Social bias affects vigilance contagion in Japanese macaques

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Abstract
In group-living animals, behavioural contagion is associated with essential functions such as information acquisition and group cohesion. Studies have shown that several social factors (e.g. familiarity, dominance, the mother–offspring relationship) affect behavioural contagion. However, as previous research has focused mostly on play signals and yawning, it is unclear whether such social biases apply to all types of contagious behaviour. Using data from a group of Japanese macaques, *Macaca fuscata*, we investigated the social biases associated with the contagion of vigilance. Our findings revealed that vigilance exhibited by a given individual was more contagious to lower-ranked than to higher-ranked individuals. In addition, vigilance was more contagious to mothers from their offspring than vice versa. Thus, the susceptibility to vigilance exhibited by others varies according to the social status of each individual and the relationship between each pair of individuals. By contrast, we did not find any effects of kinship on vigilance contagion. This implies that familiarity bias, which is often reported to be associated with the contagion of yawning and play signals, does not influence vigilance contagion. Overall, our findings indicate that behavioural contagion does not occur with equal likelihood but is affected by the interplay between the type of behaviour and social structures.

Keywords
behavioural contagion, Japanese macaque, *Macaca fuscata*, mimicry, synchronization, vigilance

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For group-living animals, coordinating one's behaviour with that of other group members is associated with essential functions such as facilitating group cohesion (Conradt & Roper, 2000) and information acquisition (Danchin, Giraldeau, Valone, & Wagner, 2004). Behavioural contagion, which is defined as the phenomenon in which one's behaviour automatically triggers similar behaviours in others (Massen, Šlipogor, & Gallup, 2016; Zentall, 2003), is an example of such coordination. As noted in several studies, behavioural contagion is a mechanism in which the behaviours of group members are synchronized (McDougall and Ruckstuhl, 2018a, 2018b). Some of the most studied topics of behavioural contagion are yawning (humans: Provine, 2005; bonobos, *Pan paniscus*: Demuru & Palagi, 2012; chimpanzees, *Pan troglodytes*: Massen, Vermunt, & Sterck, 2012; dogs, *Canis lupus familiaris*: Madsen & Persson, 2013; budgerigars, *Melopsittacus undulatus*: Gallup, Swartwood, Militello, & Sackett, 2015) and emotional behaviours (e.g. laughter in humans: Provine, 1992, 2005; emotional vocalizations in common marmosets, *Callithrix jacchus*: Watson & Caldwell, 2010; play faces and play bows in dogs: Palagi, Nicotra, & Cordoni, 2015; play faces in Tonkean macaques, *Macaca tonkeana*: Scopa & Palagi, 2016).

The terms ‘mimicry’ and ‘imitation’ are commonly considered to have a similar meaning to behavioural contagion. Mimicry can occur even without any understanding of the intentions or goals of others (Carpenter & Call, 2009), and is a reflexive rather than reflective process in which the observed behaviour of others is matched with one's own behaviour (Hecht, Patterson, & Barbey, 2012). This study uses the terms behavioural contagion and mimicry interchangeably (McDougall and Ruckstuhl, 2018a, 2018b). In comparison, the term imitation is generally defined as a process of behavioural matching based on an understanding of the others' intentions and goals (Carpenter & Call, 2009), and is controlled reflectively (Hecht et al., 2012). Based on this definition, imitation can be distinguished from behavioural contagion.

Studies of contagious behaviour, mainly in Western, educated, industrialised, rich and democratic (WEIRD) human populations (Henrich, Heine, & Norenzayan, 2010), have shown that the likelihood of behavioural contagion is not equal among all individuals but is influenced by social biases (familiarity, dominance and so forth, e.g. Weyers, Mühlberger, Kund, Hess, & Pauli, 2009; Niedenthal, Mermillod, Maringer, & Hess, 2010; Hess & Fischer, 2013). It is essential to understand how social biases affect behavioural contagion in nonhuman animals to elucidate how they cope with the problems they face in group life. Despite significant research, it is unclear whether these social biases apply to all types of contagious behaviour. This is partly because previous research has focused mostly on play signals (Palagi et al., 2015; Palagi & Mancini, 2011) and yawning (Campbell & de Waal, 2011; Romero, Konno, & Hasegawa, 2013). It is therefore important to examine the effects of social biases on other types of contagious behaviours that vary in adaptive significance. Based on the above, this study examined how social biases affect vigilance behaviour, which is contagious among individuals (e.g. Pays, Jarman, Loisel, & Gerard, 2007), but has a distinctly different adaptive significance compared to other well-studied contagious behaviours, such as yawning and play signals.

When engaging in vigilance behaviour, animals scan their surroundings to obtain environmental and social information on actual and potential threats posed by predators or conspecifics (Favreau, Goldizen, & Pays, 2010) and affiliative or agonistic interactions between group members (Schino & Scerbo, 2020; Schülke, Dumdey, & Ostner, 2020). Although it had been theoretically assumed that group members engage in vigilance independently of one another (Bednekoff & Lima, 1998; Pulliam, 1973; Scannell, Roberts, & Lazarus, 2001), empirical

research over the last two decades has shown that vigilance is rather contagious and synchronous among individuals (e.g. Fernández, Capurro, & Reboreda, 2003). For group-living animals, neighbours can be a useful source of information (Danchin et al., 2004). Thus, observing vigilant neighbours and contagiously engaging in vigilance might enable individuals to share information about their surroundings and coordinate behaviours among group members. Moreover, being vigilant simultaneously with neighbours increases each individual's fitness benefits more directly, because vigilant individuals can escape from predators' attacks faster than nonvigilant ones (Lima, 1994; Quinn & Cresswell, 2005). When there are both vigilant and nonvigilant individuals, predators preferentially target the latter (FitzGibbon, 1989). By advertising their awareness of the presence of predators, prey can also deter predators from attacking (Diana monkeys, *Cercopithecus diana*: Zuberbühler, Noë, & Seyfarth, 1997; black capuchin monkeys, *Sapajus nigritus*: Wheeler, 2008). Therefore, synchronously engaging and disengaging in vigilance is an adaptive tactic for successfully avoiding threats.

Although there is much evidence to indicate that animal vigilance is contagious (e.g. greater rheas, *Rhea americana*: Fernández et al., 2003; degus, *Octodon degus*: Ebensperger, Hurtado, & Ramos-Jiliberto, 2006; eastern grey kangaroos, *Macropus giganteus*: Pays et al., 2007; red-necked pademelons, *Thylogale thetis*: Pays, Dubot, Jarman, Loisel, & Goldizen, 2009; ring-billed gulls, *Larus delawarensis*, herring gulls, *Larus argentatus*, and greater black-backed gulls, *Larus marinus*: Beauchamp, 2009; common eiders, *Somateria mollissima*: Öst & Tierala, 2011; greater kudus, *Tragelaphus strepsiceros*: Pays, Sirot, & Fritz, 2012; bighorn sheep, *Ovis canadensis*: McDougall & Ruckstuhl, 2018a), research on the social biases associated with vigilance contagion is limited. Furthermore, results from the few studies examining how social biases affect vigilance contagion are not consistent. Take the so-called 'familiarity bias' that behavioural contagion is promoted among individuals that are socially bonded by friendship, kinship and so forth (e.g. Campbell & de Waal, 2011; Palagi et al., 2015; but see Massen & Gallup, 2017). Regarding vigilance contagion, one study showed that this was increased among familiar individuals (McDougall & Ruckstuhl, 2018a), while another indicated that vigilance synchrony was not increased, even among related individuals (Quirici, Palma, Sobrero, Faugeron, & Ebensperger, 2013).

Inconsistent support for such social biases in studies of vigilance contagion may be due to methodological problems, such as those associated with quantifying the degree of behavioural contagion. Each vigilance bout begins when an individual raises her/his head and ends when the individual lowers her/his head (Bekoff, 1995; McDougall & Ruckstuhl, 2018b). Nevertheless, most studies that have investigated vigilance contagion did not clarify whether both head-up and head-down movements or either of them are contagious, because they only focused on the proportion of time spent in a state of vigilance (e.g. Fernández et al., 2003; Pays et al., 2012; Öst & Tierala, 2011) or whether there was a tendency for vigilance to overlap (e.g. Pays et al., 2009; Quirici et al., 2013). As both head-up and head-down contagion can increase vigilance overlap, we cannot tell whether one or both occur during animal vigilance in cases where these two behaviours are not distinguished. Besides, even in cases where researchers have directly investigated contagion related to head movement, they focused only on the start of vigilance but not on its end (McDougall and Ruckstuhl, 2018a, 2018b). In this study, we focused on the contagiousness of both the start and end of vigilance bouts between two nearest neighbours by analysing data from a group of Japanese macaques, *Macaca fuscata*.

