

# Rudimentary empathy in macaques' social decision-making

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**Primates live in highly social environments, where prosocial behaviors promote social bonds and cohesion and contribute to group members' fitness. Despite a growing interest in the biological basis of nonhuman primates' social interactions, their underlying motivations remain a matter of debate. We report that macaque monkeys take into account the welfare of their peers when making behavioral choices bringing about pleasant or unpleasant outcomes to a monkey partner. Two macaques took turns in making decisions that could impact their own welfare or their partner's. Most monkeys were inclined to refrain from delivering a mildly aversive airpuff and to grant juice rewards to their partner. Choice consistency between these two types of outcome suggests that monkeys display coherent motivations in different social interactions. Furthermore, spontaneous affiliative group interactions in the home environment were mostly consistent with the measured social decisions, thus emphasizing the impact of preexisting social bonds on decision-making. Interestingly, unique behavioral markers predicted these decisions: benevolence was associated with enhanced mutual gaze and empathic eye blinking, whereas indifference or malevolence was associated with lower or suppressed such responses. Together our results suggest that prosocial decision-making is sustained by an intrinsic motivation for social affiliation and controlled through positive and negative vicarious reinforcements.**

social neuroscience | emotions | social gaze | eye blink | prosocial

Animal sociality encompasses a broad range of behaviors presumed to influence social bonds and promote group cohesion (1–5). Although higher forms of altruism, such as costly care of unknown individuals or donations to charity, may require uniquely human mentalizing abilities, evidence supports an evolutionary continuity in the motivational and affective mechanisms that regulate attachment and affiliation (6–9). In nonhuman primates, the ubiquitous social play, grooming behavior, and their hormonal correlates suggest an ability to conceive what is pleasant or unpleasant for others (10–12). Pioneering experimental studies have shown that macaques can perceive and seek to alleviate their peers' distress (13, 14) and more recent studies have attributed even to rodents the possibility of empathy and its promotion of helping behavior (2–4). Empathy is understood to refer to vicarious experiences of the affective states of others and is believed to improve adaptive social behaviors. Different components of empathy could be described, for instance, a cognitive one is related to the capacity to abstract other's experience, and another one depends on the emotional display of a conspecific. All of these components are known to be deeply influenced by the level of closeness existing between individuals (7). The ultimate, evolutionary basis of altruism and empathy is a topic of scientific interest that has been extensively discussed (7, 15–20). One of the recurrent issues is whether the motivations that drive prosocial behavior are selfish or purely altruistic. This question equally concerns the ubiquitous grooming behavior of nonhuman primates that has been shown to be pleasant for both participants (10, 12) or the nature of human altruism, as seen, for example, in the difficulty of discerning the inner motivations of blood donors (21). There are still appealing unanswered questions related to the underlying cognitive and affective mechanisms of nonhuman primates' social behaviors.

In particular, the implication of vicariously induced affective states in nonhuman primates' social decision-making remains a matter of debate (7, 16, 22). Different theories have emphasized the role of proximate affective mechanisms in shaping behavior mainly through social reinforcement (6, 7, 23, 24). For example, it has been proposed that matching a peer's affective state to one's own prior or current state might be involved in social decision-making (7, 25). In addition to that, it is not known whether a common motivation drives social behavior across different contexts, such as sharing food or avoid harming a conspecific.

We investigated the motivational and affective basis of prosocial behavior through social decisions, asking whether macaques take into account the welfare of others (defined here as the exposure to a pleasant or unpleasant experience) when making choices leading to positive or negative outcomes on others. Specifically, we sought to determine whether their motivation is consistent for different outcome valences and is predicted by their sensitivity to a peer's affective state. Pairs of animals sat face to face in a primate chair and alternately made forced-choice decisions by touching one of two visual cues that were projected on a transparent touch-sensitive panel (Fig. 1A), leading to the subsequent delivery of a combination of outcomes (Fig. 1B and C). Social decisions consisted, for one monkey (the actor), in choosing an outcome for another monkey (the partner) vs. the same outcome to nobody. The outcome was either a drop of juice or an airpuff delivered close to the eyes. From the actor's perspective, sensory events associated with partner and nobody outcomes were similar in every respect, except for their impact on the partner monkey. Choosing one or the other option did not determine the outcome for the actor monkey, who received a

