



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; Geschiere 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 m³, depending on group size) connected to indoor rooms (25.4 m³ 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

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