By focusing on Japanese macaques, it is possible to avoid the problem of ambiguity

regarding the target of vigilance, which is a common issue raised in vigilance studies (e.g. Allan & Hill, 2018; Treves, 2000). Despite the general difficulty of determining the target of a gaze in the natural environment (Emery, 2000; Watson et al., 2015), several studies have suggested that vigilance is used not only to find predators but also to monitor within-group threats (Carter, Pays, & Goldizen, 2009; Chance, 1967). This multifunctionality may lead to confounding results regarding the social biases associated with vigilance contagion. However, as some researchers have noted, vigilance in Japanese macaques is unlikely to be directed towards predators and is predominantly used to monitor group members (Kazahari & Agetsuma, 2010; Suzuki & Sugiura, 2011). This is consistent with the hypothesis that because within-group aggression in primates is considered to occur more frequently than in other taxa (Treves, 2000) and sometimes causes serious or even lethal injuries (e.g. Japanese macaques: Soltis, Thomsen, Matsubayashi, & Takenaka, 2000; chimpanzees: Muller, 2002; chacma baboons, *Papio ursinus*: Kitchen, Seyfarth, Fischer, & Cheney, 2003), primate vigilance primarily serves to monitor within-group threats rather than predators (Busia, Schaffner, & Aureli, 2016; Treves, 2000).

We conducted behavioural observations of a free-ranging wild Japanese macaque group with no predators to test the following predictions regarding social biases associated with behavioural contagion.

Prediction 1 is that vigilance is more contagious to subordinate individuals than to dominant ones. Japanese macaque society is highly despotic, and subordinate individuals face a constant risk of being attacked by dominant individuals (Thierry, 2000). Therefore, it is assumed that subordinates (i.e. individuals with low absolute dominance ranks) are more susceptible to vigilance behaviours by other individuals compared to dominant individuals (i.e. ones with high absolute dominance ranks). Hence, we predicted that head-up and head-down movements by a given individual are more contagious to subordinate than to dominant individuals.

Prediction 2 is that vigilance is more contagious from higher-ranked to lower-ranked individuals. The dominance hierarchy of Japanese macaque society is strict and linear (Chaffin, Friedlen, & De Waal, 1995). Hence, if a given individual is a threat to higher-ranking individuals, the former is also a threat to lower-ranking ones, but not necessarily vice versa. We expected that individuals would pay more attention to the vigilance of those that are more highly ranked. Therefore, we predicted that contagion of head-up and head-down movements is more likely to occur from higher-ranked to lower-ranked individuals (i.e. rank difference > 0; see Methods) than from lower-ranked to higher-ranked individuals (i.e. rank difference < 0).

Prediction 3 is that mothers are more likely to contagiously synchronize vigilance with their immature offspring than vice versa. In Japanese macaques, mothers are highly protective of their immature offspring (Thierry, 2000). They restrict contacts between their offspring and others and frequently retrieve their offspring (Thierry, 2000). Therefore, it is expected that mothers would pay special attention to their offspring's vigilant state and that offspring, in contrast, leave the appraisal of the surrounding situation to their mothers. Based on these assumptions, we predicted that head-up and head-down movements would be more contagious in the direction from the offspring to the mother, but less contagious from the mother to the offspring compared to a nonmother–offspring pair.

Prediction 4 is that kinship increases vigilance contagion. The degree of behavioural contagion and synchrony is increased by social bonds among individuals. In humans, mothers are more likely to synchronize their behaviour with their own children than with other children (Bernieri, Reznick, & Rosenthal, 1988). In bonobos, yawn contagion is more likely to occur

among related individuals than among unfamiliar individuals (Demuru & Palagi, 2012). As for vigilance, familiarity increases vigilance contagion in bighorn sheep (McDougall & Ruckstuhl, 2018a), whereas kinship does not affect vigilance contagion in degus (Quirici et al., 2013). Considering that in Japanese macaque society, there is a high degree of nepotism such that related individuals form strikingly strong social bonds (Chapais, Gauthier, Prud'homme, & Vasey, 1997), we predicted that the degree of contagion regarding head-up and head-down movements would be greater between two related individuals than between unrelated individuals.

METHODS

Study Sites and Subjects

A free-ranging provisioned group of Japanese macaques was studied in Shiga Heights, Nagano Prefecture, Japan. S.I. conducted behavioural observations from July to October 2018 and from July to September 2019. The total observation time was about 1008 h. Demographic records have been kept since 1962 and all individuals are identifiable. Because the study site is regularly visited by tourists, the individuals in the subject group are fully habituated to humans. Although it was not possible to determine the exact number of individuals in the group because mature Japanese macaque males migrate between groups and some individuals were located at the periphery of the group (Sprague, Suzuki, Takahashi, & Sato, 1998), the group comprised approximately 240 individuals. As mature males leave the natal group, there are fewer mature males than mature females (Sprague et al., 1998). In September 2019, there were 82 adult females (> 4 years old), approximately 20 adult males (> 4 years old), approximately 110 juveniles (1–4 years old) and 32 infants (<1 year old). Each day, the study group came to Jigokudani Monkey Park just before the park opened (0900 hours) and went back to the forest when the park closed (1700 hours). The group was fed barley, soybeans and apples four times daily (0900, 1200, 1500 and 1630 hours) by the staff of the park. Our subject group was the only group that regularly visited the park, and other groups rarely approached the park. For a detailed description of the research site, see Wada and Ichiki (1980).

Data Collection

Dominance rank

To estimate the dominance ranks of members of the subject group, we observed unidirectional aggressive interactions between pairs of adult individuals using the ad libitum sampling method. We considered an interaction to be unidirectional when individual A approached B, and B expressed submissive behaviour (e.g. bared teeth display) or fled, or when A unilaterally attacked B. Because the Japanese macaque is a highly despotic species, most aggressive interactions are completely unidirectional (Thierry, 2000). Therefore, it was easy for the observer to discern between the winner and loser in an aggressive interaction. Because maternal dominance rank is passed from mother to offspring in the Japanese macaque (Chapais, 1988; Kutsukake, 2000), we considered immature individuals to have the same ranks as their mothers. In a study of rhesus macaques, *Macaca mulatta*, which are phylogenetically close to Japanese macaques and have a similarly despotic society, Berman (1980) provided a further rationale for assigning immature offspring the same rank as their mothers. The study found that infants of higher-ranked mothers are less likely to be threatened and attacked by other group members than infants of lower-ranked mothers are. Overall, we observed 1112 events of unidirectionally aggressive interaction. There were no cases of mature males being defeated by females in aggressive interactions. As Japanese

macaques form matrilineal linear dominance hierarchies (e.g. Chaffin et al., 1995), dominance was indexed by an ordinal rank based on the outcome of these interactions. Owing to the small number of mature males in the dataset (N = 4 responders; see 'Video coding') and a lack of instances of multiple males foraging in a patch simultaneously, we assigned all mature males the highest rank (i.e. 0).

Vigilance behaviour

We established a regular hexagonal patch within the park area (Fig. 1). At three feeding times, i.e. 0900, 1200 and 1500 hours, the observer put barley in the patch as indicated in Fig. 1. No food was placed within 5 m around the patch. Using two digital video cameras (HDR-TD10 and HDR-PJ40V; Sony, Tokyo, Japan) recording from different angles, the observer videotaped the behaviours of individuals that entered the patch, stayed at one of the seven locations in a sitting posture and engaged in foraging in 15 min sessions. Any instances of vigilance behaviour were recorded. During all sessions, no nongroup member intrusion was observed. We did not conduct the experiment on rainy days.

Following previous studies (e.g. Beauchamp, 2017; McDougall & Ruckstuhl, 2018b), we classified vigilance behaviours into two types to investigate contagiousness and synchrony in a reliable way. The first type is 'threat-induced' vigilance. This type of vigilance occurs as a response to external threats. In this case, even if vigilance by multiple individuals is seemingly synchronous, this is mere pseudosynchrony that occurs just because the external event makes individuals vigilant simultaneously. The second type of vigilance is 'pre-emptive' vigilance. Pre-emptive vigilance occurs without any external threat being present. Therefore, if pre-emptive vigilance is synchronized across multiple individuals, we can say that this is genuine synchrony because one individual's vigilance contagiously and directly elicited another individual's vigilance. In this study, we disregarded threat-induced vigilance and analysed only pre-emptive vigilance (see also 'Video coding').

