Contagious yawning in gelada baboons as a possible expression of empathy

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Yawning in humans has been proposed to be related to our capacity for empathy. It is presently unclear whether this capacity is uniquely human or shared with other primates, especially monkeys. Here, we show that in gelada baboons (\textit{Theropithecus gelada}) yawning is contagious between individuals, especially those that are socially close, i.e., the contagiousness of yawning correlated with the level of grooming contact between individuals. This correlation persisted after controlling for the effect of spatial association. Thus, emotional proximity rather than spatial proximity best predicts yawn contagion. Adult females showed precise matching of different yawning types, which suggests a mirroring mechanism that activates shared representations. The present study also suggests that females have an enhanced sensitivity and emotional tuning toward companions. These findings are consistent with the view that contagious yawning reveals an emotional connection between individuals. This phenomenon, here demonstrated in monkeys, could be a building block for full-blown empathy.

Yawning is a common phenomenon in vertebrates, and in primates it is present since birth (1). From an ethological point of view, yawning is one of the best examples of a fixed action pattern. Once started, a yawn is unstoppable and uncontrollable. Motor patterns of yawning are stereotyped and occur in essentially the same form in different contexts, from resting to social interactions (2, 3). Yawning may also be a stress indicator and a sign of neurological pathologies (4). From a physiological perspective, it has been proposed that yawning maintains mental efficiency by regulating brain temperature through a cooling mechanism (5, 6).

There are several theories about the possible function of yawning (7, 8). Communication theories propose yawning as a way animals synchronize group behaviors during rest–activity cycles or communicate drowsiness or stress. Arousal theories propose, instead, that yawning should help subjects maintain their attention levels and that it may have evolved to promote maintenance of vigilance and/or shared alertness (2, 9).

In humans yawning is demonstrably contagious as it is easily triggered by seeing, hearing, reading, or simply thinking about another individual yawning (3, 10). More than 50% of human subjects yawned within a few minutes after having watched a video of a yawning person (10). The power of contagious yawning is suggested by interspecific effects (11), even though this phenomenon is still under debate (12).

In chimpanzees (\textit{Pan troglodytes}), yawning can be induced by observing a video of a conspecific yawn (13), even though in that study the contagious response was limited to a few of the tested individuals. Recently, however, Campbell et al. (14) demonstrated at the population level that chimpanzees show contagious yawning in response to 3D-animated chimpanzee yawns, thus confirming the results obtained in previous studies. In macaques (\textit{Macaca spp.}), yawning responses elicited by the video of unfamiliar monkeys yawning were accompanied by self-scratching, perhaps indicative of increased anxiety (15). Although these are the first attempts to investigate the phenomenon of contagious yawning in nonhuman primates, the evidence remains meager, at least in monkeys, and more data are needed to better understand the natural or naturalistic conditions under which yawning can be elicited and the possible social functions of yawning contagion.

The infectiousness of yawning and the difficulty to suppress it when we observe someone else yawning are clear signs of a connection present between two or more individuals and suggest that this phenomenon might involve not only purely motor aspects of the behavior but also more subtle emotional channels. These observations have led some researchers to hypothesize a link between contagious yawning and empathy (16–19). In humans, it has been reported that subjects showing higher levels of contagion to yawn stimuli also score higher in questionnaires evaluating empathy and mental state attribution (18). Although debated, there is no consensus about the possibility that nonhuman primates are capable of empathizing with others. However, there is a range of phenomena, from sensitivity to others’ distress to reassuring behaviors from both experimental and observational studies, which suggest some level of empathy in nonhuman primates (20–23). Moreover, in both humans and animals empathy is biased toward individuals who are more similar, familiar, or socially closer (24). It is assumed that shared representations are more easily activated the more two individuals have in common. Because empathy is biased toward such individuals, we expect that contagious yawning, if empathy-based, should be similarly biased. Although the hypothetical link between contagious yawning and empathy is appealing, it has never been empirically tested in any species, including humans.

Here, we report that yawning is contagious in a nonhuman primate, the gelada baboon, and that this response seems unrelated to external stressful events. Moreover, our data demonstrate that yawn contagion is more common between individuals with higher levels of affiliation, thus suggesting that the roots of empathy could may be present in nonhuman primates.

