



Emotional correlates of probabilistic decision making in tufted capuchin monkeys (*Sapajus* spp.)



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In humans, emotions play a fundamental role in decision making. Although there is considerable evidence that nonhuman animals exhibit emotions, studies on how emotional responses affect their choice behaviour are scant. We tested tufted capuchin monkeys in a probabilistic choice task, in which subjects were repeatedly offered a choice between a safe option (corresponding to four food units) and a risky option (corresponding to either one or seven food units). The study included three conditions that differed in the probability of receiving the larger outcome when choosing the risky option. We evaluated whether capuchins anticipated that they may experience negative consequences from their choices by scoring latency to choose, scratching and alarm vocalizations before they made their choices. Moreover, we assessed whether capuchins exhibited emotional responses to different decision outcomes by scoring scratching, alarm vocalizations, banging, and switching after the choice outcomes were revealed. We also assessed whether capuchins' motivation to choose the risky option and emotional responses were modulated by the probability of 'winning' and whether the emotional responses experienced after receiving the choice outcomes affected their subsequent decisions. Capuchins scratched more before making their choices than after choice outcomes were revealed, whereas alarm vocalizations showed the opposite pattern. Thus, the capuchins seemed more sensitive to the conflict experienced when deciding which option to choose than to the frustration of receiving an undesired outcome. The inconsistent pattern of scratching and alarm vocalizations suggests that these behaviours indicate different emotional states. Capuchins showed more emotional responses and attempts at switching their initial choice after a one-item outcome than a four-item or a seven-item outcome, suggesting that they experienced regret-like emotions. The lack of a negative impact of receiving one-item outcomes on capuchins' subsequent choices may support the view that emotional responses have a coping function, but this hypothesis remains to be demonstrated.

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Emotion and cognition have traditionally been viewed as separate entities (Descartes, 1649) and the investigation of the relationship between emotion, cognition and decision making has long been neglected (reviewed in Schwarz, 2000). Smith (1759) acknowledged that emotions influence decisions, but only in the last few decades has empirical research examined the role of emotions in decision making (Lerner, Li, Valdesolo, & Kassam, 2015).

In humans, emotions experienced at the time of a decision influence the evaluation of alternative options and, according to their valence, emotional states may differently affect risk preferences (Lerner & Keltner, 2001; Raghunathan & Pham, 1999; see also Lerner et al., 2015). In addition, people often compare the outcome of the chosen option with the outcome they could have obtained if they had chosen differently (counterfactual reasoning; Coricelli et al., 2005). The emotion of disappointment may occur when people are not shown the outcome of the option that they did not choose, but the chosen option turns out to be worse than expected. In contrast, the emotion of regret may occur when people are shown the outcome of the option that they did not choose and the outcome of that choice would have been better than the outcome of their choice (Coricelli et al., 2005, 2007; Coricelli & Rustichini,

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2010; Schwarz, 2000; Steiner & Redish, 2014). Overall, all decisions have affective consequences that can, in turn, impact subsequent decisions (Bechara, Damasio, Tranel, & Damasio, 1997; Crone, Somsen, Beek, & Van Der Molen, 2004; Schwarz, 2000).

Little is known about the role of emotional responses on decision making by nonhuman animals. Chickens, *Gallus domesticus*, exhibited physiological responses when faced with choices between a potentially high-gain 'risky' option (associated with the probabilistic delivery of an aversive air-puff) and a low-gain 'safe' option (not associated with an air-puff delivery; Davies, Radford, Pettersson, Yang, & Nicol, 2015). Specifically, when selecting the potentially high-gain option, chickens' heart rate increased both in anticipation and following the delivering of the aversive air-puff. However, experiencing these emotions did not influence their subsequent choices. Rats, *Rattus norvegicus*, showed both neural and behavioural evidence of regret when tested in a spatial decision-making task (Steiner & Redish, 2014). In regret-inducing situations, but not in control trials, rats looked backwards towards the missed option and there was a peak in the activity of the orbitofrontal cortex, an area involved in the experience of regret in human subjects (Camille et al., 2004).

Self-directed behaviours, such as scratching and self-grooming, are behavioural patterns apparently irrelevant to the situation in which they are performed and are considered indicators of anxiety (Maestripieri, Schino, Aureli, & Troisi, 1992). Some authors have examined whether self-directed behaviours observed during cognitive testing are related to task difficulty or incorrect responses. In 14 subjects representing three monkey species (lion-tailed macaque, *Macaca silenus*, common squirrel monkey, *Saimiri sciureus*, and tufted capuchin, *Cebus apella*, now *Sapajus apella*), self-directed behaviours were positively correlated with performance in a reversal learning task (Judge, Evans, Schroepfer, & Gross, 2011). In another study, a female chimpanzee, *Pan troglodytes*, tested in a matching-to-sample task showed more self-directed behaviours when she made an error than when she chose correctly (Itakura, 1993). Likewise, chimpanzees scratched more when tested in a difficult version of a matching-to-sample task than in an easy version of the same task, but only if they were presented first with the easy version of the task (Leavens, Aureli, Hopkins, & Hyatt, 2001; see also Leavens, Aureli, & Hopkins, 2004). Yamanashi and Matsuzawa (2010) observed a similar influence of task difficulty and performance in three of their six chimpanzees tested in two types of numerical tasks. In a more recent study, Wagner, Hopper, and Ross (2016) found that chimpanzees and gorillas, *Gorilla gorilla*, showed more self-directed behaviours when they made errors in a serial learning task, although task difficulty did not affect their overall rates of self-directed behaviours.