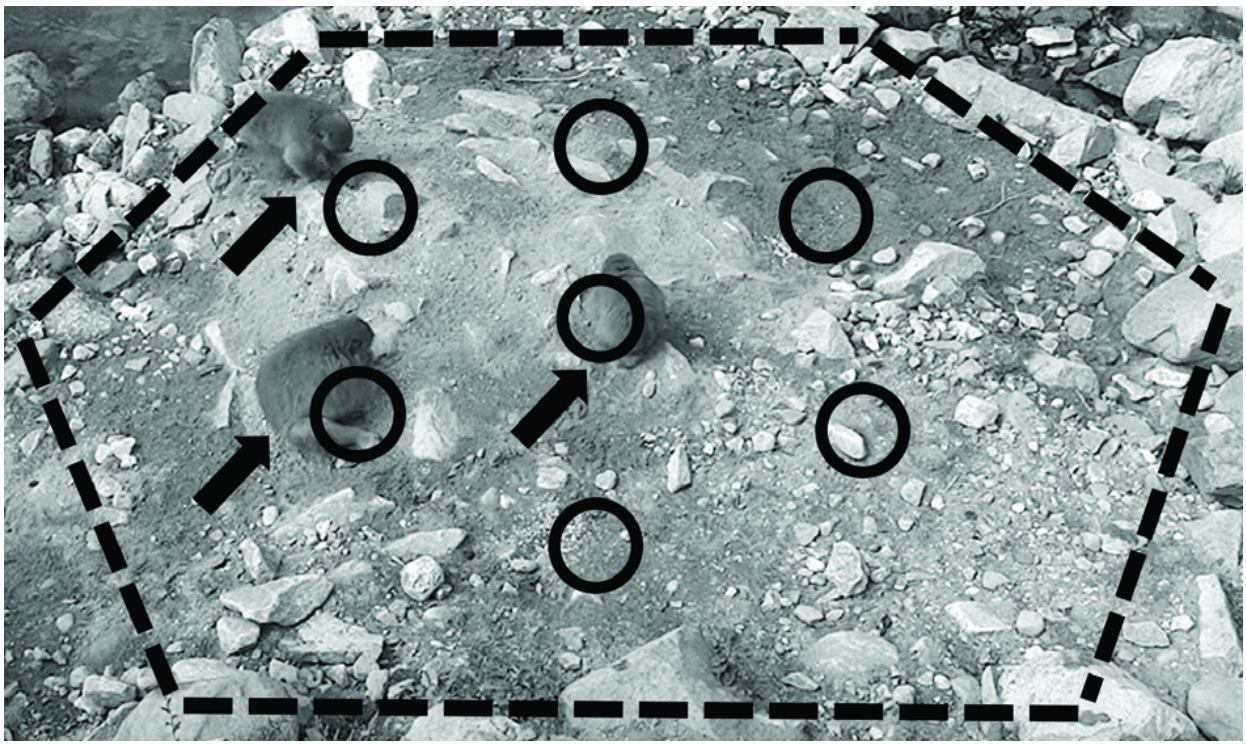


Figure 1. We established a patch (dotted line) in an area of the park below the area that human visitors were allowed to enter. Hence, visitors were not allowed near the patch and could only look down on it from more than 5 m away. The length of each side of the hexagonal patch is 2 m. The observer put 25 g of barley at each of the seven locations circled in the image. In the figure, three individuals are foraging in the patch (indicated with arrows).

Video Coding

We conducted video analyses using behavioural observation research interactive software (BORIS; Friard & Gamba, 2016). We recorded the identities of all individuals that entered the experimental patch and foraged in it. We considered that each experimental session consisted of several phases during which group composition in the patch and each individual's position remained unchanged. If an individual changed her/his position or moved out of the patch, or new individuals entered the patch to forage, this was considered a new phase. All phases that lasted less than 30 s were discarded from the analyses. Every phase during which fewer than two individuals were foraging in the patch was also discarded. For each phase, we chose two individuals situated closest together in the patch. When three or more individuals were located at almost the same distance from one another, we randomly selected two individuals from this group. We examined each phase frame by frame (30 fps) and noted instances of the start of vigilance (i.e. the time point when an individual raised her/his head) and its end (i.e. the time point when an individual lowered her/his head). For each vigilance event, we considered the first individual that raised or lowered her/his head as the initiator and the other individual as the responder. We classified the initiator's relationship to the responder into three categories: mother, offspring and other (nonmother–offspring pair).

The time window for behavioural contagion varies considerably across studies. In general, studies of yawn contagion tend to use a relatively wide time window (e.g. 3 min: Demuru & Palagi, 2012; Romero, Ito, Saito, & Hasegawa, 2014, Norscia, Demuru, & Palagi, 2016); studies of play face contagion use a narrower one (e.g. 1 s: Davila Ross, Menzler, & Zimmermann, 2008; Palagi et al., 2015; Maglieri, Bigozzi, Riccobono, & Palagi, 2020). Since vigilance

contagion involves the collection of information on the immediate surroundings, a narrow time window was considered necessary in this study. Indeed, studies of vigilance contagion have used a narrow time window of 5 s (McDougall and Ruckstuhl, 2018a, 2018b). In general, studies of behavioural contagion suffer from Type I error inflation, in which researchers falsely regard behaviours as contagious when they are really not (e.g. Kapitany & Nielsen, 2017). Since the vigilance rate in our subject group (0.13/s; Iki & Kutsukake, in press), which was much higher than that in McDougall and Ruckstuhl (2018a), can increase the risk of false positives, we considered it necessary to use a more conservative time window. Based on the above, we considered vigilance contagion to have occurred when the responder congruently moved her/his head within 1 s of the initiator's head-up or head-down movement. We did not analyse data from instances in which the initiator was behind the responder because the initiator was presumably out of the responder's line of sight. To calculate the probability of vigilance contagion, we analysed only data on an initiator's head-up and head-down movements performed while the responder's head was already lowered and raised, respectively. To distinguish pre-emptive vigilance events from threat-induced ones, we recorded whether external events (e.g. aggression among group members, approach by other monkeys, screaming, appearance of other species and the voices of park staff or visitors or other noise) were present. We considered an approach by another individual to have occurred when his/her body entered the patch. All vigilance events that might have been induced by these external events were considered threat-induced vigilance. Data pertaining to threat-induced vigilance events were discarded from the analyses and only those pertaining to pre-emptive vigilance were analysed.

Overall, we conducted 60 sessions of 15 min behavioural observations. In 111 nearest-neighbour dyads, 78 individuals were considered responders in front of whom the initiators performed head-up or head-down movements at least twice in a phase. Each responder appeared in 2.94 phases on average (SD 3.22).

Statistical Analyses

We analysed the data using generalized linear mixed models (GLMMs; glmer function in the package lme4; Bates, Mächler, Bolker, & Walker, 2015) in R version 3.6.3 (R Development Core Team, 2020). In all GLMM analyses, we included phases and the identities of the responders and initiators as random effects to deal with pseudoreplication. To obtain reliable estimates, we restricted our analyses to responders in front of whom the initiator performed head-up or head-down movements at least twice in a phase. Using a subset of the data consisting only of mother–offspring pairs, we used ANOVA to compare a model that differentiated between infants and juveniles and included responder's and initiator's age class and control factors (see below), with a model including only control factors based on the likelihood ratio test. We found that the former model did not explain more variance than the latter (head-up: $\chi^2_4 = 5.61$, P = 0.23; head-down: $\chi^2_4 = 5.62$, P = 0.23), so categorized juveniles and infants as immature individuals.

To investigate whether and what social factors affect vigilance contagion, we ran GLMMs with a binomial error structure and a logit link function. The dependent variables were the probabilities of contagion for head-up and head-down movements. The probability of contagion was calculated by dividing the number of congruent head movements by the responder within 1 s of the initiator's head-up or head-down movement by the total number of head-up or head-down movements by the initiator. We included the following social factors as fixed variables: the responder's absolute dominance rank (continuous; relevant to Prediction 1), rank difference between the responder and initiator (continuous; relevant to Prediction 2), the relationship

between the responder and the initiator (categorical: mother, offspring, and other; relevant to Prediction 3) and kinship (categorical: yes or no; relevant to Prediction 4). A responder–initiator pair was considered kin if they had a close maternal relationship (i.e. mother–offspring, grandmother–grandoffspring or maternal siblings; relatedness [r] ≥ 0.25). In addition, to control for possible confounding effects, we included the following individual factors as fixed variables: the responder's age (categorical: mature or immature), the responder's sex (categorical), the initiator's age (categorical: mature or immature), the initiator's sex (categorical), a two-way interaction between the responder's age and sex, and a two-way interaction between the initiator's age and sex. The physical distance between each responder and initiator, and the number of individuals in the patch other than the responder and initiator (continuous) were also included as fixed effects. To test for multicollinearity among the fixed effects in the global models, we calculated variance inflation factors (VIF) using the vif function in the car package (Fox & Weisberg, 2019). All the resulting VIF values were < 1.5, suggesting no multicollinearity. We fitted all possible combinations of fixed effects. For all models, we calculated and compared Akaike information criterion (AIC) scores using the dredge function in the package MuMIn in R (Barton, 2019). The model with the lowest AIC score was considered the best model, i.e. one that provides a satisfactory explanation of the variation in the data. However, models with a ΔAIC (difference between model AIC score and that of the best model) ≤ 2 are considered to have a similar level of statistical support as the best model (Burnham & Anderson, 2002). To deal with this uncertainty in model selection, we used a multi-model inference method (Burnham & Anderson, 2002). Akaike weights represent the relative likelihood of each model (Burnham & Anderson, 2002). Using Akaike weights, we calculated the relative variable importance (RVI) of models with ΔAIC ≤ 2 (Burnham & Anderson, 2002). This procedure allows us to estimate the strength of the relationship between each explanatory variable and the response variables while simultaneously taking the relative likelihood of each model into account. Figures were created with the ggplot2 package (Wickham, 2016).

Ethical Note

This study was observational and noninvasive. We conducted it in accordance with the SOKENDAI ethical guidelines for animal research. All observation protocols adhered to the ASAB/ABS Guidelines for the Use of Animals in Research.