Results

We recorded 3,229 yawns by means of all-occurrences sampling (403 h). Geladas performed three different yawning displays (see Fig. 1) with the following hourly frequencies: (i) covered teeth (CT), individual mean 0.120 ± 0.022 SE; (ii) uncovered teeth (UT), individual mean 0.115 ± 0.018 SE; and (iii) uncovered gums (UG), individual mean 0.219 ± 0.144 SE. Males and females did not differ in their baseline levels of CT and UT (CT: exact Mann–Whitney \( U = 22, \text{Nm} = 5, \text{Nf} = 9, P = 0.947 \); UT: exact Mann–Whitney \( U = 21, \text{Nm} = 5, \text{Nf} = 9, P = 0.841 \); however, sex difference was found for UG (males > females: 0.018 SE).

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exact Mann–Whitney $U = 6.5$, $N_{\text{males}} = 5$, $N_{\text{females}} = 9$, $P = 0.031$.

The concurrent presence of three observers over the whole period of observation permitted us to record the identity of each group member that was in visual and/or auditory contact with the yawner and, consequently, to assess which individuals very likely were not able to perceive the presence of the yawn. To evaluate the presence of contagion, we compared the experimental condition, defined as how often an individual X (receiver) yawns after the first individual Y (stimulus) yawned, with the baseline condition, defined as how often individual X yawns when individual Y is nearby (within ~10 m) but does not yawn. If the receiver yawned within the time window of 5 min after the yawn of the stimulus individual, the receiver response was considered as affected by the previous stimulus. Following the procedure used in previous experiments on yawning contagion in nonhuman primates (13, 15), if an individual yawned outside the time window of 5 min after the previous yawn, the yawn event was not considered as affected by the previous stimulus and was included in the baseline condition.

In geladas, each kind of yawning display can be accompanied by a loud precall and/or a long-distance vocalization (25). To evaluate the effect of such acoustic components in yawning contagion, we analyzed responses according to different sensory modalities characterizing the stimulus: (i) visual and acoustic (V+A), and (ii) acoustic alone (A).

In adults and subadults we found that receivers’ yawning responses were significantly more frequent when the stimulus individual performed a yawn than when it engaged in any other behaviors except yawning (V+A: exact Wilcoxon’s $T = 0$, $n = 14$, $P = 0.0001$; A: exact Wilcoxon’s $T = 2$, $n = 14$, $P = 0.005$) (Fig. 2). Contagion was also present when the analysis was limited to females (V+A: exact Wilcoxon’s $T = 0$, $n = 9$, $P = 0.002$; A: exact Wilcoxon’s $T = 4$, $n = 9$, $P = 0.008$). In contrast, no statistical difference was found for the immature subjects (exact Wilcoxon’s $T = 13$, $n = 7$, $P = 0.547$). For immature animals it was not possible to analyze separately the two sensory modalities characterizing the stimulus because of the extremely low frequency of response events.

We calculated the individual frequency of yawning contagion during each min of observation (for 5 min after the yawn of the stimulus individual), and we found that contagion was more frequent during the second min (exact Friedman test $\chi^2 = 10.303$, $df = 4$, $n = 14$, $P = 0.029$) (Fig. 3).

As far as the matching response is concerned (i.e., if the stimulus individual performed a CT yawn, the receiver responded with a CT yawn), we included in the analysis only those contagion events based on visual cues. We found that when the stimulus was a female, the response matched the type of yawn (CT, UT, and UG) displayed by the stimulus individual (condition UG: exact Friedman test $\chi^2 = 5.20$, $df = 2$, $n = 9$, $P = 0.013$; condition UT: exact Friedman test $\chi^2 = 7.52$, $df = 2$, $n = 9$, $P = 0.021$; condition CT: exact Friedman test $\chi^2 = 4.07$, $df = 2$, $n = 9$, $P = 0.139$) (Fig. 4A). The Dunnett test (posthoc test) revealed a trend for a matching response in the UT condition (UT-UT $>$ UT-UG: Dunnett’s $q = 1.83$, $0.05 < P < 0.1$). More interestingly, we obtained even more significant results when we restricted the analysis to the response displayed by females only. In this case the matching response was present for CT and UT (condition UG: exact Friedman test $\chi^2 = 0.00$, $df = 2$, $n = 9$, $P = 1.00$).

Fig. 1. Three different yawning displays performed by geladas. (A) A CT yawn. (B) An UT-yawning. (C) An UG-yawning.

