



## Grooming, social rank and ‘optimism’ in tufted capuchin monkeys: a study of judgement bias



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Studying the emotional consequences of social behaviour in nonverbal animals require methods to access their emotional state. One such method is provided by cognitive bias tests. We applied a judgement bias test to tufted capuchin monkeys, *Sapajus* sp., to evaluate (1) whether receiving grooming was associated with a short-term increase in ‘optimism’ (that is, a positive bias in the interpretation of ambiguous stimuli) and (2) whether interindividual differences in ‘optimism’ were related to dominance rank or overall rates of social and nonsocial behaviour. Receiving grooming had no detectable immediate consequences, but increased ‘optimism’ was observed in dominant monkeys and in monkeys that received overall larger quantities of grooming. These results provide only partial support for the hypothesis that a system of emotional bookkeeping underlies the capacity of group-living animals to reciprocate cooperative interactions.

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The study of the emotional correlates of social behaviour can help us to understand social decision making and, more generally, the proximate mechanisms underlying social interactions (Aureli & Schaffner, 2002; Aureli & Whiten, 2003). At the same time, as the fitness consequences of variation in social relationships are being increasingly recognized, so is the need to understand the causal processes that link social behaviour and Darwinian fitness (Silk, 2007). The emotional response to social interactions and its physiological correlates may well be part of these processes.

The study of animal emotions faces considerable methodological challenges. While in the field of human emotions it is possible to ask subjects to describe their emotional state verbally, nonverbal animals cannot be asked such direct questions. Thus, a variety of other methods have been developed to assess the emotional correlates of social behaviour in nonhuman animals. These methods can be grouped into four broad sets: drug discrimination tests, measures of spontaneous behaviour, measures of physiological correlates and cognitive bias tests.

The method that most closely approximates a direct question is probably the use of drug discrimination tests. In drug discrimination studies, an animal is first given a conditional discrimination task, during which it learns to choose one stimulus when administered a given psychoactive drug (e.g. an anxiogenic drug) and another stimulus when given a placebo. The animal is then tested after experiencing a social interaction (e.g. after an aggressive defeat) and its response in the conditional discrimination task is indicative of its emotional state (Vivian, Weerts, & Miczek, 1994). A second method of studying emotions in animals identifies behavioural correlates of emotions and measures behavioural variations associated with social interactions. Two groups of commonly used behavioural measures are vocalizations and displacement activities (Maestripieri, Schino, Aureli, & Troisi, 1992; Miczek, Weerts, Vivian, & Barros, 1995). The latter, in particular, have provided a simple and inexpensive way of measuring emotional responses to social interactions (e.g. Aureli, Cords, & van Schaik, 2002; but see Neal & Caine, 2015). Physiological measures of emotions are less easily applied to the study of social interactions, as they are difficult to obtain from freely interacting animals. The most commonly used are probably variations in plasma (and derived) concentrations of glucocorticoids and measures of heart rate or blood pressure (e.g. Meehan, Tornatzky, & Miczek, 1995; Shutt, MacLarnon,

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Heistermann, & Semple, 2007). The use of infrared cameras to assess cutaneous thermal variations is now opening new possibilities in the noninvasive monitoring of physiological parameters (Kano, Hirata, Deschner, Behringer, & Call, 2016). One last promising method is to rely on the cognitive distortions that are associated with emotions. These phenomena, collectively known as cognitive bias, have been initially described in psychiatric patients (MacLeod, Mathews, & Tata, 1986; Wright & Bower, 1992) and have subsequently been applied to study the emotional correlates of wellbeing in laboratory or farm animals (Harding, Paul, & Mendl, 2004; Paul, Harding, & Mendl, 2005). Pomerantz, Terkel, Suomi, and Paukner (2012) showed that behavioural and physiological indicators of stress were related to judgement bias in capuchin monkeys. However, to our knowledge, cognitive bias tests have never been applied to investigate the consequences of social interactions.

In principle, the emotional consequences of social interactions and social life can be studied along three different time frames: lifetime consequences of early events and relationships, correlates of current social relationships and immediate consequences of social interactions. The study of the lifetime consequences of early events on emotional reactivity has a long history in the framework of Bowlby's attachment theory (Bowlby, 1969). Collectively, these studies have shown how early stressors and the quality of mother–infant attachment can profoundly affect emotional reactivity to social and nonsocial stress in humans and other primates (e.g. Hinde & Spencer-Booth, 1971; Schino, Speranza, & Troisi, 2001).