## Significance

**We investigated nonhuman primate prosociality within a decision-making behavioral framework. Our results suggest that macaques have a concept of their peers' well being. The strength and originality of our experimental design is in challenging monkeys with several decisions involving both pleasant and unpleasant outcomes to self and others, thus allowing us to evaluate social motivation in different contexts. Behavioral measures, such as empathic eye blinking and mutual looking, show that the degrees of empathy and of willingness to interact with peers differ among individuals. These differences were mainly consistent with the preexisting social bonds displayed within our group-housed monkeys. Our results thus provide evidence of partner-dependent behavioral mechanisms shaping primates' social decisions.**

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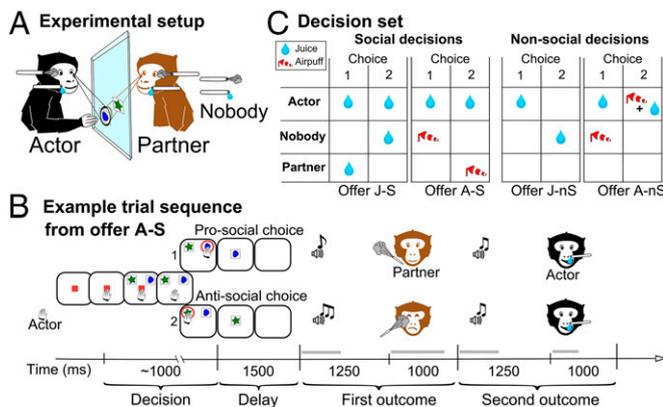
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**Fig. 1.** Task design. (A) Two monkeys (actor in black, partner in light brown) faced each other on either side of transparent touch panels on which visual stimuli were virtually projected. Both animals could observe the images and each other at all times. Tubes connected to solenoid devices allowed delivering the different outcomes. (B) Monkeys made social decisions regarding potential appetitive (offer J-S) and aversive (offer A-S) outcomes for the partner and non-social decisions regarding similar outcomes for self (offers J-nS and A-nS). For nonsocial decisions involving airpuffs and for social decisions, the actor was always rewarded with a drop of juice so as to maintain an adequate motivation level. (C) Typical trial sequence. A visual cue instructed the monkeys as to their role (actor or partner) in the current trial. The actor first touched this cue, triggering the appearance of two additional images. The monkey indicated its choice by touching one of these images. The unchosen image was then turned off and following a delay the partner's and actor's outcomes were delivered, preceded by unique 500-ms-long warning tones.

constant juice reward for touching one of the cues. Nonsocial decisions were interleaved with social decisions to control for the animals' perception of the same outcomes when delivered to self. Eye-tracking devices were used to record the monkeys' gaze and eye blinks as proxies of, respectively, social engagement and negative affect.

## Results

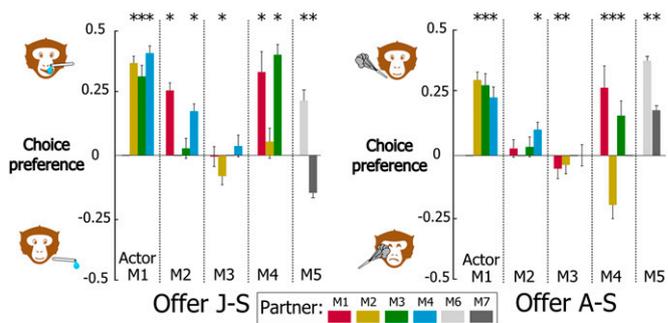
**Social and Nonsocial Decisions.** Results were analyzed for 14 dyads of monkeys (Table S1) in which the actor monkey made rational nonsocial decisions, i.e., chose to both acquire juice and avoid airpuffs for itself (respectively, offers J-nS and A-nS; Fig. S1). The dyads were formed of all pairings between four juvenile long-tailed macaques (M1–M4). Two additional dyads of adult rhesus macaques (M5 with M6 and M7) were also tested. Nonparametric tests (Wilcoxon signed-rank) were used to determine whether choices made by the actor differed significantly from indifference (mean preference score = 0.0 in Fig. 2 and Fig. S1) between the two options. Our findings show that prosocial tendencies predominated over indifferent and antisocial ones (respectively, eight, four, and two dyads for juice outcomes and eight, three, and three dyads for airpuff outcomes, significantly prosocial and antisocial decisions:  $P < 0.05$  or better), but individual monkeys exhibited different patterns of social decisions. One monkey (M1) displayed consistent prosocial choices with all of its partners, whereas all other animals showed a pattern of prosocial, antisocial, or indifferent choices that depended on partner identity and outcome valence (Fig. 2). It should be noted that monkeys were rarely as prosocial toward their partner as they were rational in their nonsocial choices (Fig. S1A). Interestingly, however, monkey M5 refrained from delivering an airpuff to M6, its female grooming partner, more than to itself (permutation test,  $P < 0.05$ ), suggesting that observing another's discomfort can be more aversive than experiencing it.

