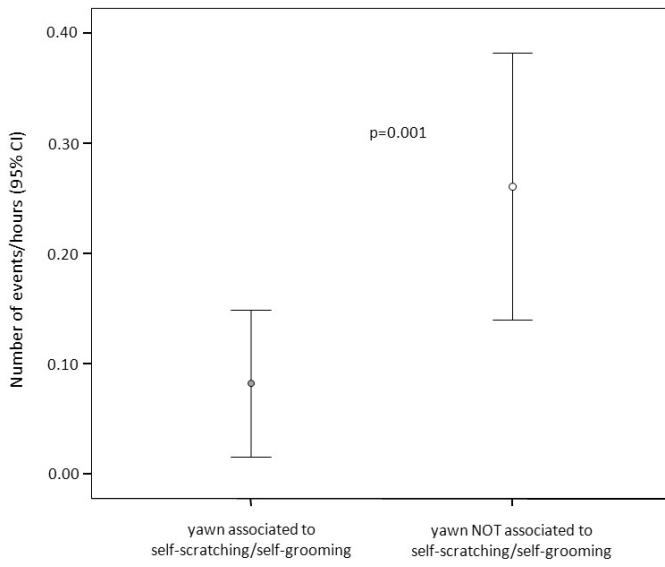


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819 Figure 3

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823 Figure 4