RESULTS

In terms of the contagiousness of head-up and head-down movements, the models with the lowest AIC scores contained two social factors (the responder's rank and relationship of the responder to the initiator; Tables 1 and 2). Regarding these two factors, the best models implied the following: regarding the responder's dominance rank, head-up and head-down movements were more contagious when the responder's absolute dominance rank was lower (Figs. 2a and 3a; Prediction 1 supported). In terms of the responder–initiator relationship, head-up and head-down movements were more contagious when the responder was the initiator's mother, whereas they were less contagious when the responder was the initiator's offspring (Figs. 2b and 3b; Prediction 3 supported). However, rank difference and kinship did not remain in the best models (Predictions 2 and 4 not supported).

Regarding the contagiousness of head-up movements, two individual factors were also highlighted in the best model (Table 1); head-up movements were more contagious to females

than to males (Fig. 2c), and more contagious when exhibited by a mature initiator versus an immature initiator (Fig. 2d).

However, the low Akaike weights produced by the best models (wi = 0.17 for head-up movement and wi = 0.07 for head-down movement) indicate that there was a considerable degree of uncertainty in model selection. Indeed, there were 11 and 25 models with ΔAIC values ≤ 2 (Table 3) for contagion associated with head-up and head-down movements, respectively. The respective null models comprising only the control factors and random effects were not included in the models with ΔAIC values ≤ 2. Despite the uncertainty in model selection, the multimodel inference analyses corroborated the above results and revealed that both head-up and head-down contagion were most strongly influenced by the two social factors mentioned above (i.e. the responder's rank and the relationship between the responder and initiator). The responder's rank and responder–initiator relationship were the two variables with the highest RVI values (Table 4). For head-up movements, the RVIs associated with the responder's rank and responder–initiator relationship were both 1.00. For head-down movements, the RVIs associated with the responder's rank and responder–initiator relationship were 0.51 and 0.97, respectively. These results imply that the probability of contagion for head-up and head-down movements was more strongly affected by these two social factors than by other individual factors. Again, rank difference and kinship had little effect on vigilance contagion, with RVIs of 0.07 and 0.09 for rank difference and kinship, respectively, for head-up movements, and values of 0.16 and 0.03, respectively, for head-down movements.

Table 1. The best model explaining the variation in the probability of head-up contagion

Best model	Estimate	SE
Intercept	−1.242	0.329
Responder's rank	0.014	0.002
Relationship of the responder to the initiator		
Mother	0	
Nonmother–offspring pair	−0.315	0.296
Offspring	−1.568	0.471
Responder's sex		
Female	0	
Male	−0.434	0.219
Initiator's age		
Mature	0	
Immature	−0.350	0.201

Model: Responder's rank + Relationship of the responder to the initiator + Responder's sex + Initiator's age. Log likelihood = −257.408. Akaike information criterion = 532.8. Sample size: N = 109 dyads (18 mother–offspring dyads, 91 nonmother–offspring dyads), N = 77 responders (53 females, 24 males), N = 82 initiators (58 females, 24 males).

Table 2. The best model explaining the variation in the probability of head-down contagion

Best model	Estimate	SE
Intercept	0.514	0.667
Responder's rank	0.013	0.009
Relationship of the responder to the initiator		
Mother	0	
Nonmother–offspring pair	−0.441	0.649
Offspring	−1.632	0.785

Model: Responder's rank + Relationship of the responder to the initiator. Log likelihood = −88.010. Akaike information criterion = 190.0. Sample size: N = 46 dyads (10 mother–offspring dyads, 36 nonmother–offspring dyads), N = 43 responders (29 females, 14 males), N = 39 responders (29 females, 10 males).

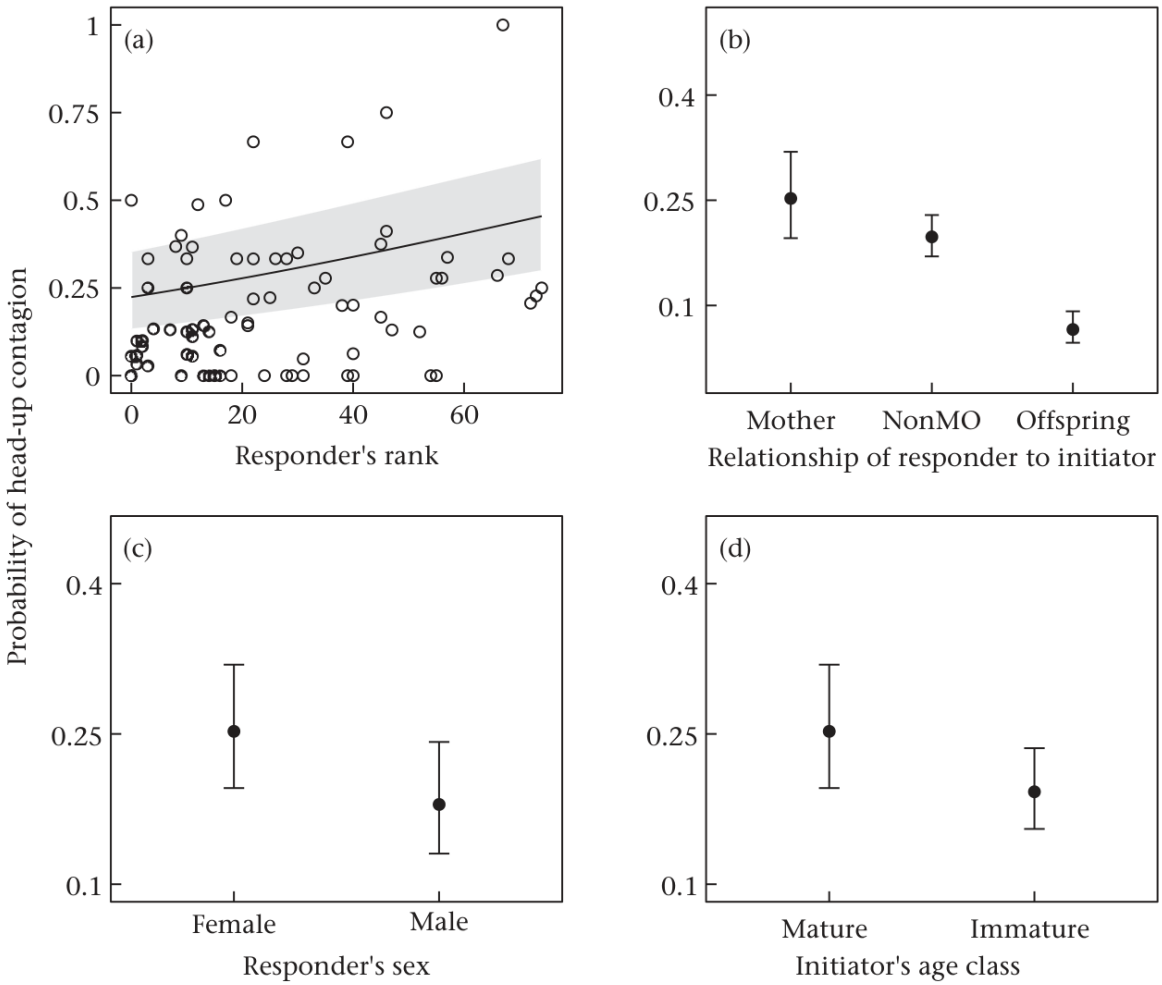


Figure 2. The predicted probabilities of head-up movement contagion according to the following fixed effects: the (a) responder's absolute rank, (b) relationship of the responder to the initiator, (c) responder's sex and (d) initiator's age class, based on the best generalized linear mixed model. In (a), smaller numbers on the x-axis indicate higher ranks. The black line and shaded area represent the fitted values and 95% confidence intervals, respectively. In (b)–(d), the black dots and error bars represent the mean probabilities and SEs, respectively. NonMO: nonmother–offspring pair.

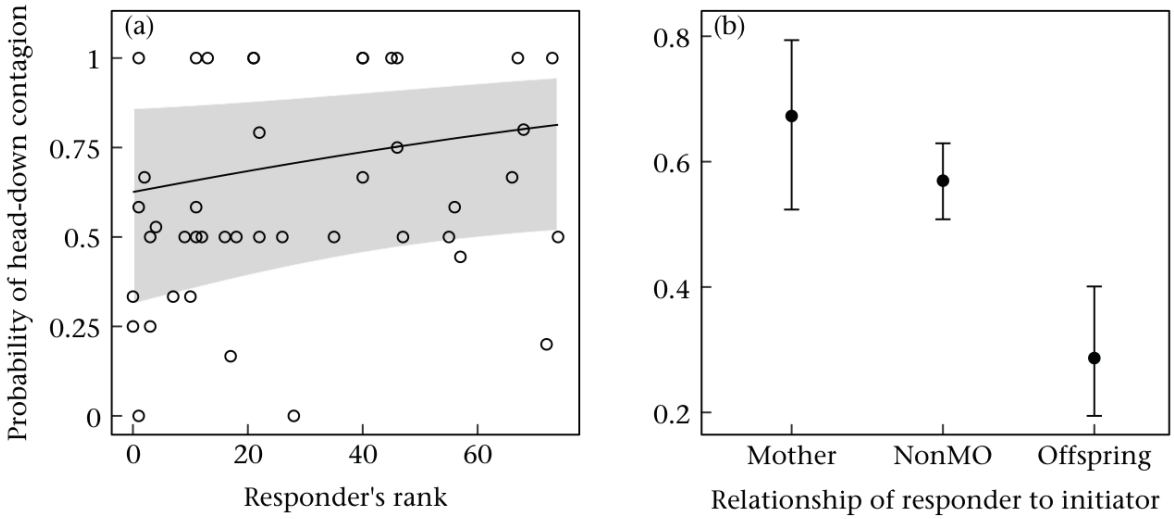


Figure 3. The predicted probabilities of head-down movement contagion according to the following fixed effects: the (a) responder's absolute rank and (b) relationship of the responder to the initiator, based on the best generalized linear mixed model. In (a), smaller numbers on the x-axis indicate higher ranks. The black line and shaded area represent the fitted values and 95% confidence intervals, respectively. In (b), the black dots and error bars represent the mean probabilities and SEs, respectively. NonMO: nonmother–offspring pair.