Fig. 2. Frequency of yawning. (A) Frequency of yawning performed in the presence and absence of the visual stimulus is shown. We considered only nonvocalized yawning as stimulus; however, we cannot exclude the influence of audible respiratory movements. (B) Frequency of yawning performed in the presence and absence of the acoustic stimulus (vocalized yawning) is shown. In this case the receiver was not able to see the first yawner so the visual cue can be excluded.
condition UT: exact Friedman test $\chi^2 = 14.00$, df = 2, $n = 9$, $P = 0.0001$; condition CT: exact Friedman test $\chi^2 = 10.67$, df = 2, $n = 9$, $P = 0.0017$). For the CT and UT conditions the Dunnett test (posthoc test) gave the following results: condition CT-CT: Dunnett’s $q = 1.96$, $P < 0.05$) and condition CT-UT: Dunnett’s $q = 2.6$, $P < 0.01$; CT-CT vs. CT-UG: Dunnett’s $q = 3.52$, $P < 0.01$; UT-UT vs. UT-UG: Dunnett’s $q = 2.84$, $P < 0.01$.

On the contrary, we did not find any statistical evidence for a matching response when the stimulus was a male (condition UG: exact Friedman test $\chi^2 = 1.33$, df = 2, $n = 9$, $P = 0.60$; condition UT: exact Friedman test $\chi^2 = 1.63$, df = 2, $n = 9$, $P = 0.58$; condition CT: exact Friedman test $\chi^2 = 1.73$, df = 2, $n = 9$, $P = 0.53$) (Fig. 4B), even when we restricted the analysis to the response displayed by males only (condition UG: exact Friedman test $\chi^2 = 3.18$, df = 2, $n = 9$, $P = 0.20$; condition UT: exact Friedman test $\chi^2 = 2.60$, df = 2, $n = 9$, $P = 0.44$; condition CT: exact Friedman test $\chi^2 = 0.20$, df = 2, $n = 9$, $P = 1.00$).

To calculate the level of reciprocal contagion for each dyad we divided the number of XY contagion events plus number of YX contagion event per the number of opportunities in which Y perceived X’s yawns plus number of opportunities in which X perceived Y’s yawns.

Last, we found a positive correlation between hourly grooming frequency and yawning contagion based on visual contact, so that we were confident that the receiver was aware of the stimulus’ identity [row-wise permutation test $K_r = 57$, Tau$_{wr} = 0.18$, $n = 10$ individuals (45 dyads), $P = 0.02$] (Fig. 5). However no correlation was found between yawning contagion and individual spatial association (proximity plus contact sitting frequency) [row-wise permutation test $K_r = 1$, Tau$_{wr} = -0.0033$, $n = 10$ individuals (45 dyads), $P = 0.50$]. This analysis was performed on the unit A ($n = 10$) because there was not any grooming exchange between the individuals of the two units. We did not perform the same analysis on the unit B because of the low sample size ($n = 4$) and the absence of grooming interactions in two dyads. In other words, the more two individuals groomed each other, the more they responded with a yawn to the other’s yawn. One could argue that individuals groom each other more when they are in proximity, and that proximity exposes them more toward the other’s yawning. However, the correlation between the frequency of grooming and yawning contagion remained significant even after controlling for interindividual spatial association (proximity plus contact sitting frequency) not involving grooming interactions [partial row-wise matrix permutation $K_r = 18$, Tau$_{wr} = 0.21$, $n = 7$ individuals (21 dyads), $P = 0.001$; proximity plus contact sitting frequency and yawning contagion: row-wise permutation test $K_r = 40$, Tau$_{wr} = 0.48$, $n = 7$ individuals (21 dyads), $P = 0.03$]. Thus, proximity does not seem to explain the level of yawning contagion. We obtained even a higher level of significance when we limited the analyses to the females [grooming frequency and yawning contagion: row-wise permutation test $K_r = 40$, Tau$_{wr} = 0.48$, $n = 7$ individuals (21 dyads), $P = 0.001$; proximity plus contact sitting frequency and yawning contagion: row-wise permutation test $K_r = 18$, Tau$_{wr} = 0.21$, $n = 7$ individuals (21 dyads), $P = 0.001$].

**Fig. 3.** Frequency of contagion distribution as a function of the minutes of observation is shown.

**Fig. 4.** Matching response. (A) Type of yawning response as a function of type of previous yawning when the first yawner (stimulus) was a female is shown. A matching response is present only for CT and UT. (B) Type of yawning response as a function of type of previous yawning when the first yawner (stimulus) was a male is shown. There is no matching response for any of the three types of yawning.