Furthermore, with a few exceptions (e.g., M2 toward M1 and M5 toward M7), in a majority of dyads (10/14), the actor monkey showed consistent tendency toward its partner for the social decisions involving juice and airpuff outcomes (respectively, offers J-S and A-S). As a check for possible uncontrolled factors biasing the

monkeys' decisions, we ran a number of sessions with monkeys facing an empty primate chair and found that their choices did not depart from indifference, whereas nonsocial decisions remained rational (Fig. S1B).

To investigate further what motivated these decisions, the results were analyzed on a session-by-session basis using multilevel models (26) that controlled for individual differences by considering actor and partner identity as a random effect. We found that the tendency to provide a pleasant stimulus to one's partner reliably predicts withholding of an unpleasant one ( $P < 0.001$ ; Table 1, Table S2, and Fig. S2 A and B). Consequently, actors' social tendencies were characterized as "benevolent," when significantly choosing mostly the prosocial options, "indifferent," when choosing about equally the prosocial and antisocial options or "malevolent," when choosing mostly the antisocial options. We then examined the monkey's oculomotor behavior as potential marker of the underlying affective and motivational process explaining the actor's decisions.

**Social Gaze.** A social region of interest (ROI) was defined as the area encompassing the partner's face and corresponding to ~15% of the visual field. Social gaze was defined as the percentage of time a monkey fixated into this ROI, and mutual gaze as the percentage of time the gaze of both monkeys coincided. Social and mutual gaze increased during the delay period and was enhanced on trials in which the actor chose to grant juice to the partner, compared with nobody (Fig. 3 and Fig. S3A; permutation test,  $P < 0.05$ ). Logically, when both monkeys' social gaze increases, the probability of gaze coincidence is expected to increase as well. However, if mutual looking is an actively controlled social interaction (i.e., if monkeys deliberately chose to sustain or avoid each other's gaze), its occurrence might be expected to be different from predicted by chance. This hypothesis was tested using a permutation-based analysis (Fig. S3B). For every trial in the dataset, actual mutual gaze rate was compared with its theoretical distribution and considered to be below or above chance if it was, respectively, inferior or superior to a CI set at  $P < 0.05$  (two-tailed test). For more than 70% of trials, mutual gaze rates could not be explained by random intersection of the actor's and the partner's gaze. Interestingly, when the actor chose to grant juice to its partner, the proportion of trials with above- and below-chance mutual gaze rates, respectively, increased and decreased, compared with when the actor withheld juice from its partner. This result suggests that when prosocial decisions were made, both animals actively sought to interact more with each other through gaze. Further analyses show that mutual gaze rate predicts, on a session-by-session basis, the animals' degree of prosociality (Table 1, Table S2, and Fig. S2A;  $P < 0.001$ )



**Fig. 2.** Social choice preferences. Positive values indicate prosocial decision-making, i.e., preference for granting juice (offer J-S) and avoiding airpuff (offer A-S) to the partner. Data are presented for M1-5 as actor and M1-4 and M6-7 as partner. Mean preference scores for each monkey pair across all experimental sessions were computed as  $[\text{choice}_1 / (\text{choice}_1 + \text{choice}_2)] - 0.5$ . \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ . Significant preference for one of the two options (Wilcoxon signed-rank test); error bars represent SEM.