Table 3. Details of the models with $\Delta AIC \leq 2$

Models	df	AIC	ΔAIC	w_i
Head-up contagion				
1. Rank + RS + Rsp sex + Init age	9	532.8	0.00	0.17
2. Rank + RS + Rsp sex + Init age + No. indv	10	533.7	0.87	0.11
3. Rank + RS + Rsp sex	8	533.8	0.94	0.11
4. Rank + RS + Rsp sex + No. indv	9	533.9	1.04	0.10
5. Rank + RS + Rsp sex + Init age + Kin	10	534.1	1.32	0.09
6. Rank + RS + Rsp sex + Init age + Dist	10	534.6	1.83	0.07
7. Rank + RS + Rsp sex + Init age + No. indv + Dist	11	534.7	1.85	0.07
8. Rank + RS + Init age	8	534.7	1.86	0.07
9. Rank + RS + Rsp sex + Init age + Rank diff	10	534.7	1.86	0.07
10. Rank + RS + Rsp sex + Rsp age + Init age	10	534.7	1.87	0.07
11. Rank + RS + Rsp sex + Init sex + Init age	10	534.8	1.95	0.07
Head-down contagion				
1. Rank + RS	7	190	0.00	0.07
2. RS	6	190.4	0.36	0.06
3. RS + Rsp sex + Init sex	8	190.5	0.50	0.06
4. Rank + RS + Init sex	8	190.5	0.50	0.06
5. RS + Rsp sex	7	190.5	0.53	0.06
6. Rank + RS + Init age	8	190.7	0.68	0.05
7. Rank + RS + Rsp sex	8	190.7	0.71	0.05
8. RS + Init sex	7	190.8	0.77	0.05
9. Rank + RS + Rsp sex + Init sex	9	190.8	0.82	0.05
10. RS + Init age	7	191	1.01	0.04
11. RS + Rsp sex + Init sex + Rank diff	9	191.1	1.05	0.04
12. RS + Init sex + Rank diff	8	191.4	1.40	0.04
13. RS + Rsp sex + Init age	8	191.6	1.54	0.03
14. Rank + RS + Dist	8	191.7	1.65	0.03
15. Rank + RS + Rsp sex + Init age	9	191.7	1.67	0.03
16. RS + Rank diff	7	191.7	1.69	0.03
17. Rank + RS + Init sex + Init age	9	191.8	1.75	0.03
18. RS + Rsp sex + Rank diff	8	191.9	1.90	0.03
19. Rank	5	191.9	1.93	0.03

Models	df	AIC	ΔAIC	w_i
20. RS + Init sex + Init age	8	192	1.98	0.03
21. Rank + RS + Kin	8	192	1.98	0.03
22. Rank + RS + No. indv	8	192	1.99	0.03
23. RS + Rsp sex + Init sex + Init age	9	192	1.99	0.03
24. Rank + RS + Rank diff	8	192	2.00	0.03
25. Rank + RS + Rsp age	8	192	2.00	0.03

Models with ΔAIC > 2 are not presented. AIC: Akaike information criterion; w_i: Akaike weight; RS: relationship of the responder to the initiator; Rank: responder's rank; Rsp sex: responder's sex; Rsp age: responder's age; Init sex: initiator's sex; Init age: initiator's age; No. indv: number of individuals; Rank diff: rank difference between the responder and initiator; Dist: distance between the responder and initiator.

Table 4. Relative importance of variables in models with ΔAIC ≤ 2.

	Head up	Head down
RS	1	0.97
Rank	1	0.51
Rsp sex	0.93	0.37
Rsp age	0.07	0.03
Init sex	0.07	0.37
Init age	0.79	0.24
No. indv	0.29	0.03
Kin	0.09	0.03
Rank diff	0.07	0.16
Dist	0.14	0.03

RS: relationship of the responder to the initiator; Rank: responder's rank; Rsp sex: responder's sex; Rsp age: responder's age; Init sex: initiator's sex; Init age: initiator's age; No. indv: number of individuals; Rank diff: rank difference between the responder and initiator; Dist: distance between the responder and initiator. Variables that were omitted in the models with ΔAIC ≤ 2 are not shown.

DISCUSSION

Our results imply that both head-up and head-down contagion are influenced by the dominance relationship, with lower-ranked individuals (in terms of absolute ranking) being more susceptible to vigilance behaviours by other individuals (Figs. 2a and 3a). The Japanese macaque society is highly despotic, and attacks are unilaterally directed from higher-ranked to lower-ranked individuals (Thierry, 2000). Therefore, the lower the rank of a macaque, the more threats there are around her/him to be wary of. Hence, to immediately detect a threat, lower-ranked individuals may pay more attention to what their neighbours are looking at than higher-ranked individuals. Although we also expected that vigilance contagion is more likely to occur from higher-ranked to lower-ranked individuals than vice versa, we failed to observe this effect (Tables 1, 2 and 4). Instead, our results showed that both head-up and head-down movements were likely to be contagious to lower-ranked individuals regardless of the initiator's rank. These results are even more interesting compared to those reported by Scopa and Palagi (2016). They compared Japanese macaques, a despotic species, to Tonkean macaques, an egalitarian species, and showed that behavioural contagion of play face does not occur in Japanese macaques. Since play face is a positively valenced behaviour directed towards the interaction partner, while vigilance is a scanning behaviour directed towards the surrounding environment, these behaviours obviously differ markedly in terms of adaptive significance. Combining the findings of the previous study of play faces with ours reinforces the idea that whether behavioural contagion occurs depends on the interplay between the type of behaviour and social structures.

In addition, our results showed that both head-up and head-down movements were more contagious from offspring to their mothers than from mothers to their offspring (Figs. 2b and 3b).

This implies that mothers were likely to be vigilant when their offspring were vigilant, but not necessarily vice versa. Japanese macaque mothers are highly protective of their offspring (Thierry, 2000) and our results imply that they may pay special attention to their offspring's vigilance. In contrast, offspring likely leave appraisal of the surrounding environment to their mothers and not pay attention to their mothers' vigilant state. In contrast to this result, research on the contagion of smiles in humans has shown that these behaviours are contagious not only from immature offspring to their mothers but also from the mothers to their offspring, although cultural differences must be carefully considered (e.g. Wörmann et al., 2012). This bidirectional susceptibility to contagion between mothers and their offspring can also be observed in play faces in nonhuman primates (e.g. Mancini, Ferrari, & Palagi, 2013). Taken together, our results indicate that although it is generally believed that mother–offspring dyads are characterized by a high susceptibility to reciprocal and bidirectional behavioural contagion, this is not the case with vigilance. While we did not find any difference between juveniles and infants in the context of vigilance contagion between mothers and offspring (see 'Statistical analyses'), the ontogenetic variation of individual vigilance levels in the early life stages is an interesting question, apart from the context of contagion.

A number of studies have reported on familiarity bias, i.e. behavioural contagion is more likely to occur among individuals with stronger social bonds (Bernieri et al., 1988, Demuru & Palagi, 2012, Campbell & de Waal, 2014, McDougall & Ruckstuhl, 2018a; but see Neilands et al., 2020). Because Japanese macaque societies are characterized by a high degree of nepotism and related individuals form strong social bonds (Chapais et al., 1997), we predicted that kinship would increase vigilance contagion. However, no effects of kinship were observed (Tables 1, 2 and 4). There are several possible explanations for this result. First, this negative result might have been due to our method of examining vigilance contagion between two nearest individuals. In primates, individuals in close proximity tend to have a strong social bond (e.g. bonnet macaque, *Macaca radiata*: Silk, 1994; yellow baboons, *Papio cynocephalus*: Silk, Alberts, & Altmann, 2003; chimpanzees: Langergraber, Mitani, & Vigilant, 2009; see Massen, Sterck, & de Vos, 2010 for a review). Hence, we might not have detected any effects associated with familiarity because all dyads we examined exhibited a certain level of social bonding, whether they were kin or nonkin. Second, familiarity bias may not affect vigilance contagion, unlike the contagion of play signals and yawning (Demuru & Palagi, 2012; Campbell & de Waal, 2014; but see Massen et al., 2012; Massen & Gallup, 2017). However, this possibility seems unlikely in light of previous studies showing that in some species, negative valence responses (e.g. alertness and escape behaviour) increased in familiar pairs when witnessing the distressed state of another individual (dogs: Quervel-Chaumette, Faerber, Faragó, Marshall-Pescini, & Range, 2016; mice, *Mus musculus*: Gonzalez-Liencres, Juckel, Tas, Friebe, & Brüne, 2014, Pisansky, Hanson, Gottesman, & Gewirtz, 2017). In any case, additional detailed studies are needed to further test these possibilities.