We have a less clear picture of the emotional correlates of current social relationships during the adult life. Dominance rank is associated with variations in impulsivity, stress and anxiety, although some of these effects appear to be modulated by individual, possibly genetic, predispositions, and the direction of the causal relations is often unclear (Diezinger & Anderson, 1986; Fairbanks et al., 2004; Gesquiere et al., 2011; Sapolsky, 2005). Dominance rank is associated with both structural and functional variations in brain structures involved in the response to socio-emotional stimuli (Morgan et al., 2002; Noonan et al., 2014). Variations in social networks also appear to affect both stress-mediated health and socioemotional neural structures (Bickart, Wright, Dautoff, Dickerson, & Barrett, 2011; House, Landis, & Umberson, 1988; Sallet et al., 2011).

The study of the immediate emotional consequences of social interactions has most often been based on measuring variations in the rate of displacement activities, thought to index emotional states related to motivational conflict or anxiety (Maestriperieri et al., 1992). This method has been extremely successful in understanding the emotional consequences of agonistic interactions and of conflict management strategies. Postconflict increases in anxiety (as measured by increases in scratching rates) have been shown to be related to the quality of the relationship between aggressor and victim, and to be decreased by reconciliation (Aureli, 1997; Kutsukake & Castles, 2001). In contrast, the emotional consequences of affiliative interactions such as grooming have been more difficult to identify. While earlier reports highlighted a relaxing effect of receiving grooming as evidenced by decreases in both displacement activities and heart rate (Aureli, Preston, & de Waal, 1999; Schino, Scucchi, Maestriperieri, & Turillazzi, 1988), more recent studies focusing on displacement activities have reported conflicting results (Molesti & Majolo, 2013; Semple, Harrison, & Lehmann, 2013). Given their relation to anxiety, displacement activities may not be the best tool to investigate positive emotional responses.

The difficulty in pinpointing the emotional consequences of cooperative interactions such as grooming is particularly troublesome as identifying these emotional consequences is crucial to

testing current hypotheses about the proximate mechanisms underlying reciprocal cooperation. Schino and Aureli (2009, *in press*) hypothesized that a mechanism of 'emotional bookkeeping' could underlie reciprocity in group-living animals. A central prediction of this hypothesis is that the receipt of cooperative interactions should elicit a positive emotional response. In this study, we investigated the emotional consequences of grooming as measured by a judgement bias test. In this test, monkeys were asked to interpret an ambiguous stimulus as signalling either a more positive ('optimistic' interpretation) or less positive ('pessimistic' interpretation) outcome. We evaluated both the short- and long-term effects of receiving grooming, as well as the correlates of social dominance and of behavioural measures of stress and anxiety.

## METHODS

### *Ethical Note*

This study complied with protocols approved by the Italian Ministry of Health (Permit number 122/2014-C to G. Schino). All procedures were performed in full accordance with the Directive 2010/63/EU on the protection of animals used for scientific purposes and conformed to ASAB/ABS guidelines.

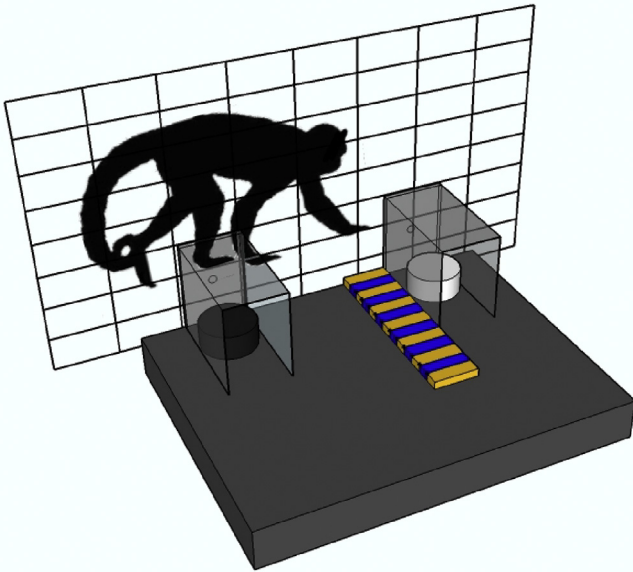
Differently from other studies on judgement bias, monkeys had to choose between options leading to positive reinforcement of different sizes, not to positive or negative reinforcement. Monkeys were thus generally willing to participate in the test, but could easily refuse by simply not entering the indoor compartments.