**Table 1. Multilevel model analysis of monkey's decisions and oculomotor behaviors**

Observation	Fixed predictor	<i>P</i>	<i>t</i>	<i>R</i> <sup>2</sup>
Choice preference in offer J-S	Mutual gaze rate in offer J-S	<0.001	6.24	0.44
	Choice preference in offer A-S	<0.001	5.43	
Choice preference in offer A-S	Actor's blink rate in offer A-S	<0.001	2.76	0.55
	Actor's and partner's blink rate in offer A-S	<0.001	3.11	
	Choice preference in offer J-S	<0.001	3.5	
Choice preference in offer A-S	Actor's blink rate in offer A-S	<0.001	5.46	0.56
Mutual gaze rate in offer J-S	Actor's blink rate in offer A-S	<0.001	7.2	0.31
Actor's blink rate in offer A-S	Partner's blink rate in offer A-S	<0.05	1.94	0.09

All of the models considered actor's and partner's identity as random predictors. These models were compared with null models including only the random effects (Table S2, theoretical likelihood ratio test). Then, to find the best fitting model, we compared models with different sets of predictors (Table S2, theoretical likelihood ratio test). Where needed, the pseudo-*R*<sup>2</sup> algorithms of McFadden's were used to compute *R*<sup>2</sup>. See Fig. S2 for a graphical representation.

and discriminates between different actors' decisional tendencies [ANOVA,  $F(2) = 3.77$ ,  $P < 0.01$ , before juice delivery;  $F(2) = 3.07$ ,  $P < 0.05$ , after juice delivery]. This modulation is apparent in Fig. 3, *Right*, showing that mutual gaze increases before and during juice delivery in dyads that include a benevolent actor.

**Eye Blinks.** Eye blinking is a primary response to an airpuff near the eyeball. A large increase in eye blinking rate was recorded in the actor monkey when occasionally delivering itself an airpuff (up to 21% of nonsocial decision trials; Fig. S4, dotted curves). This response reached significance (permutation test,  $P < 0.05$ ) around the onset of the warning tone, indicating that the monkeys anticipated the event. Anticipatory blinking was also associated with increased airpuff avoidance (Table 1 and Fig. S2C;  $R^2 = 0.56$ ,  $P < 0.001$ ), consistent with a negative affective state being induced by the aversive outcome prediction. More interestingly, observing an airpuff being delivered to the partner was also associated with changes in blink rate, and the strength of this response was a distinctive feature of the actors' prosocial tendencies: benevolent monkeys showed larger blink response in anticipation of, and in reaction to, the partner's airpuff [Fig. 4; ANOVA, before airpuff delivery:  $F(2) = 3.96$ ,  $P < 0.05$ , after airpuff delivery:  $F(2) = 9.04$ ,  $P < 0.001$ ; Fig. S4; permutation test,  $P < 0.05$ ]. This response was smaller than during an airpuff to self ( $P < 0.05$ ), but significantly higher than during an airpuff to nobody ( $P < 0.05$ ). By contrast, when exhibiting indifferent and malevolent social decision tendencies, monkey actors, respectively, did not react or, surprisingly, underreacted ( $P < 0.05$ ) to an aversive stimulus on their partner. The specificity of such anticipatory an enhanced blink response to observed airpuffs strongly argues for an intrinsically social underlying process. As the partner monkey, to whom the airpuff was directed, also showed anticipatory blinks, it is possible that the actor's behavior was mirroring its partner's. This effect would be consistent with work on motor mimicry in monkeys (27, 28) and with the observation that humans with higher empathy score are more likely to mimic other's eye blinks (29). The statistical model that best account for social choices involving aversive stimuli includes the interaction of actor and partner anticipatory blinking (Table 1, Table S2, and Fig. S2B), and we found a significant but quite weak degree of synchronization of the actor and partner's anticipatory blink rates (Table 1 and Fig. S2E;  $R^2 = 0.09$ ,  $P < 0.05$ ). This low correlation suggests that more covert aspects of the actor monkey's affective state is involved in the generation of empathic blinking. Overall, these results argue for eye blinking as a meaningful indicator of monkeys' negative affective reaction to others' discomfort and suggest that the decision to avoid inflicting an unpleasant stimulus to a conspecific might be dependent both on the partner's affective display and the actor's prior experience with aversive stimuli.

