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Observing grooming promotes affiliation in Barbary macaques

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Observing friendly social interactions makes people feel good and, as a result, then act in an affiliative way towards others. Positive visual contagion of this kind is common in humans, but whether it occurs in non-human animals is unknown. We explored the impact on female Barbary macaques of observing grooming, a behaviour that physiological and behavioural studies indicate has a relaxing effect on the animals involved. We compared females' behaviour between two conditions: after observing conspecifics groom, and in a matched control period. We found that observing grooming was associated with reduced behavioural indicators of anxiety, suggesting that seeing others groom is, in itself, relaxing. Observing grooming was also associated with a shorter latency to becoming involved in a grooming bout (and higher likelihood both of initiating that bout and being the groomer rather than groomee), and with elevated rates of other affiliative behaviours. These results provide evidence for positive visual contagion; this phenomenon may contribute fundamentally to group cohesion not just in this species, but also in the many mammal and bird species where grooming occurs. Our study highlights the importance of exploring social behaviour beyond the level of the interacting individuals, within the broader social context where it occurs.

1. Introduction

Repeated interactions between individual animals underlie their social relationships, which in turn underpin species' social structure [1]. Understanding how and why animals engage socially with each other is, as a result, a central goal of behavioural ecology [2]. Studies of animal social interactions typically focus only on the individuals immediately involved; such interactions do not usually occur in isolation, however, but rather in the presence of other group members. Seeing or hearing conspecifics interacting can alter the affective state and behaviour of these bystanders, leading to contagion—the spread of affect and behaviours from one individual to others in the group [3,4]. This phenomenon may have important impacts on individual animals, and more broadly at the level of their social networks, and such effects have been well studied in humans [5]. In non-human species, they are much less well understood, but there is increasing evidence that contagion—of negative and positive affective states and behaviours—occurs in a range of taxa.

Evidence that negative interactions of conspecifics lead to contagion among bystanders has been found in a range of taxa. In rats, *Rattus norvegicus*, behavioural, pharmacological and brain stimulation studies indicate that specific 22 kHz vocalizations given in aversive social interactions reflect underlying negative affective states [6], and individuals hearing these calls in an experimental setting showed behavioural indicators of anxiety, namely a reluctance to enter and explore an open arena [7]. In primates, there is behavioural and pharmacological evidence that self-directed behaviours such as scratching indicate affective state: decreases in these behaviours from normal levels reflect feelings of relaxation [8], while increases indicate anxiety [9,10]. In a number of primate species, e.g. hamadryas baboons, *Papio hamadryas* [11] and Japanese

macaques, *Macaca fuscata* [12], it has been found that bystanders witnessing an aggressive interaction between other group members showed elevated levels of self-directed behaviours.

Studies exploring how positive interactions of conspecifics may lead to contagion in bystanders have focussed on a range of behaviours associated with positive affect, and their associated acoustic cues. For example, in common marmosets, *Callithrix jacchus*, playbacks of chirp calls given during affiliation led to an increase in rates of positive social behaviours [13], and in zoo-housed groups of chimpanzees, *Pan troglodytes*, the frequency of grooming behaviour was found to be positively related to the number of grooming-related vocalizations from a neighbouring group [14]. In kea parrots, *Nestor notabilis*, individuals hearing the playback of calls given in the context of social play showed an increase in likelihood of playing with conspecifics [15] and in rats, playbacks of ultrasonic calls given during play led to an increase in prosocial approach behaviour [16].

A notable gap in our knowledge relates to positive contagion through visual observation of conspecific interactions. This phenomenon is central to human social interactions [17–19]; seeing friendly interactions can make people feel positive emotions and, as a result, they then act in an affiliative way to others [20,21]. To our knowledge, only one study has explored such positive visual contagion beyond our own species, despite the fact that many group-living species rely heavily on vision to monitor conspecifics' behaviour [22–24]. In that study, Watson [25] found that laboratory-housed common marmosets shown videos of conspecifics grooming showed elevated rates of grooming, but did not show reduced levels of self-scratching as would be expected if they experienced a positive shift in affective state [8]. Moreover, prolonged exposure to videos led to an increase in self-scratching, suggesting that the video presentations were stressful; the increase in grooming associated with such presentations may consequently represent a behavioural coping strategy to alleviate such stress [26].