### *Subjects and Housing*

Subjects were 13 adult tufted capuchin monkeys, *Sapajus* sp., (five males and eight females) belonging to the colony housed at the Primate Centre of the Institute of Cognitive Sciences and Technologies in Rome, Italy. They were part of three social groups (numbering five to nine monkeys) living in outdoor compartments (53.2–374.0 m<sup>3</sup>, depending on group size) connected to indoor rooms (25.4 m<sup>3</sup> for each group). All compartments were furnished with wooden perches, tree trunks, ropes and branches. Testing occurred between 0930 and 1330 hours. Capuchins were fed with fresh fruits, vegetables and monkey chow once a day in the afternoon, always after the tests. Water was available *ad libitum*. Most of the subjects had taken part in previous cognitive experiments.

### *Experimental Procedure*

Monkeys were tested alone in their indoor compartments and voluntarily participated in the tests. The experimental procedure was adapted from Pomerantz et al. (2012) and De Petrillo et al. (2015). Monkeys were presented with an apparatus (Fig. 1) that allowed a choice between two options. It consisted of a platform (62 × 40 cm and 15 cm high) with two transparent boxes (12 × 20 cm and 15 cm high), 28 cm apart, that contained two differently coloured cups (black and white), covering the rewards. The apparatus was positioned in the area in front of the indoor compartment. Tests were conducted by two experimenters: experimenter 1 sat in front of the subject, behind the apparatus, and experimenter 2 sat next to experimenter 1. In each trial, experimenter 2 blocked the subject's visual access to the apparatus by means of an opaque screen, while experimenter 1 baited the apparatus. After baiting, experimenter 2 lifted the opaque screen and experimenter 1 pushed the apparatus towards the wire mesh, allowing the subject to make its choice. The subject made its choice by inserting its finger in a small hole in the selected transparent



**Figure 1.** Schematic representation of the experimental apparatus.

box. Experimenter 1 then proceeded to uncover the reward and to give it to the subject.

During the training phase, monkeys were presented with a conditional discrimination task with differently sized rewards. They had to attend to the position of a striped yellow-and-blue rectangle that was positioned close to either of the two transparent boxes and indicated the position of the reward. The baited cup was always the one close to the striped rectangle, but the size of the reward varied. In  $S+$  trials the subject could obtain a larger reward (two Cheerios) if it chose the correct box or no reward if it chose the wrong box. The position of the larger reward (right or left) was always the same for each subject, and was counterbalanced across subjects. In  $S-$  trials the subject could obtain a smaller reward (one Cheerio) if it chose the correct box or no reward if it chose the wrong box. The position of the smaller reward (left or right; opposite to that of  $S+$  trials) was always the same for each subject, and was counterbalanced across subjects. On each test day, the subject received 24 trials (12  $S+$  and 12  $S-$ ) in a pseudo-random order. The subject was considered to have passed the training phase when it chose the correct box in at least 10 of 12 trials for each type of trial ( $S+$  or  $S-$ ) for at least three consecutive sessions.

During tests, subjects were presented with 'ambiguous' trials in which the striped rectangle was positioned midway between the two boxes and thus did not give any indication of the position (and, therefore, size) of the reward. If a subject chose the box that was associated with the larger reward, it was considered to have given an 'optimistic' interpretation of the ambiguous stimulus. If it chose the box that was associated with the smaller reward, it was considered to have given a 'pessimistic' interpretation of the ambiguous stimulus. During ambiguous trials both cups were baited with a quarter of a Cheerio in order to maintain motivation. Each test session consisted of three ambiguous trials interspersed between 22  $S+$  and  $S-$  trials.

Tests were conducted under two different experimental conditions: after receiving grooming and in the absence of grooming. On each test day, the observer monitored the enclosure looking for any grooming received by one of the experimental subjects. When a monkey received grooming, the observer recorded its duration and the identity of the groomer and, at the end of the grooming bout,

proceeded to call the subject into the indoor room. Grooming preceding tests lasted between 20 s and 21 min. Time between the end of grooming and the beginning of the test ranged between 2 and 11 min. Control tests were conducted after the subject had been monitored for at least 30 min without being involved in any grooming event, either as a groomer or as a groomee. Given that tests following grooming were conducted in a somewhat opportunistic way, it was not always possible to counterbalance precisely the two experimental conditions (see the Data Analysis section for how this problem was dealt with).