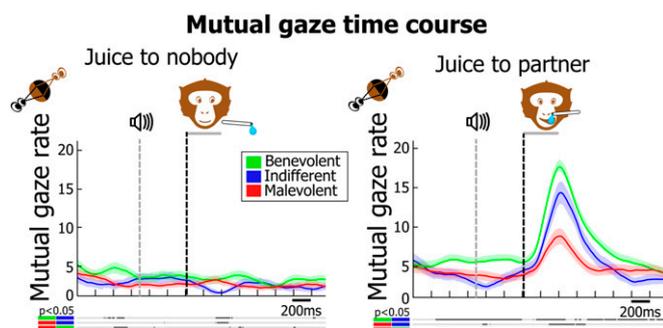
Mutual gaze and eye blinking thus provide two windows into a monkey's internal affective state. As both are modulated in accordance with the animal's social tendencies, one could hypothesize a

shared motivational basis. Results in Table 1 and Fig. S2D indeed show a relation between mutual gaze (offer J-S) and eye blinking in the context of airpuff avoidance (offer A-S;  $R^2 = 0.31$ ,  $P < 0.001$ ).

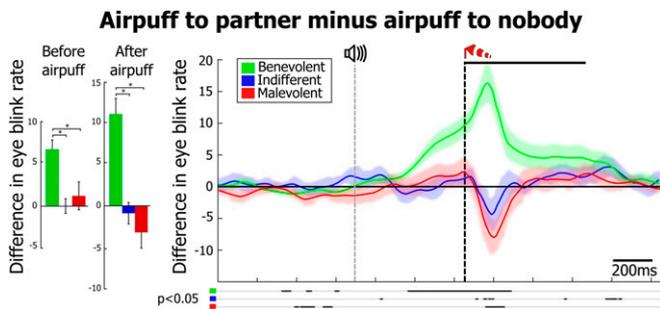
**Social Network Structure.** Social organization and affiliative behavior patterns of the four long-tailed macaques were assessed using manual and automatic scoring of their spontaneous interactions (30). (Fig. 5A and Fig. S5). These analyses highlight several characteristics of the studied macaque group: (i) monkeys that cared about others' welfare in the laboratory spent more time in social grooming than other dyads (Fig. 5B and C; Spearman rank correlation permutation test,  $R = 0.77$ ,  $P < 0.05$  for offer A-S; the correlation for offer J-S did not reach significance,  $R = 0.49$ ,  $P > 0.1$ ); (ii) the only dyad showing mutually benevolent decision tendencies for both juice granting and airpuff avoidance involved the two monkeys who exhibited the strongest mutual grooming interactions (M1 and M4; Fig. 5A); and (iii) the only monkey who showed benevolent decision tendencies toward all of its partners was M1, the dominant member of the group. These observations, together with the positive correlation found between social grooming and mutual gaze rate (Fig. 5D, Spearman rank correlation permutation test,  $R = 0.83$ ,  $P < 0.05$ ), highlights the consistency between actual social affiliation patterns in the monkeys' living space and the valuation process taking place during social decisions. The observation that the dominant member of this long-tailed minicolony is also the most benevolent monkey is somewhat anecdotal but consistent with prior work (31–33).

## Discussion

In this study, we showed that macaques were spontaneously inclined to act prosocially, even in the absence of explicit, immediate incentives to do so. Whichever decision was taken, the consequence to



**Fig. 3.** Mutual looking rate for the different social decider profiles for juice to nobody and juice to partner choices. Thick lines below the plot indicate significant pairwise differences (permutation test,  $P < 0.05$ ); shading overlays on the traces represent SEM. The number of sessions considered for benevolent, indifferent, and malevolent actors is, respectively, equal to 97, 30, and 37 sessions.