**Fig. 5.** Grooming and contagion. The scatter-plot shows the correlation between the frequency of grooming interchange ($y$ axis) and the level of contagion ($x$ axis).
dyads), $P = 0.106$; grooming and yawning frequency controlled for proximity plus contact sitting; partial row-wise matrix permutation $\text{Tau}_{kr} = 0.42$, $n = 7$ (21 dyads), $P = 0.005$]. This analysis was restricted to the females of the unit A only ($n = 7$) because of the absence of grooming exchange between the members of the two units. The same analysis could not be performed on males because of the low sample size (males of the unit $A = 3$; males of the unit $B = 2$).

**Discussion**

The present findings indicate that yawning in gelada baboons is contagious and can be elicited via both visual and acoustic modalities. This latter result is in line with previous data (4) on contagious yawning by blind human subjects, thus suggesting the importance of multimodal perception in yawning triggering. Furthermore, activation of matched motor programs via different sensory modalities has been shown in monkeys. For example, pig-tailed macaques (*Macaca nemestrina*) increased feeding behavior, even though they were fully satiated, after just hearing another monkey eat without visual input (26). Motor facilitation to specific acoustic stimuli has also been demonstrated in the macaque motor cortex, suggesting that motor output may be facilitated by multiple sensory modalities (27).

The contagion effect of yawning may be interpreted as a type of response occurring in highly social animals that need to synchronize behavioral activities (20). Coordinating activities among group members has an undoubted advantage because it promotes social cohesiveness. In fact, we observed such coordination in the social context of our baboons, when they were awake and relaxed, often coinciding with grooming sessions or with transitions from rest to activity, or vice versa.

Yawn contagion was present only in adults. The absence in infants and juveniles has also been reported for humans, in which children aged younger than 5 years do not show this contagion (28). The relative insensitivity of immature subjects to yawning may reflect a developmental immaturity of their social cognitive skills and/or brain structures involved in processing social information. In most social animals, including primates, adults have the main role in group decision-making and regulating the group daily activities, whereas the young tend to passively follow adults, especially the mother (29). Thus, synchronizing and coordinating one’s own behavior with that of conspecifics could be less relevant for young individuals, which are rather more sensitive to maintain proximity with their mothers in their first years of life before weaning (30).

The criteria we adopted for the analysis of contagion allowed us to exclude that yawning responses were elicited by any kind of stressful event. In fact, we excluded all yawning events associated with behavior indicative of stressful conditions (e.g., raised eye browse, self-scratching, self-grooming, body shaking, lip flip, urination, defecation, gravel digging, etc.).

Even though yawning contagion requires the reenactment of a behavior, it cannot be considered an imitative or mimetic process because of the reflexive and stereotypical nature of this chain reaction. However, this phenomenon could be compatible with the idea of a common mechanism active during the perception and reenactment of yawning. The discovery of mirror neurons in macaques has prompted the idea that an action-perception mechanism could be responsible for important cognitive functions such as action understanding, response facilitation, and other behavioral matching (31, 32). A human mirror mechanism for action understanding and imitation homologous to that of the macaque has been supported by several neurophysiological and brain imaging studies (33). Only recently, however, has the hypothesis that a similar mechanism may account for contagious yawning been empirically investigated in humans. The findings obtained so far failed to find activation in the traditional parietal-premotor areas populated by mirror neurons. However, a more recent study (34) found that the observation of yawning in humans activates these specific areas. More data are clearly needed, but overall it seems imitation and contagion are different types of phenomena, even though they may share some neural mechanisms (34–36).

In gelada baboons, yawning contagion was particularly evident when the analysis was limited to adult females, which also showed an additional feature: they tended to match the type of yawn. This finding further supports the notion that a neural mechanism involved in behavioral matching is probably involved in this phenomenon. If mirror neurons are involved in contagion they very likely can act, through an indirect pathway (32), on limbic structures and subcortical areas that are involved in the generation and control of the yawning motor patterns.

