Research report

Social modulation of risky decision-making in rats (Rattus norvegicus) and tufted capuchin monkeys (Sapajus spp.)

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ABSTRACT

Both human and non-human animals frequently deal with risky decisions in a social environment. Nevertheless, the influence of the social context on decision-making has been scarcely investigated. Here, we evaluated for the first time whether the presence of a conspecific influences risk preferences in rats and in tufted capuchin monkeys. Subjects received a series of choices between a constant, safe option and a variable, risky option, both alone (Alone condition) and when paired with a conspecific (Paired condition). The average payoff of the risky option was always lower than that of the safe option. Overall, the two species differed in their attitude towards risk: whereas rats were indifferent between options, capuchins exhibited a preference for the safe option. In both species, risk preferences changed in the Paired condition compared to the Alone condition, although in an opposite way. Whereas rats increased their risk preferences over time when paired with a conspecific, capuchins chose the risky option less in the Paired condition than in the Alone condition. Moreover, whereas anxiety-like behaviours decreased across sessions in rats, these behaviours where more represented in the Paired condition than in the Alone condition in capuchins. Thus, our findings extend to two distantly-related non-human species the evidence, so far available for human beings, that a decrease in anxiety corresponds to an increase in risk preferences, and vice versa. This suggests that the modulation of risk preferences by social influences observed in rats and capuchin monkeys may rely on a common, evolutionarily ancient, mechanism.

1. Introduction

In view of the severe mental and social consequences of gambling disorder in humans (DSM-5, [1]), and the lack of evidence-based guidance for its treatment, it is urgent to deepen our understanding of this condition. In this respect, evidence obtained on non-human subjects is crucial for at least two reasons [2]. Firstly, comparative studies are essential to shed light on the evolutionary origins of human attitudes towards risk and, in this respect, several species have been studied extensively (rats, Rattus norvegicus; e.g., [3,4]; starlings, Sturnus vulgaris: [5]; pigeons, Columba livia; e.g., [6,7]; rhesus macaques, Macaca mulatta: e.g., [8]; capuchin monkeys, Sapajus spp.: [9–11]; great apes: [12,13]). Secondly, the development of refined protocols, aimed at reproducing gambling proneness in animal models, is fundamental to unravel the psychobiological underpinnings of human pathological gambling.

Not only factors such as age, sex, personality and genotype affect decision-making (i.e., the cognitive process resulting in the selection of a course of action among several alternative possibilities; e.g., [14,15]), but also the social environment plays a crucial role. The modulating role of the social environment on decision-making processes is explicated through (i) direct/indirect social influences (i.e., social facilitation, conformity, cooperation and competition), and (ii) social stress effects [14,15].

In humans, social influences play a powerful role in decision-making. Adult humans were more risk-seeking when choosing among...
lotteries with different risk levels in the presence of other people than alone [16], or when tested with a probabilistic choice questionnaire and offered the possibility of outperforming a social competitor [17]. Moreover, adult humans presented with a series of choices between a constant option and a variable option were more risk seeking when the experimenter made them believe that a person of equal social status was observing them and possibly competing for the same resource [18]. Furthermore, adolescents, young adults and adults made riskier decisions when in peer groups than alone and peer effects on risk taking were stronger among adolescents and young adults than adults [19], possibly because the presence of peers may render potentially risky activities far more rewarding for young people [20].

Also social stress effects influence decision-making. Social stressors may involve conflicts with conspecifics in the context of both dominance-submission interactions and competition over resources, when performing a task in front of conspecifics and if witnessing aggression [14]. Notably, van den Bos et al. [21] pointed out that social stress seemed to affect decision-making in a different way in paradigms where subjects were tested singly vs. paradigms involving social interaction. No animal studies have explicitly looked at the effects of social stress on decision-making. However, studies in rats where non-social stress paradigms were employed showed that, as in humans, stress disrupts reward-based decision-making [22,23].

Although the social context has an important role in modulating decision-making, to date, only one animal study, involving great apes, has investigated how social influences affect individual risk preferences [24]. Specifically, chimpanzees (Pan troglodytes) and bonobos (Pan paniscus) presented with a series of choices between a constant option (yielding an immediately preferred food item) and a variable option (yielding either a low-preferred or a high-preferred food item, with the same probability), chose the risky option more often in a competitive context than in a neutral context, whereas a play context did not increase risk proneness. However, it should be noted that such competitive interaction involved a human opponent and not a conspecific. Thus, further studies on the social modulation of risky decision-making in non-human animals in the presence of a conspecific are needed.