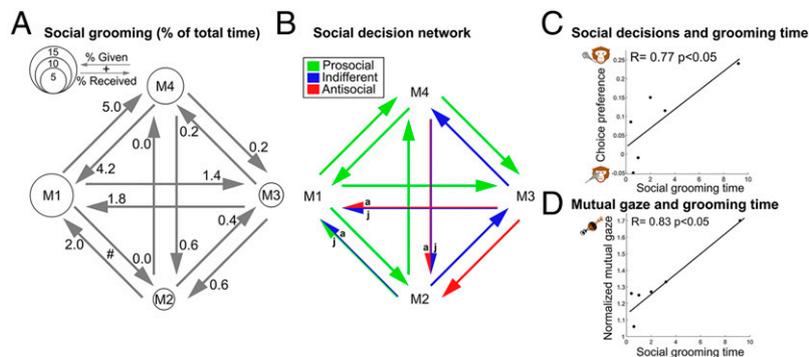


**Fig. 4.** Eye blink behavior when experiencing and when observing an airpuff. Net effect on blink rate of observing the partner receiving an airpuff, computed as the difference [*airpuff to partner* – *airpuff to nobody*] for benevolent, indifferent, and malevolent actors ( $n = 97, 30,$  and  $37$  sessions, respectively). Shading overlays on the traces represent SEM. Bar graphs show mean blink rate differences computed 300 ms before and after airpuff delivery. Thick lines below the plot indicate significant pairwise differences (permutation test,  $P < 0.05$ ). \*Significant pairwise difference (Wilcoxon rank sum test,  $P < 0.05$ ); error bars represent SEM.

self, i.e., the expected value, of each option was the same: a fixed amount of juice. Thus, according to a strict utility hypothesis, monkeys should have shown no systematic choice preference: the consequence to the partner was task irrelevant and the two monkeys did not have to coordinate their actions or adopt a joint strategy. Despite this, what happened to the partner shaped decisions in a large majority of the monkey pairs tested (11/14; Fig. 2), with a significant and consistent prosocial bias in more than half of cases. Prior experiments that have used appetitive (32–38) or aversive outcomes (13) to study prosocial behavior in nonhuman primates raise the question of the underlying mechanisms: why do animals make generous choices or refrain from causing harm to others? The observation that monkeys chose to grant juice (or food) to a partner is offered as evidence of motivation for object giving or sharing, but an alternative explanation is that social stimuli preferentially attract the monkeys' attention, such that the differential salience of the two outcomes is sufficient to positively reinforce prosocial choices. Monkeys might enjoy watching a partner eating or drinking more than waiting passively for the next trial or than seeing a drop of juice falling into a container. However, social decisions involving aversive stimuli, such as older studies that challenged monkeys to forego a food reward to save a partner from electrical shock (13), are more difficult to reconcile with a purely attentional interpretation. The present results clearly refute it, as the monkeys did not consistently

choose the outcomes that include the social stimulus across appetitive and aversive social decisions. The partner licking a drop of juice in the first case, or wincing in response to an airpuff in the second, were both more salient than their respective alternatives. However, rates of juice giving and of airpuff avoidance to the partner were correlated, which implies that the monkeys' choice preferences must have been influenced by the social significance, not only by the salience of those events. The kind of social dilemmas that these monkeys were challenged with have no obvious equivalence in more ecological settings, but nevertheless shed light on the cognitive and affective mechanisms underlying prosocial behavior. Previous studies using allocation tasks also reported that, under certain circumstances, monkeys can grant juice or food to their conspecifics. Massen et al. (31, 32, 34, 39) observed such prosocial behavior, especially among dominant animals and between kin in a colony of 20 long-tailed macaques, and Chang et al. (33) found that individually housed, unrelated rhesus monkeys allocated juice to a partner, but needed no reward to reveal a prosocial tendency. Despite differences in experimental procedures, choice contexts, living conditions or species, which might influence the social decision framework of macaques, choices in such tasks appear to involve intrinsically social mechanisms. Interesting partner-dependent and individual differences in decision-making pattern were observed. However, given the relatively small number of animals tested, defining the role of sex difference, hierarchy, or developmental stage in nonhuman primates' social decisions must await further investigations. The unique features of the present study, particularly the combination of appetitive and aversive social outcomes, the analysis of multiple behavioral markers, and the assessment of social decisions between group-housed animals with well-defined network structure, allowed us to address the following unresolved issues.