Our results also imply that the contagiousness of head-up movements is affected by individual factors related to the initiators and responders, although we did not make any specific predictions about these individual factors. Head-up movements were more contagious to female responders than to male ones, and more contagious from mature initiators than from immature ones. Several studies have reported a greater susceptibility to behavioural contagion in females (Demuru & Palagi, 2012; Romero et al., 2014), but many others have reported the absence of this bias (Gallup & Massen, 2016; Massen & Gallup, 2017; Neilands et al., 2020). Further research is

needed to clarify whether the sex bias demonstrated in this study applies to the phenomenon of behavioural contagion in general regardless of species and the type of behaviour, or whether it is derived from factors specific to Japanese macaques and vigilance. With respect to the age class of the initiators, our results imply that mature initiators are a more reliable source of information in terms of appraising the surrounding situations than immature initiators. For group-living animals, group members can be a useful source of information (Danchin et al., 2004). Japanese macaques inherit their rank from their mothers over the course of ontogeny (Chapais, 1988; Kutsukake, 2000). Hence, mature individuals that are fully incorporated into the dominance relationship and have a fixed rank may be a more reliable source of information.

Although it was not a major focus of this study, the adaptive significance of contagion may differ between head-up and head-down movements. Considering that vigilant individuals can escape attacks faster than nonvigilant individuals (Lima, 1994; Quinn & Cresswell, 2005), it may cost more not to be vigilant when neighbours are vigilant than not to relax vigilance when neighbours relax vigilance. Unfortunately, our results are of little help in addressing this issue: the same social biases (i.e. responder's rank and the mother–offspring relationship) affected both head-up and head-down movements (Tables 1 and 2). The differences in factors influencing head-up versus head-down movements were also unclear: the initiator's age and responders' sex, which were included in the best model for head-up movement, were not included in the best model for head-down movement (Tables 1 and 2). However, the RVI values for these individual factors in the context of head-down contagion were higher than those for almost all other factors (Table 4), which was also the case for head-up contagion. Other indicators, such as foraging efficiency and success rates at avoiding attacks, may provide greater insight into this issue.

Note that we saw social bias only in the context of the contagion of vigilance ‘behaviour’, not that of vigilance as an internal state. Although some researchers have assumed that behavioural contagion drives empathic processes such as emotional contagion (yawning in humans: Platek, Critton, Myers, & Gallup, 2003; play signals in dogs: Palagi et al., 2015; play faces in Tonkean macaques: Scopa & Palagi, 2016), the relationship between these processes is still debated (e.g. Massen & Gallup, 2017; Tamietto et al., 2009). In any case, more detailed studies are needed to clarify the relationship between vigilance contagion and emotional contagion.

We did not focus on the possibility that vigilance is contagious among more than two individuals; research on that topic could clarify how individual or dyadic behaviour is extended to the group level. Studies on antipredator vigilance have assumed that vigilance contagiously spreads out like a wave through the group (Beauchamp, Alexander, & Jovani, 2012; Sirot & Touzalin, 2009). Although predators can be a threat to any individual in a group, threats from conspecifics depend on the social relationships among individuals. Therefore, the way by which social vigilance is spread within a group may be different from that associated with anti-predator vigilance. Investigations on social vigilance contagion among more than two individuals constitute an interesting area of future research.

As this study focused on the contagion of head movements, we did not analyse gaze direction in detail. However, an important question in ecological and cognitive terms is whether vigilance contagion is merely a copy of head movements or involves more specific mechanisms of gaze direction matching (McDougall & Ruckstuhl, 2018b). Sharing vigilance targets would benefit responders but augmenting the vigilance of others by looking in a different direction would also be of some benefit. Depending on whether the vigilance is induced or pre-emptive,

the benefits of sharing gaze direction may vary. To address these issues, more detailed experiments, such as those used in studies of gaze following, are essential (e.g. Bugnyar, Stöwe, & Heinrich, 2004; Catala, Mang, Wallis, & Huber, 2017). Based on some evidence of gaze following in Macaca species (e.g. Tomasello, Call, & Hare, 1998), our subjects might first check the direction of an initiator's glance, and then turn their gaze in the same direction.

In conclusion, this study found that vigilance in Japanese macaques was more contagious among lower-ranked individuals. We also revealed that vigilance was more contagious in the direction from the offspring to the mother, but there was no familiarity bias. These findings suggest that social biases do not apply to all types of behavioural contagion, instead varying by the type of behaviour and adaptive significance thereof.

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References

Allan, A. T. L., & Hill, R. A. (2018). What have we been looking at? A call for consistency in studies of primate vigilance. American Journal of Physical Anthropology, 165, 4–22. https://doi.org/10.1002/ajpa.23381

Barton, K. (2019). MuMIn: Multi-Model Inference. R package version 1.43.15 https://CRAN.R-project.org/package=MuMIn.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Beauchamp, G. (2009). Sleeping gulls monitor the vigilance behaviour of their neighbours. Biology Letters, 5(1), 9–11. https://doi.org/10.1098/rsbl.2008.0490

Beauchamp, G. (2017). What can vigilance tell us about fear? Animal Sentience, 15(1), 1–31.

Beauchamp, G., Alexander, P., & Jovani, R. (2012). Consistent waves of collective vigilance in groups using public information about predation risk. Behavioral Ecology, 23(2), 368–374. https://doi.org/10.1093/beheco/arr194

Bednekoff, P. A., & Lima, S. L. (1998). Randomness, chaos and confusion in the study of antipredator vigilance. Trends in Ecology & Evolution, 13(7), 284–287. https://doi.org/10.1016/S0169-5347(98)01327-5

Bekoff, M. (1995). Vigilance, flock size, and flock geometry: Information gathering by western evening grosbeaks (aves, fringillidae). Ethology, 99(1–2), 150–161. https://doi.org/10.1111/j.1439-0310.1995.tb01096.x

Berman, C. M. (1980). Early agonistic experience and rank acquisition among free-ranging infant rhesus monkeys. International Journal of Primatology, 1(2), 153–170. https://doi.org/10.1007/BF02735595

Bernieri, F. J., Reznick, J. S., & Rosenthal, R. (1988). Synchrony, pseudosynchrony, and dissynchrony: Measuring the entrainment process in mother-infant interactions. Journal of Personality and Social Psychology, 54(2), 243–253. https://doi.org/10.1037/0022-3514.54.2.243

Bugnyar, T., Stöwe, M., & Heinrich, B. (2004). Ravens, *Corvus corax*, follow gaze direction of humans around obstacles. Proceedings of the Royal Society B: Biological Sciences, 271(1546), 1331–1336. https://doi.org/10.1098/rspb.2004.2738

Burnham, K. P., & Anderson, D. R. (2002). Model Selection and Multimodel Inference: a Practical Information-theoretic Approach (2nd ed.). New York, NY: Springer-Verlag.

Busia, L., Schaffner, C. M., & Aureli, F. (2016). Watch out or relax: Conspecifics affect vigilance in wild spider monkeys (*Ateles geoffroyi*). Behaviour, 153(1), 107–124. https://doi.org/10.1163/1568539X-00003329

Campbell, M. W., & de Waal, F. B. M. (2011). Ingroup-outgroup bias in contagious yawning by chimpanzees supports link to empathy. PLoS One, 6(4), 19–22. https://doi.org/10.1371/journal.pone.0018283

Campbell, M. W., & de Waal, F. B. M. (2014). Chimpanzees empathize with group mates and humans, but not with baboons or unfamiliar chimpanzees. Proceedings of the Royal Society B: Biological Sciences, 281(1782). https://doi.org/10.1098/rspb.2014.0013

Carpenter, M., & Call, J. (2009). Comparing the imitative skills of children and nonhuman apes. Revue de Primatologie, 1(1). https://doi.org/10.4000/primatologie.263

Carter, A. J., Pays, O., & Goldizen, A. W. (2009). Individual variation in the relationship between vigilance and group size in eastern grey kangaroos. Behavioral Ecology and Sociobiology, 64(2), 237–245. https://doi.org/10.1007/s00265-009-0840-4

Catala, A., Mang, B., Wallis, L., & Huber, L. (2017). Dogs demonstrate perspective taking based on geometrical gaze following in a Guesser–Knower task. Animal Cognition, 20(4), 581–589. https://doi.org/10.1007/s10071-017-1082-x

Chaffin, C. L., Friedlen, K., & De Waal, F. B. M. (1995). Dominance style of Japanese macaques compared with rhesus and stumptail macaques. American Journal of Primatology, 35(2), 103–116. https://doi.org/10.1002/ajp.1350350203

Chance, M. R. A. (1967). Attention structure as the basis of primate rank orders. Man, 2(4), 503–518. https://doi.org/10.2307/2799336

Chapais, B. (1988). Experimental matrilineal inheritance of rank in female Japanese macaques. Animal Behaviour, 36(4), 1025–1037. https://doi.org/10.1016/S0003-3472(88)80062-9