Here, we tested for evidence of positive visual contagion among Barbary macaques, *Macaca sylvanus*, by investigating their response to observing grooming interactions. Grooming occurs in a wide range of mammal and bird species [27–31] and there is evidence that this behaviour provides hedonic benefits, relaxing those involved [32]. Being groomed is associated with a reduced heart rate in pigtail macaques, *Macaca nemestrina* [33], rhesus macaques, *Macaca mulatta* [34] and Camargue horses, *Equus caballus* [35], a release of opioids in the blood in pigtail macaques [36], and lower rates of self-directed behaviour in long tailed macaques, *Macaca fascicularis* [37] and green woodhoopoes, *Phoeniculus purpureus* [31]. The giving of grooming has been found to be associated with reduced rates of self-directed behaviour in crested macaques, *Macaca nigra* [38] and green woodhoopoes [31], and with lower stress hormone levels in Barbary macaques [39]. In chimpanzees, grooming with a closely bonded social partner—regardless of the direction of grooming—is associated with an increase in peripheral oxytocin levels [40].

In this observational study of semi-free-ranging adult female Barbary macaques, we tested the hypothesis that observing grooming leads to positive contagion. Such contagion could result in positive changes in affective state, promote grooming, increase rates of other affiliative behaviour, or inhibit agonistic behaviour; we explored predictions related to each of these four possibilities. We predicted firstly

that the observation of grooming would reduce bystanders' rates of self-directed behaviour (*prediction 1*). We also predicted that observing grooming would reduce the time to bystanders' next grooming bout (*prediction 2a*), that levels of visual attention while observing grooming would be negatively related to the time to the next grooming bout (*prediction 2b*), and that observing grooming would increase the likelihood both of bystanders initiating grooming (*prediction 2c*) and of them being the groomer rather than groomee (*prediction 2d*). We predicted that observing grooming would increase bystanders' rates of approaching other individuals (*prediction 3a*), the proportion of time they spent in close proximity to others (*prediction 3b*) and their rates of (non-grooming) affiliative behaviour (*prediction 3c*), but would reduce their rates of aggressive behaviour (*prediction 4*).

2. Methods

(a) Study site and animals

We conducted this study in the semi-free ranging population of Barbary macaques at Trentham Monkey Forest (Stoke-on-Trent, UK). Barbary macaques live in multi-male, multi-female groups in which grooming is a key social behaviour. Importantly, unlike many other primate species, Barbary macaques do not have grooming-specific vocalizations, and it is extremely rare for any vocal signals to be given during a grooming bout, so acoustic cues are unlikely to underpin any observed contagion effects. At Trentham, two groups of Barbary macaques range within a fenced 24 ha area of grassland, oak and cedar forest. Visitors to the park must stay on designated paths and are not allowed to touch or feed the animals. The macaques are provisioned with fruit, vegetables, pellets and cereals. Each monkey has an individual code tattooed on the inside of their thigh, allowing individual identification. Subjects of this study were 20 adult females, aged from 4 to 27 years old (mean \pm s.d.: 12.8 ± 6.7 years old); females were chosen as subjects as they are involved in grooming more frequently than males. These animals lived in the same group, which comprised 68 individuals at the start of the study: 31 adult females (greater than 4 years of age), 22 adult males (greater than 4 years of age) and 15 individuals less than 4 years of age (nine females and six males). During the study period, three infants were born.

(b) Data collection

We conducted behavioural observations daily from 9.00 to 5.00 between 1 April and 15 June 2017. The procedure used to collect data was adapted from the well-established post-conflict/matched-control (PC-MC) method, first used by de Waal & Yoshihara [41] to study post-conflict behaviour. In the PC-MC method, observational data are collected on the behaviour of individually recognized animals during a defined period of time after they have been involved in a conflict (PC), and then compared to data collected for the same animal during an MC before which no conflict occurred. In our study, instead of collecting data following conflicts involving our focal animals, we did so after the start of their observation of a grooming bout.