No monkey was ever tested more than once a day and more than twice a week. Test sessions were always separated by at least two reminder training sessions during which no ambiguous trial was presented to the subject.

#### *Observations of Social Behaviour*

In the same period in which the experiment was carried out, we also conducted focal animal observations in the outdoor compartments, i.e. when subjects were together with their group mates. In part, these focal animal observations were conducted on the same day of testing, either before or after the test. A total of 509.8 h of observation were made (range 12.9–21.4 per subject). We obtained individual hourly rates of scratching, head stereotypies and aggression received (episodes/h), and grooming received (min/h). For the subset of tests that were accompanied by observations conducted on the same day, we also obtained rates of scratching and head stereotypies relative to each test day.

#### *Data Analysis*

Given that the order of presentation of the two experimental conditions was not perfectly counterbalanced, mean session number was not exactly the same for the two conditions for all subjects. We therefore included session number as an independent variable in all analyses in order to control for its influence and avoid problems deriving from the two experimental conditions not being perfectly counterbalanced.

We used conditional within-subject logistic regressions with bootstrap standard errors to investigate short-term variations in the subject's choice during ambiguous trials. Individual choices ('optimistic' or 'pessimistic', a binary dependent variable scored as 1 and 0, respectively) were the unit of analysis. Analyses evaluated the effects of the experimental condition (immediately after grooming versus control), of behavioural indicators of stress/anxiety (scratching and head stereotypies) measured during focal observations conducted on the same day of testing, or of characteristics of the received grooming. The latter included grooming duration, the identity of the groomer (i.e. whether the groomer was the subject's preferred grooming partner or not), and the time elapsed between the end of grooming and the beginning of the test.

We used mixed-effect linear regressions with bootstrap standard errors to investigate long-term interindividual variations in the mean proportion of 'optimistic' choices. Individual mean values recorded over the entire study were the unit of analysis. Analyses evaluated the effects of social variables (dominance rank, rate of grooming received, rate of aggression received), or of behavioural indicators of stress/anxiety (scratching and head stereotypies). Group membership was inserted as a random effect in these analyses.

David's score (Gammel, de Vries, Jennings, Carlin, & Hayden, 2003) was used to arrange animals in dominance hierarchies. In our sample, sex was perfectly collinear with dominance rank (i.e. all males were dominant to all females). Therefore, sex was not

included in the analysis. All statistical analyses were run in Stata 14.1 (StataCorp, 2015).

## RESULTS

A preliminary analysis showed that trial number within each session and the type of trial (S+ or S-) immediately preceding the ambiguous trial had no effect on the interpretation capuchin monkeys gave to ambiguous stimuli (trial number: odds ratio = 0.740,  $z = -1.60$ ,  $P = 0.109$ ; type of preceding trial: odds ratio = 1.145,  $z = 0.84$ ,  $P = 0.402$ ). In contrast, monkeys reduced their optimistic interpretation of ambiguous stimuli along test sessions (session number: odds ratio = 0.820,  $z = -3.21$ ,  $P = 0.001$ ;  $N = 367$  choices). Therefore, we included session number as a control variable in all subsequent analyses.

### Short-term Within-individual Variation

Receiving grooming had no short-term detectable effect on the interpretation of ambiguous stimuli (experimental condition: odds ratio = 0.938,  $z = -0.24$ ,  $P = 0.813$ ,  $N = 354$  choices; Fig. 2). In an analysis that only included tests conducted after receiving grooming, the characteristics of the grooming episode did not affect the interpretation of ambiguous stimuli (grooming duration: odds ratio = 1.001,  $z = 0.55$ ,  $P = 0.580$ ; identity of the groomer: odds ratio = 1.840,  $z = 1.69$ ,  $P = 0.090$ ; time elapsed between grooming and testing: odds ratio = 1.054,  $z = 0.64$ ,  $P = 0.523$ ;  $N = 176$  choices). Given that grooming exerted no detectable short-term effect, we included tests conducted in both experimental conditions in all subsequent analyses.

Within-individual day-to-day variations in emotional state (as measured by the rate of scratching and head stereotypies recorded on the same day of testing) were unrelated to the interpretation of ambiguous stimuli (scratching: odds ratio = 1.012,  $z = 1.61$ ,  $P = 0.108$ ; head stereotypies: odds ratio = 1.000,  $z = -0.01$ ,  $P = 0.990$ ;  $N = 313$  choices).