Chapais, B., Gauthier, C., Prud'homme, J., & Vasey, P. (1997). Relatedness threshold for nepotism in Japanese macaques. Animal Behaviour, 53(5), 1089–1101. https://doi.org/10.1006/anbe.1996.0365

Conradt, L., & Roper, T. J. (2000). Activity synchrony and social cohesion: A fission-fusion model. Proceedings of the Royal Society B: Biological Sciences, 267(1458), 2213–2218. https://doi.org/10.1098/rspb.2000.1271

Danchin, E., Giraldeau, L. A., Valone, T. J., & Wagner, R. H. (2004). Public information: From nosy neighbors to cultural evolution. Science, 305(5683), 487–491. https://doi.org/10.1126/science.1098254

Davila Ross, M., Menzler, S., & Zimmermann, E. (2008). Rapid facial mimicry in orangutan play. Biology Letters, 4(1), 27–30. https://doi.org/10.1098/rsbl.2007.0535

Demuru, E., & Palagi, E. (2012). In bonobos yawn contagion is higher among kin and friends. PLoS One, 7(11), Article e49613. https://doi.org/10.1371/journal.pone.0049613

Ebensperger, L. A., Hurtado, M. J., & Ramos-Jiliberto, R. (2006). Vigilance and collective detection of predators in degus (*Octodon degus*). Ethology, 112(9), 879–887. https://doi.org/10.1111/j.1439-0310.2006.01242.x

Emery, N. J. (2000). The eyes have it: The neuropathology, function and evolution of social gaze. Neuroscience & Biobehavioral Reviews, 24(6), 581–604. https://doi.org/10.1016/S0149-7634(00)00025-7

Favreau, F. R., Goldizen, A. W., & Pays, O. (2010). Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos. Proceedings of the Royal Society B: Biological Sciences, 277(1690), 2089–2095. https://doi.org/10.1098/rspb.2009.2337

Fernández, G. J., Capurro, A. F., & Reboreda, J. C. (2003). Effect of group size on individual and collective vigilance in greater rheas. Ethology, 109(5), 413–425. https://doi.org/10.1046/j.1439-0310.2003.00887.x

FitzGibbon, C. D. (1989). A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. Animal Behaviour, 37, 508–510. https://doi.org/10.1016/0003-3472(89)90098-5

Fox, J., & Weisberg, S. (2019). An [R] Companion to Applied Regression (3rd ed.). Thousand Oaks, CA: Sage https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Friard, O., & Gamba, M. (2016). Boris: A free, versatile open-source event-logging software for video/audio coding and live observations. Methods in Ecology and Evolution, 7(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Gallup, A. C., & Massen, J. J. M. (2016). There is no difference in contagious yawning between men and women. Royal Society Open Science, 3(9), 160174. https://doi.org/10.1098/rsos.160174

Gallup, A. C., Swartwood, L., Militello, J., & Sackett, S. (2015). Experimental evidence of contagious yawning in budgerigars (*Melopsittacus undulatus*). Animal Cognition, 18(5), 1051–1058. https://doi.org/10.1007/s10071-015-0873-1

Gonzalez-Liencres, C., Juckel, G., Tas, C., Friebe, A., & Brüne, M. (2014). Emotional contagion in mice: The role of familiarity. Behavioural Brain Research, 263, 16–21. https://doi.org/10.1016/j.bbr.2014.01.020

Hecht, E. E., Patterson, R., & Barbey, A. K. (2012). What can other animals tell us about human social cognition? An evolutionary perspective on reflective and reflexive processing. Frontiers in Human Neuroscience, 6, 224. https://doi.org/10.3389/fnhum.2012.00224

Henrich, J., Heine, S. J., & Norenzayan, A. (2010). The weirdest people in the world? Behavioral and Brain Sciences, 33(2–3), 61–83. https://doi.org/10.1017/S0140525X0999152X

Hess, U., & Fischer, A. (2013). Emotional mimicry as social regulation. Personality and Social Psychology Review, 17(2), 142–157. https://doi.org/10.1177/1088868312472607

Iki, S., & Kutsukake, N. (in press). Japanese macaques relax vigilance when surrounded by kin. Animal Behaviour.

Kapitany, R., & Nielsen, M. (2017). Are yawns really contagious? A critique and quantification of yawn contagion. Adaptive Human Behavior and Physiology, 3(2), 134–155. https://doi.org/10.1007/s40750-017-0059-y

Kazahari, N., & Agetsuma, N. (2010). Mechanisms determining relationships between feeding group size and foraging success in food patch use by Japanese macaques (*Macaca fuscata*). Behaviour, 147(11), 1481–1500. https://doi.org/10.1163/000579510X521573

Kitchen, D. M., Seyfarth, R. M., Fischer, J., & Cheney, D. L. (2003). Loud calls as indicators of dominance in male baboons (*Papio cynocephalus* ursinus). Behavioral Ecology and Sociobiology, 53(6), 374–384. https://doi.org/10.1007/s00265-003-0588-1

Kutsukake, N. (2000). Matrilineal rank Inheritance varies with absolute rank in Japanese macaques. Primates, 41(3), 321–335. https://doi.org/10.1007/BF02557601

Langergraber, K., Mitani, J., & Vigilant, L. (2009). Kinship and social bonds in female chimpanzees (*Pan troglodytes*). American Journal of Primatology, 71(10), 840–851. https://doi.org/10.1002/ajp.20711

Lima, S. L. (1994). On the personal benefits of anti-predatory vigilance. Animal Behaviour, 48(3), 734–736. https://doi.org/10.1006/anbe.1994.1293

Madsen, E. A., & Persson, T. (2013). Contagious yawning in domestic dog puppies (*Canis lupus familiaris*): The effect of ontogeny and emotional closeness on low-level imitation in dogs. Animal Cognition, 16(2), 233–240. https://doi.org/10.1007/s10071-012-0568-9

Maglieri, V., Bigozzi, F., Riccobono, M. G., & Palagi, E. (2020). Levelling playing field: Synchronization and rapid facial mimicry in dog-horse play. Behavioural Processes, 174, 104104. https://doi.org/10.1016/j.beproc.2020.104104

Mancini, G., Ferrari, P. F., & Palagi, E. (2013). Rapid facial mimicry in geladas. Scientific Reports, 3(1), 1–6. https://doi.org/10.1038/srep01527

Massen, J. J. M., & Gallup, A. C. (2017). Why contagious yawning does not (yet) equate to empathy. Neuroscience & Biobehavioral Reviews, 80, 573–585. https://doi.org/10.1016/j.neubiorev.2017.07.006

Massen, J. J. M., Šlipogor, V., & Gallup, A. C. (2016). An observational investigation of behavioral contagion in common marmosets (*Callithrix jacchus*): Indications for contagious scent-marking. Frontiers in Psychology, 7, 1–11. https://doi.org/10.3389/fpsyg.2016.01190

Massen, J. J. M., Sterck, E. H. M., & de Vos, H. (2010). Close social associations in animals and humans: Functions and mechanisms of friendship. Behaviour, 147(11), 1379–1412. https://doi.org/10.1163/000579510X528224

Massen, J. J. M., Vermunt, D. A., & Sterck, E. H. M. (2012). Male yawning is more contagious than female yawning among chimpanzees (*Pan troglodytes*). PLoS One, 7(7), Article e40697. https://doi.org/10.1371/journal.pone.0040697

McDougall, P. L., & Ruckstuhl, K. E. (2018a). Doing what your neighbour does: Neighbour proximity, familiarity and postural alignment increase behavioural mimicry. Animal Behaviour, 135, 177–185. https://doi.org/10.1016/j.anbehav.2017.11.009

McDougall, P. L., & Ruckstuhl, K. E. (2018b). Vigilance behaviour is more contagious when chewing stops: Examining the characteristics of contagious vigilance in bighorn sheep. Behavioral Ecology and Sociobiology, 72(9), 143. https://doi.org/10.1007/s00265-018-2536-0

Muller, M. N. (2002). Agonistic relations among Kanyawara chimpanzees. In C. Boesch, G. Hohmann, & L. Marchant (Eds.), Behavioural Diversity in Chimpanzees and Bonobos (pp. 112–124). Cambridge, U.K.: Cambridge University Press. https://doi.org/10.1017/cbo9780511606397.012.