We recorded these post-observing-grooming (POG) samples opportunistically, starting them either (i) when a grooming interaction started between two individuals, with one of our study subjects less than 7 m from the grooming dyad; or (ii) when a study subject moved to a distance less than 7 m from two individuals already involved in a grooming interaction. We decided on the maximum distance of 7 m between the focal individual and the grooming dyad following a brief pilot study. Bystanders frequently attended to grooming interactions over

distances up to 7 m and while they sometimes appeared to look at more distant grooming bouts, we felt the accuracy of assessment of gaze direction reduced markedly beyond this distance.

For a POG to be used in the study, the grooming interaction observed by the study subject had to involve at least one adult individual (male or female) and to last at least 1 min after the start of the POG. In addition, the subject had to be awake, to look at the grooming dyad at least once, and to stay in a 7 m radius of them for at least 1 min. In order to assess the looking behaviour of the subject, where possible the observer stood such that the grooming animals were between them and the subject; thus the observer looked beyond the grooming pair to the subject, and a look was scored when the gaze of the subject was assessed to be directly at the grooming interaction. In a very small number of cases, such alignment was not possible, and here a look was scored when the orientation of the subject's head was judged to be directly towards the grooming animals.

For each POG, we recorded the length of the grooming bout (or the time until the focal animal moved away to greater than 7 m) and the number of times the subject looked directly at the grooming dyad. We followed the subject until the start of their next grooming interaction with another individual, which marked the end of the POG. For this next grooming interaction, we recorded whether the subject was groomer or graminee, and whether they did, or did not, initiate the bout (the subject was considered as initiator if they approached another individual and either started grooming them, or presented to be groomed by them). If no grooming bout involving the subject occurred within one hour of the start of the POG, data collection was stopped.

On the day following the POG, or as soon as was possible thereafter, we carried out MC observations, starting at about the same time of day (± 30 min), collecting the same type of data and for the same amount of time as the corresponding POG. We followed the focal individual for 10 min before the beginning of the MC to be sure they were not a bystander of a grooming interaction or themselves involved in grooming during this period; if they were, the MC was postponed to the next day. Similarly, if the subject was involved in an intense fight or conflict in this time, the MC was postponed. If, during the MC, the subject was located within 7 m of individuals involved in grooming and obvious visual attention towards the grooming dyad was detected, we abandoned the MC and started a new POG; two MCs were then subsequently collected in chronological order for the two POGs (i.e. the first MC was matched to the first POG). If no visual attention towards the grooming bout was detected, the MC continued until the end. If it was not possible to carry out an MC within two weeks after the date of a POG, we discarded that POG (mean interval between POG and MC was 4.11 days). We stopped data collection on those subjects who gave birth during the study period ($n = 3$) after the birth of their infant, and discarded any POGs which had been recorded before the birth but for which the MCs had not yet been collected.

During the POG and MC observation periods, we recorded all occurrences of self-directed behaviours (scratching, self-grooming, yawning and body shake) shown by the focal animal. Occurrences of self-directed behaviours had to be separated by a minimum of 5 s to be considered two separate events. We also noted the occurrence of any non-grooming affiliative behaviours (body contact, affiliative facial expression, embrace, affiliative touch, mount and co-feeding), and aggressive behaviours (bite, chase, contact aggression, mock hit, aggressive facial expressions, lunge and scream). We recorded all occurrences of subjects approaching another individual (to within 1 m). We used scan sampling to assess the proximity of the subject to adult males or females during POGs and MCs, noting every minute the presence of all such animals within 1 m and within 5 m of the focal individual (with distances estimated by eye).

Behavioural observations were recorded using an iPod Touch equipped with the application ANIMAL BEHAVIOUR PRO© v.1.2 [42],

with the exception of three observations which, owing to an iPod malfunction on one day, were recorded by voice onto mobile phone. Treated data are available in the electronic supplementary material, and all raw data files are deposited at https://figshare.com/articles/Berthier_and_Semple_-_raw_data_files/7029269.