Thus far, the only study providing a detailed behavioural analysis of nonhuman primate emotional responses in a probabilistic choice task showed that great apes exhibited a rich pattern of emotional responses following their decisions (Rosati & Hare, 2013). Chimpanzees and bonobos, *Pan paniscus*, that faced a series of choices between a safe option and a risky option showed negative emotional responses (i.e. negative vocalizations, scratching and banging, see below) more often after choosing a low-value risky option than after choosing a high-value risky option or a safe option. In addition, individual chimpanzees and bonobos attempted to switch their initial choices for a risky option more often after receiving a low-value outcome. Moreover, bonobos, but not chimpanzees, modulated their choices based on the outcome of their previous decisions. However, the above study did not examine whether emotions play a causal role in decision making under risk.

Here, we scored capuchin monkeys' (*Sapajus* spp.) emotional and motivational responses before choices were made and after choice outcomes were revealed in a probabilistic choice task.

Subjects were presented with a series of choices between safe options and risky, variable options (De Petrillo, Ventricelli, Ponsi, & Addressi, 2015). The study involved three conditions varying in the probability of receiving either a seven-item or a one-item outcome when selecting the risky option: (1) Neutral: the individual had the same probability of receiving either a seven-item or a one-item outcome; (2) Advantageous: the individual had 2/3 probability of receiving a seven-item outcome; (3) Disadvantageous: the individual had 1/3 probability of receiving a seven-item outcome. In each trial we scored, for each individual, Latency to choose, Scratching behaviour (a self-directed behaviour that indexes emotional states related to motivational conflict or anxiety, Maestripieri et al., 1992; Troisi, 2002; but see Neal & Caine, 2016) and Hiccup vocalizations (i.e. vocalizations produced by capuchins in stressful situations; Di Bitetti, 2001; Wheeler, 2010) that occurred before the subject made its choice. Then, after the choice outcome was revealed, we again scored Scratching and Hiccup vocalizations. We also scored Banging, a tantrum response to an unfavourable outcome. Moreover, we recorded Switching behaviour (i.e. if the subject attempted to modify the initial choice by selecting the previously unchosen option).

The first goal of our study was to examine whether capuchins anticipated negative consequences from their choices, as do humans (e.g. Bechara et al., 1997). Based on Davies et al.'s (2015) findings in chickens, we expected this was also the case for capuchins. The second goal was to evaluate whether capuchins exhibited emotional responses to different decision outcomes. As reported for apes (Rosati & Hare, 2013), we expected capuchins to exhibit more emotional responses after choosing the risky option and receiving a one-item outcome than after receiving a seven-item outcome or after choosing the constant four-item option. The third goal was to assess whether capuchins' motivation to choose the risky option and their emotional responses were modulated by the probability of 'winning' in the three conditions. Capuchins preferred the risky option in both the Advantageous and Neutral conditions and had no preference for either option in the Disadvantageous condition (De Petrillo, Ventricelli et al., 2015). Thus, we expected them to be similarly motivated towards both choice options and their emotional responses not to be consistently affected by condition. Finally, the fourth goal was to test whether capuchins' emotional responses shown after receiving the choice outcomes affected their subsequent decisions on a trial-by-trial basis, as advocated by Rosati and Hare (2013). Similar to what has been observed in humans (Lerner & Keltner, 2001; Maner et al., 2007), we expected a behavioural response indicative of anxiety (Scratching) to be related to increased risk aversion, and vocalizations probably indicating frustration (Hiccups, Di Bitetti, 2001; Wheeler, 2010) to be related to increased risk proneness.

Capuchin monkeys are an ideal candidate for this investigation since, in the probabilistic choice task described in De Petrillo, Ventricelli et al. (2015), they showed a similar pattern of risk preferences to chimpanzees (Heilbronner, Rosati, Stevens, Hare, & Hauser, 2008) when the expected values of the safe and risky options were the same. Thus, we evaluated whether Rosati and Hare's (2013) findings in chimpanzees (reported above) could be replicated and extended in a distantly related primate species showing the same attitude towards probabilistic rewards.

METHODS

Ethical Note

The data originally collected for this study complied with protocols approved by the Italian Health Ministry (DM 123/214-C to E.A.). All procedures were performed in full accordance with the

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