From a social perspective, the matching responsiveness shown by gelada females may be interpreted in light of the female social network characteristic of this species. The relationships within the typical gelada one-male unit (OMU) revolve around adult females, who form the core of the cohesion and stability typical of OMUs (37). In some cases, the strength of female bonds suffices to maintain OMU integrity despite the absence of the male (25). Thus, the matching response recorded between females probably reflects the need and ability of females to stay in tune with each others’ behavioral activities and to form coalitions and alliances based on a precise reading of others’ behavior. An important implication of the present findings is that the contagion effect triggered by yawning has not only a main consequence to synchronize two individuals but it seems also to influence affective components of the behavior. Through the involuntary reenactment of an observed behavior, emotional states related to the behavior may be arise in the observer. This idea has been theorized by Preston and de Waal (24) and likely involves neural mechanisms that, during the perception of an action or of a facial expression, activate shared representations (31, 38).

Recently, this hypothesis has been tested in tufted capuchin monkeys (*Cebus apella*). When monkeys were being imitated by a human experimenter they increased their liking and interactions toward the imitator compared with a nonimitator (39). It has been proposed that in a highly social species, such as the capuchin monkey, activities are highly synchronized and this might provide a sufficient degree of behavioral matching to promote affiliative behaviors between individuals. Similar effects may be produced by yawning contagion. Even though our study could not disentangle the cause–effect relationship between yawning contagion and affiliation, the correlation between the level of contagion and the rate of grooming suggests that yawning contagion is facilitated by an emotional connection between stimulus animals and receivers.

An alternative explanation, however, is that individuals who often groom each other have more opportunities to observe and catch the yawns of the other. However, reduced interindividual distances (measured by proximity and contact sitting) did not correlate with yawning contagion and the correlation between grooming and yawning contagion persisted after statistically controlling for spatial association. Thus, social closeness seems to predict yawning contagiousness, which is consistent with the idea that yawning contagion is mediated by empathy (24).

Another hypothesis, not necessarily mutually exclusive with the emotional connection hypothesis, is that yawning contagion in geladas can be a sign of mood convergence. Because gelada baboons are highly social animals, which behave in a highly synchronized and cohesive way, the capacity to communicate a sleepy mood may result in a better coordinated group activity for sleeping or waking. However, this hypothesis cannot explain the results presented here because the data were cleaned from the resting–activity transition phases (mainly morning and evening).
and included events that did not necessarily follow sleep-resting activities.

Yawning has been conserved in its stereotypic forms throughout mammals and other vertebrate taxa, demonstrating its important basic physiological function. In primates, its function has been extended to the social domain. The demand for synchronizing activities in highly social species requires that individuals read each others’ behaviors and match it accurately. Matching one’s own behavior with that of others, independently on whether this occurs consciously or not, has recently been shown to promote affiliation between individuals through an empathic connection (39). The presence of yawning contagion in gelada baboons and its relation with the degree of bonding between individuals suggests that in this species are probably present the basic components of the multilayered empathy well known of humans and, at least in part, of the great apes.

Methods

Subjects and Housing. The colony of gelada baboons (T. gelada) housed at the NaturZoo (Rheine, Germany) was made up of two OMUs, which comprised two adult males, one subadult female, three immature males, and four immature females (Table S1). The two OMUs were housed in the same enclosure with both an indoor (a room ~36 m²) and outdoor facility (an island of ~2,700 m² surrounded by a boundary ditch). The animals of the two OMUs could interact freely with one another. The size of the island allowed the scattering of geladas and, consequently, the formation of small groups of animals that frequently changed. This situation, together with the good observability conditions, allowed us to easily define the stimulus animal (the first yawner) and the potential receivers.

The enclosures were equipped with everything necessary to allow the geladas to move freely in all three dimensions. Specifically, the outside enclosure was located in an open naturally hilly area equipped with trees, branches, ropes, and dens (Fig. S1). The animals were fed with grains, vegetables, and pellets, which were scattered on the ground three times a day (8:30 AM, 11 AM, 2:30 PM). Water was available ad libitum. No stereotypic or aberrant behaviors characterized the study group.

The research complied with current laws of Germany and Italy.

Data Collection. We collected behavioral data during 4 months of observation (June to October 2007) on all of the subjects of the colony. We concurrently used two methods of observation: all-occurrences sampling and focal-animal sampling (40). During all-occurrences sampling (a total of 403 h of observation) we recorded all of the yawns performed by each subject. Data were collected vocally through a voice recorder, and the records were later computer-transcribed. Before starting systematic data collection, the three observers underwent a training period (~90 h).