(c) Data analyses

To ensure that in each POG-MC pair the duration of behavioural observation was the same, in cases where grooming involving the focal individual occurred earlier during an MC than during the corresponding POG, we reduced the length of the latter to the same length as the former. Following de Waal & Yoshihara [41], we then classified each POG-MC pair as: 'attracted' (when a grooming interaction involving the subject occurred during the POG period but not in the corresponding MC), 'dispersed' (when a grooming interaction involving the focal individual occurred before the end of the MC period; this includes POG-MC pairs for which no grooming interaction involving the focal occurred during the POG but one did occur during the MC), or 'neutral' (grooming did not happen in either the POG or MC; $n = 7$ in total, one from each of seven females). To avoid pseudoreplication, for each study animal we calculated an average of each behaviour (or proportion of attracted/dispersed pairs) across their POGs and their MCs, and used these individual-level matched pairs of data to test most of the study predictions, with paired *t*-tests used when difference scores were found (using the Shapiro–Wilk test) to be normally distributed, and Wilcoxon matched-pairs tests used when difference scores were not normally distributed. Statistical tests were two-tailed with alpha set at 0.05, and conducted in SPSS v.22. We tested predictions as follows.

- (i) *Prediction 1*: we used a paired *t*-test to determine whether rates of self-directed behaviours were lower in POGs than MCs.
- (ii) *Prediction 2a*: we used a Wilcoxon matched-pairs test to determine whether the proportion of 'attracted' POG/MC pairs was higher than that of 'dispersed' POG/MC pairs.
- (iii) *Prediction 2b*: we tested whether visual attention of subjects towards the grooming bouts observed in POGs was negatively related to time to the next grooming bout, following the method described by Carder & Semple [43] and Hohmann *et al.* [44]. First, for each subject with at least five POGs ($n = 19$), Spearman's rank correlations were carried out to assess the relationship between the number of times subjects looked towards the grooming bout, and the time to their next grooming interaction (the latter set at 60 min if no grooming occurred during a POG). We then used a one-sample *t*-test to test whether the mean of subjects' correlation coefficients was significantly lower than 0, as predicted if the overall pattern of relationships between visual attention and time to next grooming bout is negative.
- (iv) *Prediction 2c*: we used a paired *t*-test to determine whether the proportion of POGs for which the subjects were the initiator of the next grooming interaction was higher than the proportion for which other individuals were the initiator of the next grooming interaction. One female for which only one grooming interaction was observed in POGs was excluded from this analysis (all other females had at least four grooming interactions in total in POGs). We repeated this analysis for MCs, predicting here that proportions of grooming bouts initiated versus not initiated by subjects would not be different, reflecting an overall baseline pattern of animals initiating on average half of the grooming bouts they are involved in. In MCs, the next grooming bouts involving subjects were frequently not observed; thus, only those subjects

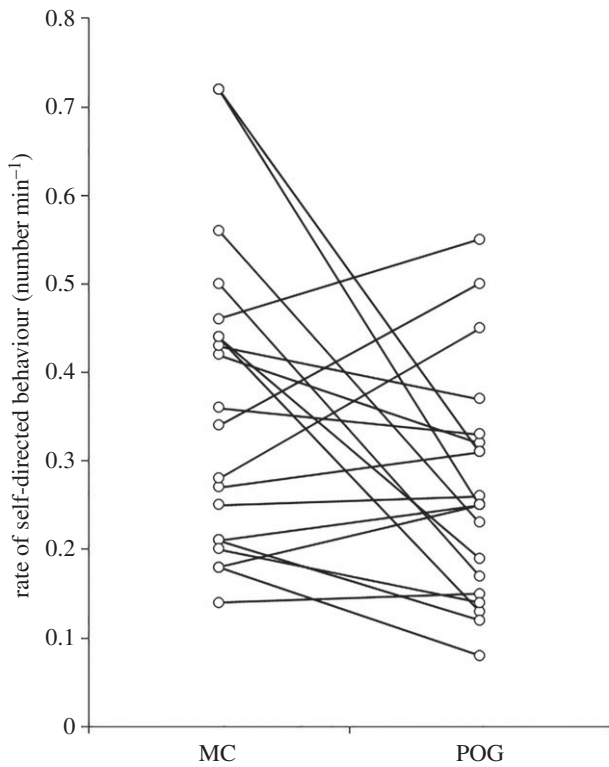


Figure 1. Rates of self-directed behaviour in post-observing-grooming (POG) samples and matched controls (MC). Lines join data points for individual females ($n = 20$).

for which at least three grooming interactions were seen were considered in these analyses ($n = 10$).