**Are Social Stimuli Vicarious Reinforcers?** The quest for proximal mechanisms of prosociality has led authors to hypothesize that prosocial behavior is shaped by the reinforcing value of certain social events (33). For instance, the view of a conspecific receiving a drop of juice could be experienced as pleasant, recruit brain reward circuits and lead to a preference for the prosocial option (33). Conversely, a conspecific receiving an airpuff could be perceived as unpleasant, deactivate reward circuits, and negatively reinforce the antisocial option. The view that prosocial actions generate their own rewards is somewhat related to the “warm glow” hypothesis of human altruism: doing good makes us feel good (40, 41). Similarly, empathy theories (7, 8) postulates that prosocial behavior aimed at suffering individuals alleviates vicariously experienced pain (23). In



**Fig. 5.** Social affiliation structure of long-tailed macaques and relation to social decision-making tendencies. (A) Social grooming network. Circle diameter is proportional to the total percentage of time (in a 3-h cycle, 10 recording sessions) spent in allo-grooming activity by each monkey. Arrows show directionality of grooming and numbers, the percentage of time dedicated to grooming a given partner. (B) Schematic of the social decision network based on data from Fig. 2, allowing direct comparisons between spontaneous social behavior and decision tendencies. (C) Correlation between social decisions regarding aversive outcomes (offer A-5) and mean social grooming time in the home environment ( $R = 0.77, P < 0.05$ ). (D) Correlation between mutual gaze rate of monkeys in the social decision task and mean social grooming time in the home environment ( $R = 0.83, P < 0.05$ ). Mutual gaze (MG) was normalized using the ratio:  $MG_{[juice\ to\ partner]} / (MG_{[juice\ to\ partner]} + MG_{[juice\ to\ nobody]})$ . The dataset includes 10 recording sessions conducted during the same period that social decisions data were collected. Each dot in the correlations represents a monkey dyad.

this study, what is the evidence for the involvement of such empathy-like mechanisms and are these satisfactory explanations of macaque prosocial decision-making? The behavioral data presented here suggest that granting juice to a partner triggers social interactions that might act as positive or negative vicarious reinforcers, depending on preexisting bonds. We also found that viewing a partner experiencing an airpuff triggers a defensive blinking response, indicative of the negative affective impact of the partner's discomfort upon the observer. However, the monkey's social decision-making clearly exhibited partner selectivity, as previously observed in primates and rodents (4, 31–33, 35, 42, 43). There thus seems to be more at play than vicarious rewarding or punishing "social stimuli." Factors related to personality traits and preexisting social bonds should also modulate social decision-making, suggesting that macaque's vicarious affect is cognitively controlled. These different points are discussed next.

**Is Mutual Gaze a Marker of Social Reward?** In a social context, gaze is used both to gather information and to communicate with peers, mainly through gaze following and joint attention as well as direct eye contact (44–47). Social gaze started during the delay following the actor's choice, ruling out exclusively stimulus-driven responses, and was particularly enhanced in the partner monkey. In agreement with other observations (46), we found that macaques actively control their social looking. Indeed, actor and partner monkeys either avoided meeting the other's gaze or sustained it more than would be predicted if their respective gaze patterns were independently generated. This interaction is expected because, in the social environment of macaques, staring at conspecifics may be risky and its potential cost needs to be balanced with its usefulness (47). Indeed, during negative social interactions, eye contact is generally threatening for macaques. Here, we find that mutual gaze rate is correlated with prosociality and with another proxy of affiliation: the rate of social grooming. These associations indicate that, in the context of juice allocation, mutual gaze could express an intrinsic motivation for social affiliation. Thus, consistently with other observations, we suggest that monkeys' eye contact can also represent a form of positive social interaction (44, 48–50). The vicarious reward hypothesis suggests that viewing a conspecific receiving juice might activate, through some form of mirror mechanism, the same reward circuit as an actual drop of juice (33). Here, consistently with other nonhuman primate study (22), we propose that, rather than the mere sight of juice delivery, it is the social attention received from the partner and the gaze exchanges that act as social rewards or punishment, promoting or preventing prosocial behavior through the monkeys' social attachment system. In other words, our results suggest that voluntary social interaction through gaze might be a social reinforcer and thus play an important role in the experience of juice allocation in macaques. This hypothesis is coherent with the fact that macaques display partner-dependent cofeeding tolerance (42) (a tendency which might be evolutionary rooted as humans and bonobos are usually seeking to eat in social context rather than alone) (51, 52).