During the training phase (the trainer was E.P.), the same focal animal was followed by the observers simultaneously, and the data were then compared. Training was considered to have been completed when at least 90% of cases were agreed upon by the interobserver reliability according to Martin and Bateson (41). The observations took place daily over 6-hr periods that spanned morning (from 6 AM) and evening (until 10 PM).

During each yawning occurrence we recorded the exact time of the yawning, the posture assumed by the yawner (defined as sitting, standing, and lying), the identity of the yawner, the presence of vocalization, the level of mouth opening (CT, UT, UG) (Fig. 1). Each type of yawn (CT, UT, UG) could be accompanied by a vocalization (precall and/or yawning vocalizations) (25).

Moreover, we sampled the behavioral item occurring during the 10 s before and 10 s after the yawn (7) that included further ethogram items. Specifically, we recorded a series of state of activity and behaviors classified into social and nonsocial. Resting, sleeping, walking, standing, grooming, feeding, contact sitting, and proximity were scored as states. Other behavioral items, such as raised eye brows, scratching, self-grooming, body shake, lip flip, urination, defecation, gravel digging, and copulation were scored as events. For each behavioral item we recorded the identity of the actor and the receiver.

The analysis of contagion in presence of the visual cue has been performed according to the following criteria: (i) absence of external stimuli (including visitors) alerting the attention of the first yawner (stimulus) and the receiver (at least from the observer perspective); and (ii) the stimulus yawner had to maintain its gaze toward the target of its activity/behavior (without shifting its gaze toward other stimuli). Obviously, in this analysis the acoustic component caused by audible respiratory movements could not be completely excluded.

The analysis of contagion in presence of acoustic cues (and in absence of visual cues) has been performed according to the following criteria: (i) absence of visual contact between the first yawner (stimulus) and the potential receiver (presence of visual barriers); (ii) a vocalized yawn (recorded by observer 1 was considered “not perceived,” when observer 2, which followed the potential receiver, did not hear any vocalization. Moreover, both the analyses were performed according to the following criteria: (i) the yawn was not accompanied by or associated with signs of stress or arousal such as raised eye brows, scratching, self-grooming, body shake, lip flip, urination, defecation, gravel digging, and copulation and (ii) the whole yawn sequence had to occur when the animals involved in the observation were awake and relaxed (i.e., not engaged in feeding activities or in agonistic, sexual, and play encounters).

By focal animal sampling (30 h of observation per subject), we were able to record all of the proximity and grooming sessions performed by each focal animal with any other group member. Each subject was followed every day and at different times to obtain data covering the entire day in balanced proportions as much as possible.

Data Analysis and Statistics. When the analyses were carried out at the individual level, we used nonparametric statistical approach (42). The Wilcoxon matched pairs sign rank test and Mann-Whitney U test were used to determine whether the frequency of yawns performed after a previous yawn (experimental condition) and those performed without the presence of any previous yawn (baseline condition), Friedman’s two-way ANOVA was used to test for differences in the latency of yawning response within a 5-min time window and evaluate whether a matching response in the type of yawn (CT, UT, and UG) between the stimulus yawner and the receiver was present. In the case of a significant main effect, we used the Dunnett multiple comparison test (post hoc test) to determine which responses were significantly different (42).

We used exact tests according to the threshold values suggested by Mundry and Fischer (43). Statistical analyses were performed by using Microsoft Excel and SPSS 12.0.

To control for the possible correlation between the level of affiliative relationships and the yawning contagion we applied the row-wise matrix permutation test. In interaction matrices data are not independent because observations concerning the same individual recur. This results in dependency within and between rows and columns of the same individual. The row-wise matrix correlation compares only the values within the same row, overcoming the problem of the interdependency of the data. The Kr row-wise matrix correlation coefficient is based on a weighted sum of the correlation between all dyads of corresponding rows of the two matrices and it is defined by using Kendall’s rank order correlation coefficient (44). This method, applied to square matrices, can be used with small sample sizes because no assumptions are made about the underlying distribution (the smallest sample size for square matrices that can acquire a probability value <5% is four). The matrices were permuted 10,000 times. Each analysis was carried out with the software MatMan 1.0.

As a second step, we used the Tau K, matrix partial correlation (44) to test the null hypothesis that the potential correlation between the levels of grooming and contagion was unaffected by the reduced interindividual spatial distribution. For this test we constructed a third matrix of the association frequency measured by proximity plus contact sitting levels shown by each dyadic pair.

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