- (v) *Prediction 2d*: we used a paired t -test to determine whether the proportion of POGs for which the subjects were the groomer in the next grooming interaction was higher than the proportion in which they were the groomee (as above, the female for which only one grooming interaction was observed in POGs was excluded from analysis). For the corresponding analysis of MCs (for which we used a Wilcoxon matched-pairs test), as before subjects' next grooming bouts were often not observed, and only subjects for which at least three grooming interactions were seen were considered ($n = 11$).
- (vi) *Predictions 3a-3c*: we used Wilcoxon matched-pairs tests to determine whether rates of approaching another individual (to within 1m) (*prediction 3a*), the proportion of time spent with at least one neighbour within 1 m, and within 5 m (*prediction 3b*), and rates of (non-grooming) affiliative behaviours (*prediction 3c*) were higher in POGs than MCs.
- (vii) *Prediction 4*: we used a Wilcoxon matched-pairs test to determine whether rates of aggressive behaviours were lower in POGs than MCs.

3. Results

In total, 154 POG/MC pairs were collected over the 20 adult females in this study (range: 2–10 pairs per female), representing a total of 82 h 7 min of observation. Each individual was followed for a mean of 4 h 27 min (range 2 h 6 min–7 h 44 min). For 15 out of 154 POGs (9.7% of the dataset), no grooming interaction involving the focal individual was observed after 1 h of observation; for seven of these (one from each of seven females) no grooming was seen also in the MC.

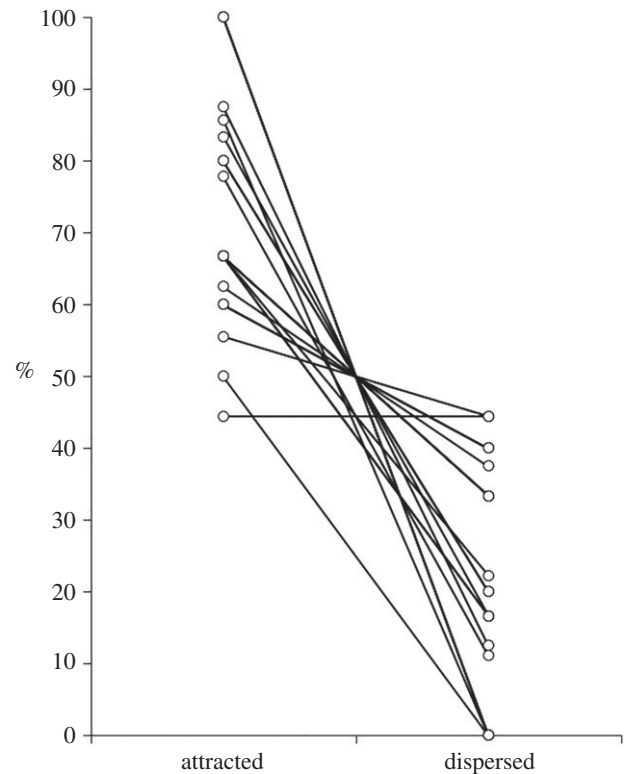


Figure 2. Proportion of 'attracted' and 'dispersed' post-observing-grooming (POG) and matched controls (MC) pairs. Lines join data points for individual females ($n = 20$). Note that as POG/MC pairs could also be 'neutral', values for individual females do not necessarily total 100%.