### Long-term Between-individual Variations

Capuchin monkeys varied widely in their average interpretation of ambiguous stimuli (range 7.7–86.7% of optimistic choices). Mean individual interpretation of ambiguous stimuli was affected by dominance rank and grooming received, but not by aggression

received (rank: coefficient =  $-0.034$ ,  $z = -3.01$ ,  $P = 0.003$ ; grooming: coefficient = 0.020,  $z = 2.03$ ,  $P = 0.043$ ; aggression: coefficient =  $-0.335$ ,  $z = -1.49$ ,  $P = 0.137$ ;  $N = 13$  individuals; Figs. 3 and 4). Thus, high-ranking monkeys and monkeys that received more grooming were more likely to interpret ambiguous stimuli optimistically.

Mean interpretation of ambiguous stimuli was also related to mean individual behavioural measures of emotional state (scratching: coefficient =  $-0.006$ ,  $z = -2.89$ ,  $P = 0.004$ ; head stereotypies: coefficient =  $-0.001$ ,  $z = -2.58$ ,  $P = 0.010$ ;  $N = 13$  individuals). Thus, monkeys that showed more indications of being stressed or anxious were less likely to interpret ambiguous stimuli optimistically.

## DISCUSSION

This study shows that high-ranking capuchin monkeys and monkeys that received more grooming were more likely to give a positive, 'optimistic' interpretation of ambiguous stimuli. Also, individuals that showed higher levels of behavioural indicators of stress and anxiety were less likely to interpret ambiguous stimuli optimistically, confirming an earlier report by Pomerantz et al. (2012). In contrast, we were unable to detect any immediate effect of receiving grooming on the interpretation of ambiguous stimuli. These results suggest that being dominant and receiving high rates of grooming translate into a positive long-term emotional state, or mood, while receiving a single grooming bout did not have any immediate detectable effect on the emotional state of capuchin monkeys. No previous study had investigated the social correlates of judgement bias, either in the short or in the long term.

Schino and Aureli (2009, in press) hypothesized that an emotionally based bookkeeping system may support reciprocal cooperation in group-living animals. A complete test of this hypothesis would require: (1) demonstrating the positive emotional valence of receiving cooperative behaviours; (2) demonstrating that the elicited emotions are partner specific and, in the long term, contribute to the formation of social bonds; (3) demonstrating that social bonds are instrumental in guiding cooperative behaviour. At the moment, while the last of the points above is relatively well supported (Berghänel, Ostner, Schröder, & Schülke, 2011; Sabbatini, De Bortoli Vizioli, Visalberghi, & Schino, 2012), we have no clear evidence to support or refute the first two points.

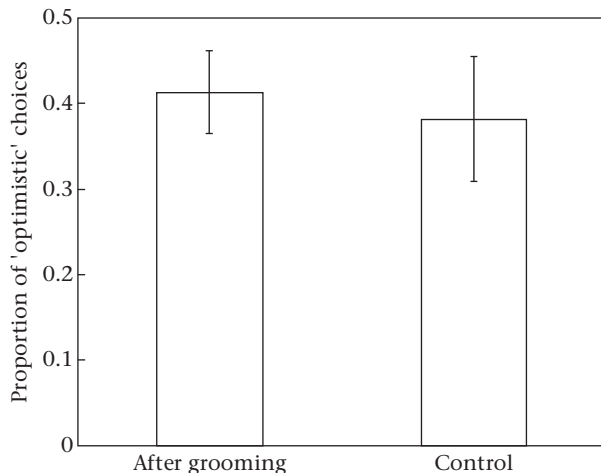


Figure 2. Proportion of 'optimistic' choices immediately after receiving grooming and in the absence of grooming (Control). Means and SEs are reported.