**Is Eye Blinking a Marker of Negative and Vicarious Affect?** Enhanced eye blinking when watching a peer receiving an airpuff offers evidence of induced negative affect in the observer. Our finding of similar, and correlated behavioral responses to the direct experience of an aversive stimulus and to the observation of its impact upon a peer would appear consistent with simulation theories of empathy (7–9, 21). Empathic-like responses have already been reported in others animal studies (2, 5, 7, 53–56). Such behavioral responses are usually either contagious, modulated by past experience, and/or dependent on the partner identity. The singular empathic response that we have described here contains all of these features. However, further experiment would be needed to know to which extent the macaques' empathic response reflected their understanding of what their peers

were experiencing. In addition, eye blinking is also related to the generalized startle reflex, which has been shown to be gated by affective states (57, 58). Thus, anticipatory eye blinking to observed airpuffs may involve a form of conditioned startle response modulated by the perceived facial affective state of the partner monkey. Regardless of its nature, the fact that the presence and amplitude of this physiological response were related to the monkeys' prosocial tendencies further argues for the implication of vicarious mechanisms in shaping nonhuman primates social decisions.

**Why Is Rudimentary Empathy Involved in Macaques' Social Decision-Making?** Ethological observations of complex social behaviors such as coalition building or reconciliations (59, 60) emphasize that nonhuman primates maintain preferential relationships that can be influenced by diverse social variables such as personality traits, rank, or services that a peer can provide (61, 62). Hence, to act in accordance with their motivation for social interaction, macaques need to be able to predict the consequences of their behavior on future social bonds. Moreover, greeting rituals constitute evidence that macaques react to other's absence, suggesting a persistent mental representation and a specific need to interact with a given conspecific (63, 64). Beyond the claim that macaques are natural born politicians, we believe that a cognitive control of vicarious affect allows macaques to include (or discard) others' welfare into their social decision framework and thus shape their social network. From an evolutionary and ecological perspective, the cognitive abilities of each species should be adapted to their social challenges. Different factors can strengthen or weaken social cohesion, including the affective state of individual group members (65–69). Seemingly gratuitous aggressions are used, especially in despotic species, to maintain the group's hierarchy, but a disproportionate use of aggressive behaviors would needlessly weaken the troop's cohesion. We can thus propose that the evolutionary benefit of rudimentary empathy would be linked to a better management of social structure which consequently might increase individual fitness.

To conclude, the convergence of our measures of social decision-making, online social interaction, vicarious affect, and social affiliation demonstrate the existence of internal states that coherently shape the value nonhuman primates assign to others' welfare and to their social interactions, together fostering prosocial behaviors. Our results provide insights into the proximal mechanisms that drive primate social preferences and pave the way toward understanding the biological basis of the cognitive and affective mechanisms involved in nonhuman primates' social decision-making.

## Methods

Four nonkin juvenile male long-tailed macaques (*Macaca fascicularis*) and three rhesus macaques (*Macaca mulatta*) were used as subjects. The social status and interaction patterns of the long-tailed macaques were characterized by both manual and automated ethological measures using a custom-designed multicamera 3D tracking system (30) (Fig. 5A and Fig. 5B). Choice preferences, eye position, and eye blink signals of actor and partners monkeys in the social decision task were recorded and processed using experimental and data analysis procedures detailed in *SI Methods*. All experimental procedures were approved by the animal care committee (Department of Veterinary Services, Health & Protection of Animals, permit no. 69 029 0401) and the Biology Department of the University Claude Bernard Lyon 1, in conformity with the European Community standards for the care and use of laboratory animals (European Community Council Directive No. 86–609).

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