In support of *prediction 1*, rates of self-directed behaviours were lower during POGs than during MCs (paired t -test: $t_{19} = -2.276$, $p = 0.035$; figure 1). In support of *predictions 2a* and *2b*, the average proportion of attracted POG/MC pairs was significantly higher than the average proportion of dispersed pairs (attracted: median = 0.67, range = 0.44–1.00; dispersed: median = 0.20, range = 0.00–0.44; Wilcoxon matched-pairs test: $Z = -3.827$, $n = 20$, $p < 0.001$; figure 2), and the rate of visual attention towards the grooming bout was negatively associated with the time to the next grooming interaction (one sample t -test: $t_{18} = -2.226$, $p = 0.039$). Supporting *prediction 2c*, in POGs the proportion of grooming interactions initiated by the focal individual was significantly higher than the proportion initiated by another individual (initiated by focal: mean = 0.62, range = 0.33–1.00; initiated by other: mean = 0.38, range = 0.00–0.67; paired t -test: $t_{18} = 2.852$, $p = 0.011$); by contrast, in MCs the proportion of grooming interactions initiated by the focal individual was not significantly different to the proportion of grooming interactions initiated by another individual (initiated by focal: mean = 0.57, range = 0.00–1.00; initiated by other: mean = 0.43, range = 0.00–1.00; paired t -test: $t_9 = 0.749$, $p = 0.473$). Supporting *prediction 2d*, in POGs the proportion of grooming interactions for which the focal individual was the groomer was significantly higher than the proportion for which the focal individual was the groomee (groomer: mean = 0.72, range = 0.33–1.00; groomee: mean = 0.26, range = 0.00–0.67; paired t -test: $t_{18} = 5.603$, $p < 0.001$); in MCs, by contrast, the proportion of grooming interactions for which the focal individual was the groomer was not significantly different to the proportion for which the focal individual was the groomee (groomer: median = 0.60, range = 0.00–0.71; groomee: median = 0.33, range = 0.00–0.67; Wilcoxon matched-pairs

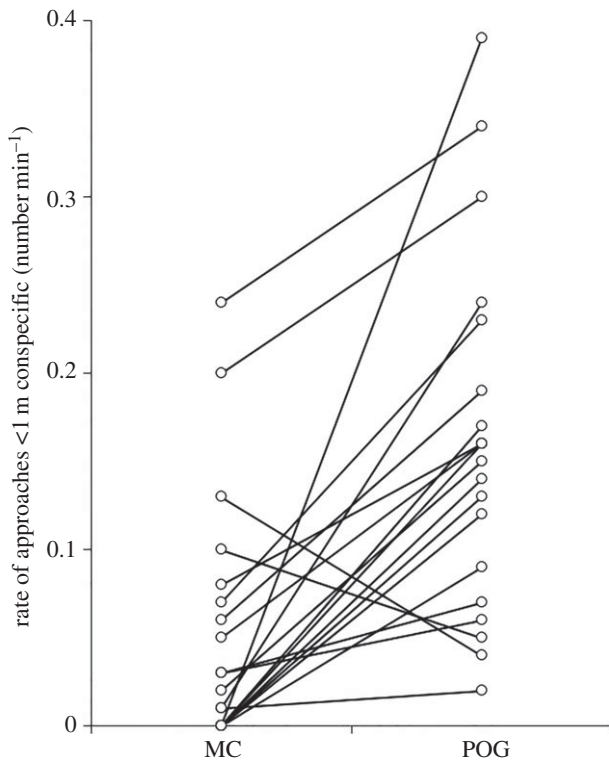


Figure 3. Rates of approaching conspecifics in post-observing-grooming (POG) samples and matched controls (MC). Lines join data points for individual females ($n = 20$).

test: $Z = -1.429$, $n = 11$, $p = 0.153$). Predictions 3a-3c were all supported: females approached other individuals more frequently during POGs than MCs (Wilcoxon matched-pairs test: $Z = -3.530$, $n = 20$, $p < 0.001$; figure 3), spent significantly more time with at least one conspecific in proximity during POGs than MCs (within 1 m—Wilcoxon matched-pairs test: $Z = -1.972$, $n = 20$, $p = 0.049$; within 5 m—Wilcoxon matched-pairs test: $Z = -2.688$, $n = 20$, $p = 0.007$), and were involved in significantly more (non-grooming) affiliative interactions during POGs than MCs (Wilcoxon matched-pairs test: $Z = -2.112$, $n = 20$, $p = 0.035$; figure 4). Finally, prediction 4 was not supported as females were not less aggressive in POGs compared to MCs (Wilcoxon matched-pairs tests: $Z = -0.699$, $n = 20$, $p = 0.485$).

4. Discussion

In this study of adult female Barbary macaques, we tested whether observing grooming—an affiliative behaviour that behavioural and physiological studies suggest has a relaxing effect on the animals involved—leads to positive contagion among bystanders. Our results indicate that seeing conspecifics groom was associated with a reduction in a behavioural indicator of anxiety among bystanders, suggesting that seeing others groom is, in itself, relaxing. In addition observation of grooming bouts was associated with increases in a range of affiliative behaviours, including grooming itself. These findings provide evidence from a non-human species that observing affiliative interactions of conspecifics can lead to positive contagion. This work further highlights the importance of exploring animal social behaviour not just at the level of the interacting individuals, but also within the broader social environment in which the behaviour occurs.