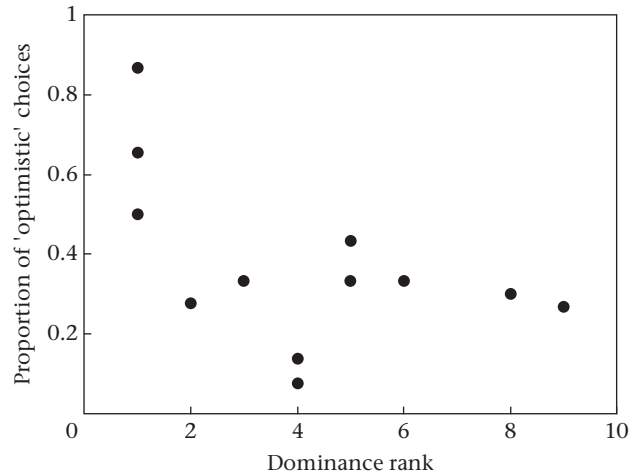
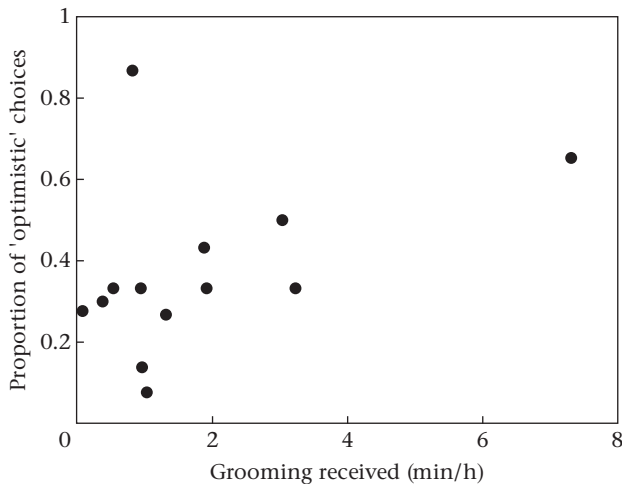


Figure 3. Proportion of 'optimistic' choices in relation to dominance rank. Each point represents a different individual.





**Figure 4.** Proportion of 'optimistic' choices in relation to overall amount of grooming received. Each point represents a different individual.

Overall, our results provide only partial support for the hypothesis that receiving cooperative behaviour such as grooming elicits positive emotions. On the one hand, monkeys that received overall more grooming showed a positive cognitive bias, an indicator of a better mood. On the other hand, receiving grooming had no detectable immediate consequence on cognitive bias, suggesting grooming was not associated with any short-term emotional variation. These results might be considered as parallel to the observed time frame of grooming reciprocity, where short-term imbalances in grooming given and received often coexist with long-term reciprocity. Note, however, that the latter results imply that interdyadic differences in grooming rates translate into differential social bonds among different group mates, while our results show that interindividual differences in total amount of grooming received (by whatever group mate) are associated with a better mood. In both cases, however, grooming seems to have negligible immediate consequences. The relation between the long-term formation of social bonds and the improvement in mood remains to be clarified.

The difficulties of identifying the immediate emotional consequences of receiving grooming contrast sharply with the feeling of extreme relaxation that monkeys receiving grooming convey. One possibility is that such emotional consequences are extremely short lived and thus difficult to measure reliably. If this hypothesis were correct, then tests or behavioural measures that typically span over 5–15 min postgrooming would be unable to highlight an emotional state that fades very rapidly. Interestingly, both behavioural and physiological measures taken during the receipt of grooming seem to confirm the relaxing effect of grooming (Aureli et al., 1999; Schino et al., 1988). As already noted, it remains to be seen whether such short-lived emotions do contribute to the formation of social bonds. In this regard, recent evidence points to a possible role of oxytocin, which is released in association with the exchange of cooperative interactions such as grooming and food sharing (Crockford et al., 2013; Wittig et al., 2014) and is instrumental in the formation of social memories (Ferguson et al., 2000).

We found that dominant monkeys were consistently more optimistic than subordinates. This seemed to be especially true for alpha males, since the three alpha males were the most optimistic subjects in our sample (see Fig. 2). While these results do not by themselves demonstrate a special effect specific to the alpha status (given also the collinearity between sex and rank in our sample) they are coherent with recent evidence showing that alpha status

may have specific costs and benefits that do not just represent an extreme of the distribution of dominance rank (Gesquiere et al., 2011).

Understanding the emotional consequences of social interactions is a priority in the field of animal behaviour. We have shown how a cognitive bias test can be used to explore the emotional correlates of aspects of the social life of monkeys, notably dominance and cooperative behaviour. Further methodological progresses will help in investigating the details of the emotional causes and consequences of social interactions.

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### Supplementary Material

Supplementary material related to this article can be found, in the online version at, <http://dx.doi.org/10.1016/j.anbehav.2016.06.017>.

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