Neilands, P., Claessens, S., Ren, I., Hassall, R., Bastos, A. P. M., & Taylor, A. H. (2020). Contagious yawning is not a signal of empathy: No evidence of familiarity, gender or prosociality biases in dogs. Proceedings of the Royal Society B: Biological Sciences, 287(1920). https://doi.org/10.1098/rspb.2019.2236

Niedenthal, P. M., Mermillod, M., Maringer, M., & Hess, U. (2010). The simulation of smiles (SIMS) model: Embodied simulation and the meaning of facial expression. Behavioral

and Brain Sciences, 33(6), 417–433. https://doi.org/10.1017/S0140525X10000865
Norscia, I., Demuru, E., & Palagi, E. (2016). She more than he: Gender bias supports the empathic nature of yawn contagion in Homo sapiens. Royal Society Open Science, 3(2). https://doi.org/10.1098/rsos.150459
Öst, M., & Tierala, T. (2011). Synchronized vigilance while feeding in common eider brood-rearing coalitions. Behavioral Ecology, 22(2), 378–384. https://doi.org/10.1093/beheco/arq223
Palagi, E., & Mancini, G. (2011). Playing with the face: Playful facial 'chattering' and signal modulation in a monkey species (Theropithecus gelada). Journal of Comparative Psychology, 125(1), 11–21. https://doi.org/10.1037/a0020869
Palagi, E., Nicotra, V., & Cordoni, G. (2015). Rapid mimicry and emotional contagion in domestic dogs. Royal Society Open Science, 2(12), 150505. https://doi.org/10.1098/rsos.150505
Pays, O., Dubot, A. L., Jarman, P. J., Loisel, P., & Goldizen, A. W. (2009). Vigilance and its complex synchrony in the red-necked pademelon, *Thylogale thetis*. Behavioral Ecology, 20(1), 22–29. https://doi.org/10.1093/beheco/arn110
Pays, O., Jarman, P. J., Loisel, P., & Gerard, J. F. (2007). Coordination, independence or synchronization of individual vigilance in the eastern grey kangaroo? Animal Behaviour, 73(4), 595–604. https://doi.org/10.1016/j.anbehav.2006.06.007
Pays, O., Sirot, E., & Fritz, H. (2012). Collective vigilance in the greater kudu: Towards a better understanding of synchronization patterns. Ethology, 118(1), 1–9. https://doi.org/10.1111/j.1439-0310.2011.01974.x
Pisansky, M. T., Hanson, L. R., Gottesman, I. I., & Gewirtz, J. C. (2017). Oxytocin enhances observational fear in mice. Nature Communications, 8(1), 1–11. https://doi.org/10.1038/s41467-017-02279-5
Platek, S. M., Critton, S. R., Myers, T. E., & Gallup, G. G. (2003). Contagious yawning: The role of self-awareness and mental state attribution. Cognitive Brain Research, 17(2), 223–227. https://doi.org/10.1016/S0926-6410(03)00109-5
Provine, R. R. (1992). Contagious laughter: Laughter is a sufficient stimulus for laughs and smiles. Bulletin of the Psychonomic Society, 30(1), 1–4. https://doi.org/10.3758/BF03330380
Provine, R. R. (2005). Contagious yawning and laughing: Everyday imitation-and mirror-like behavior. Behavioral and Brain Sciences, 28(2), 142. https://doi.org/10.1017/S0140525X05390030
Pulliam, H. R. (1973). On the advantages of flocking. Journal of Theoretical Biology, 38(2), 419–422. https://doi.org/10.1016/0022-5193(73)90184-7
Quervel-Chaumette, M., Faerber, V., Faragó, T., Marshall-Pescini, S., & Range, F. (2016). Investigating empathy-like responding to conspecifics' distress in pet dogs. PLoS One, 11(4), 1–15. https://doi.org/10.1371/journal.pone.0152920
Quinn, J. L., & Cresswell, W. (2005). Escape response delays in wintering redshank, *Tringa totanus*, flocks: Perceptual limits and economic decisions. Animal Behaviour, 69(6), 1285–1292. https://doi.org/10.1016/j.anbehav.2004.10.007
Quirici, V., Palma, M., Sobrero, R., Faugeron, S., & Ebensperger, L. A. (2013). Relatedness does not predict vigilance in a population of the social rodent *Octodon degus*. Acta Ethologica, 16(1), 1–8. https://doi.org/10.1007/s10211-012-0131-3

R Core Team. (2020). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Romero, T., Ito, M., Saito, A., & Hasegawa, T. (2014). Social modulation of contagious yawning in wolves. PLoS One, 9(8), Article e105963. https://doi.org/10.1371/journal.pone.0105963

Romero, T., Konno, A., & Hasegawa, T. (2013). Familiarity bias and physiological responses in contagious yawning by dogs support link to empathy. PloS One, 8(8), Article e71365. https://doi.org/10.1371/journal.pone.0071365

Scannell, J., Roberts, G., & Lazarus, J. (2001). Prey scan at random to evade observant predators. Proceedings of the Royal Society B: Biological Sciences, 268(1466), 541–547. https://doi.org/10.1098/rspb.2000.1388

Schino, G., & Scerbo, M. (2020). Monitoring of group mates in relation to their behavior in mandrills. American Journal of Primatology, 82(6). https://doi.org/10.1002/ajp.23129

Schülke, O., Dumdey, N., & Ostner, J. (2020). Selective attention for affiliative and agonistic interactions of dominants and close affiliates in macaques. Scientific Reports, 10(1), 1–8. https://doi.org/10.1038/s41598-020-62772-8

Scopa, C., & Palagi, E. (2016). Mimic me while playing! social tolerance and rapid facial mimicry in macaques (*Macaca tonkeana* and *Macaca fuscata*). Journal of Comparative Psychology, 130(2), 153–161. https://doi.org/10.1037/com0000028

Silk, J. B. (1994). Social relationships of male bonnet macaques: Male bonding in a matrilineal society. Behaviour, 130(3–4), 271–291. https://doi.org/10.1163/156853994X00569

Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. Science, 302(5648), 1231–1234. https://doi.org/10.1126/science.1088580

Sirot, E., & Touzalin, F. (2009). Coordination and synchronization of vigilance in groups of prey: The role of collective detection and predators' preference for stragglers. The American Naturalist, 173(1), 47–59. https://doi.org/10.1086/593358

Soltis, J., Thomsen, R., Matsubayashi, K., & Takenaka, O. (2000). Infanticide by resident males and female counter-strategies in wild Japanese macaques (*Macaca fuscata*). Behavioral Ecology and Sociobiology, 48(3), 195–202. https://doi.org/10.1007/s002650000224

Sprague, D. S., Suzuki, S., Takahashi, H., & Sato, S. (1998). Male life history in natural populations of Japanese macaques: Migration, dominance rank, and troop participation of males in two habitats. Primates, 39(3), 351–363. https://doi.org/10.1007/BF02573083

Suzuki, M., & Sugiura, H. (2011). Effects of proximity and activity on visual and auditory monitoring in wild Japanese macaques. American Journal of Primatology, 73(7), 623–631. https://doi.org/10.1002/ajp.20937

Tamietto, M., Castelli, L., Vighetti, S., Perozzo, P., Geminiani, G., Weiskrantz, L., et al. (2009). Unseen facial and bodily expressions trigger fast emotional reactions. Proceedings of the National Academy of Sciences of the United States of America, 106(42), 17661–17666. https://doi.org/10.1073/pnas.0908994106

Thierry, B. (2000). Covariation of conflict management patterns across macaque species. In F. Aureli, & F. B. M. de Waal (Eds.), Natural conflict resolution (pp. 106–128). Berkeley, CA: University of California Press.

Tomasello, M., Call, J., & Hare, B. (1998). Five primate species follow the visual gaze of conspecifics. Animal Behaviour, 55(4), 1063–1069.

https://doi.org/10.1006/anbe.1997.0636
Treves, A. (2000). Theory and method in studies of vigilance and aggregation. Animal Behaviour, 60(6), 711–722. https://doi.org/10.1006/anbe.2000.1528
Wada, K., & Ichiki, Y. (1980). Seasonal home range use by Japanese monkeys in the snowy Shiga Heights. Primates, 21(4), 468–483. https://doi.org/10.1007/BF02373835
Watson, C. F., & Caldwell, C. A. (2010). Neighbor effects in marmosets: Social contagion of agonism and affiliation in captive *Callithrix jacchus*. American Journal of Primatology, 72(6), 549–558. https://doi.org/10.1002/ajp.20805
Watson, K. K., Li, D., Brent, L. J. N., Horvath, J. E., Gonzalez-Martinez, J., Ruíz-Lambides, A. V., et al. (2015). Genetic influences on social attention in free-ranging rhesus macaques. Animal Behaviour, 103, 267–275. https://doi.org/10.1016/j.anbehav.2015.02.012
Weyers, P., Mühlberger, A., Kund, A., Hess, U., & Pauli, P. (2009). Modulation of facial reactions to avatar emotional faces by nonconscious competition priming. Psychophysiology, 46(2), 328–335. https://doi.org/10.1111/j.1469-8986.2008.00771.x
Wheeler, B. C. (2008). Selfish or altruistic? An analysis of alarm call function in wild capuchin monkeys, *Cebus apella nigritus*. Animal Behaviour, 76(5), 1465–1475. https://doi.org/10.1016/j.anbehav.2008.06.023
Wickham, H. (2016). ggplot2: Elegant graphics for data analysis. New York, NY: Springer-Verlag.
Wörmann, V., Holodynski, M., Kärtner, J., & Keller, H. (2012). A cross-cultural comparison of the development of the social smile. A longitudinal study of maternal and infant imitation in 6- and 12-week-old infants. Infant Behavior and Development, 35(3), 335–347. https://doi.org/10.1016/j.infbeh.2012.03.002
Zentall, T. R. (2003). Imitation by animals: How do they do it? Current Directions in Psychological Science, 12(3), 91–95. https://doi.org/10.1111/1467-8721.01237
Zuberbühler, K., Noë, R., & Seyfarth, R. M. (1997). Diana monkey long distance calls: Messages for conspecifics and predators. Animal Behaviour, 53(3), 589–604. https://doi.org/10.1006/anbe.1996.0334