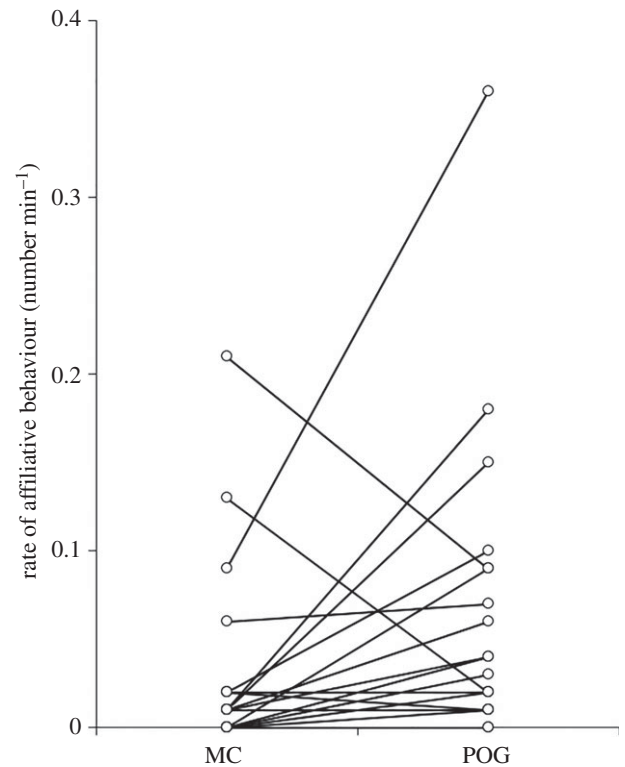


Figure 4. Rates of (non-grooming) affiliative behaviour in post-observing-grooming (POG) samples and matched controls (MC). Lines join data points for individual females ($n = 20$).

Female Barbary macaques showed lower rates of self-directed behaviours after observing others grooming than in corresponding control periods. This mirrors the decrease in self-directed behaviours from baseline levels seen in captive long-tailed macaques that had been given lorazepam [8,10], a drug which in healthy humans has a relaxing effect, leading to feelings of calmness [45]. Our results indicate, therefore, that seeing others grooming has a calming effect. This is at least suggestive of the occurrence of emotional contagion—sharing the emotional state of another [46]—but to provide strong evidence for this phenomenon, it would be necessary to assess simultaneously the emotional state of the grooming animals and bystanders, and to demonstrate a change in the emotional state of the latter towards the state of the former [47]. For this, measures of emotion that reflect valence as well as arousal should be used [47,48]; these could be provided by combining behavioural indices with non-invasive physiological measures, for example through remote assessment of heart rate [49] or quantification of urinary levels of oxytocin [40] or cortisol [50].

We also found evidence that grooming was itself contagious: subjects observing others grooming were quicker to become involved in a grooming bout themselves, and more likely to be both the initiator of this bout and the giver rather than the receiver of grooming. Moreover, the more frequently a bystander looked at a grooming interaction, the shorter was the time to their next grooming bout, suggesting that intensity of visual attention is an important factor in grooming contagion. Animals that had seen others grooming were also more likely to approach and to spend time in close proximity to conspecifics, and to engage with them in (non-grooming) affiliative behaviours. Taken together, these findings indicate that animals become more tolerant and prosocial after seeing others interacting in a positive way,

perhaps as a result of reduced anxiety levels. Interestingly, rates of aggression did not appear to be impacted by observing grooming interactions. This suggests that contagion effects related to grooming may be valence-specific, i.e. they manifest themselves as increased rates of socio-positive behaviours, but not reduced rates of socio-negative behaviours.

Positive visual contagion of the kind for which we have provided evidence here is likely to play a key role in maintaining group cohesion [51]. In humans, it has been found that positive contagion influences work group dynamics, in particular, increasing levels of within-group cooperation [52]. Our study suggests that a similar phenomenon may arise in non-human animals, as a result of the impacts of observing others engaged in positive social interactions. The contagion of affiliation in general, and grooming, in particular, would be expected to strengthen social bonds and promote cooperation among group members. In primates, the giving of grooming leads not just to the reciprocation of grooming [53] but also to increased social tolerance and support in conflicts [54,55], access to infants [56] and mating opportunities [57]. Visual contagion related to grooming may therefore give rise to a multi-faceted ripple effect, extending throughout the social network of the group—from bystanders to their subsequent grooming partners, to the bystanders of those grooming interactions and beyond. Exploring the nature and reach of such chains of behavioural contagion will provide valuable new insights into the importance of visual contagion effects in shaping both within- and between-species differences in affiliative tendencies. Variation in the strength of such effects may, for example, drive differences in affiliation between populations of the same species, or within such populations over time. Moreover, interspecific differences in visual contagion may underpin variation in social style across species, with higher levels of positive contagion characterizing more tolerant societies.

It is important to consider the adaptive significance for bystanders of the positive visual contagion effects we document. Important benefits may arise from bystanders' consequent affiliative social interactions; in Barbary macaques, animals that groom others are more likely to be tolerated around valuable food resources and to receive support in agonistic encounters [55]. Additionally, the costs associated with grooming may be reduced if it occurs when group mates are also grooming. For example, the time cost of searching for a willing grooming partner, and/or the risk of receiving aggression from a potential partner, may be lower in such contexts as other animals in the group have demonstrated a readiness to engage in grooming at that particular time. The relative opportunity costs of grooming may also be reduced by engaging in this behaviour when others are doing so, as these individuals will also be incurring such costs, being similarly not able to exploit the alternative opportunities available.

Grooming is one of the most commonly studied social behaviours in animals, with data on patterns of grooming used to test predictions from a range of theoretical frameworks including reciprocal altruism, kin selection and biological markets (e.g. [58–62]). To date, such work has typically focussed on the animals directly involved in the interaction, with little attention paid to the ways that bystanders might influence—or be influenced by—grooming bouts. The impact of bystanders on grooming interactions has

recently started to be explored, and evidence indicates that these individuals can have direct effects by intervening to disrupt ongoing grooming bouts [63], or indirect effects by their presence affecting grooming partner choice [64] or the nature of the grooming interaction [65,66]. Our study indicates the value of exploring now the other side of the coin—the impact of grooming interactions on bystanders. Furthermore, the evidence we present that observing grooming has an impact on bystanders raises an intriguing possibility, namely that grooming may have a signalling function, and that in some situations bystanders are not mere eavesdroppers but rather intended receivers. Theoretical and empirical studies to assess potential benefits to groomers of the impact of their behaviour on bystanders are needed to test this idea.

Overall, the findings of this study further highlight the importance of moving the analysis of animal social behaviour beyond the level of the interacting individuals, to take into account the broader social environment; in doing so, we feel there are a number of key avenues for future exploration. Firstly, it would be valuable to explore inter-individual variability in the extent to which observing affiliative interactions leads to positive contagion, and to investigate the biological correlates of such variation; key variables that have been linked previously to variation in affective response, and that might therefore be important here, include sex [67], age [68] and physiological parameters such as levels of circulating oxytocin [69]. Secondly, it would be interesting to investigate the factors—for example, the rank, identity of, or relatedness to, the animals being observed—that may mediate the occurrence or intensity of such contagion. Finally, it would be valuable to explore interspecific variation in this phenomenon to test, for example, whether propensity to positive contagion covaries with species' social style (e.g. tolerant/despotic). Studies of these kinds are needed if we are to appreciate the role that positive visual contagion plays in the life of social animals.

Ethics. Ethical approval was provided by the University of Roehampton. Permission to conduct the research was granted by the Trentham Monkey Forest and the Department of Life Sciences at the University of Roehampton. The study animals were fully habituated to visitors and researchers, and all data were collected using behavioural observations only. The observer attempted to keep a minimum distance of 5 m from all monkeys at all times, and physical and direct eye contact with study animals was strictly avoided.

Data accessibility. Treated data are available in the electronic supplementary material; all raw data files are deposited at https://figshare.com/articles/Berthier_and_Semple_-_raw_data_files/7029269.

Authors' contributions. J.M.B. and S.S. designed research and wrote the paper; J.M.B. collected and analysed data.

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