We addressed this issue in two mammalian species. Specifically, we investigated whether the presence of a conspecific (hystander) affected risk preferences and emotional responses in rats (Rattus norvegicus) and tufted capuchin monkeys (Sapajus spp.) by using a probabilistic choice task in which the focal subject could choose between a safe, constant option and a risky, variable option either alone or in view of a conspecific. We chose rats and capuchin monkeys because both are socially-living species, they make feeding decisions in the presence of others and the social context is known to influence their behaviour (e.g., [73,74]; for a review see [25]). Moreover, importantly for this study, the risk preferences of both species have been extensively investigated in previous research (e.g., [2,9–11,15,26–28]). We took great care in using as much as possible a common methodology, by employing the same food comparisons and probability associated to the larger option, and testing individuals belonging to both species in the first part of their diurnal cycle (i.e., maintaining rats on a 12-h reversed light/dark cycle). Notwithstanding, it was inevitable to introduce some methodological differences in the experimental procedure (e.g., automated vs. non-automated task administration) to account for the different testing experience of the two species.

We aimed to fulfill the following goals. First, we evaluated whether subjects modulated their decisions and exhibited different behavioural responses based on the outcome of their previous choices. We expected them to show more negative emotional responses after choosing the risky option and receiving one food item than after choosing a risky option and receiving seven food items or after choosing a safe option, as recently reported for individually tested capuchin monkeys [10]. Second, we evaluated whether the social environment could modulate subjects’ risk preferences and emotional responses. By comparing two distantly related mammal species, we aimed to uncover whether this modulation was mediated by similar behavioural mechanisms. As both rats and capuchin monkeys are socially-living species whose eating behaviour is socially-facilitated (e.g., [73,74]), we expected social influences to affect their choice behaviour. On the basis of the human literature [16–19] and of the only study currently available in non-human primates [24], we expected risk proneness to increase in the social context compared to the solo testing. In any case, the results of the present study will allow a better understanding of decision-making under risk in a more ecologically valid setting than the individual testing, which is commonly employed in captive non-human animals.

**Experiment 1. Social influences on risky decision-making in rats**

**2. Methods**

**2.1. Ethical note**

All experimental procedures were approved by the Institutional Animal Survey Board on behalf of the Italian Ministry of Health (DM 05/2014 B to GL) and performed in full accordance with the Directive 2010/63/EU on the protection of animals used for scientific purposes.

**2.2. Subjects and housing**

We tested 30 adult Wistar-Han male rats (Charles River, France) housed at the ISS (Rome, Italy). They belonged to two different cohorts (mean bodyweight of the 20 rats belonging to the first cohort before the beginning of the experiment 480.2 ± 8.4 g; mean bodyweight of the 10 rats belonging to the second cohort before the beginning of the experiment 728.8 ± 14.1 g; the difference in bodyweight between the two cohorts reflected an age difference, see the paragraph 2.4.2 for further details on the role played by rats belonging to the two different cohorts). All animals were accommodated in pairs (by maintaining the two cohorts separated) inside polycarbonate cages (42.5 × 26.6 × 18.5 cm) with sawdust bedding, in an air-conditioned room (temperature 21 ± 1°C, relative humidity 60 ± 10%), on a 12-h reversed light/dark cycle (lights off at 8:00 a.m.). Water was always available ad libitum, whereas food (Altromin-R, A. Rieper S.p.A., Vandoies, Italy) was available ad libitum until the start of the experiment, when a mild food restriction was imposed to increase the animal’s motivation to work for food delivery. This mild food restriction was applied to all 30 rats involved in the experiment, regardless of the role played. In order to allow the mean bodyweight of animals to remain constant (90–95% of the free feeding bodyweight) over the sessions, rats were given an appropriate amount of standard food at around 4:30 p.m., after testing was completed. All rats were weighted throughout the experiment on a regular basis. The food-restriction schedule was continued seven days a week.

**2.3. Apparatus**

As shown in Fig. 1, the testing apparatus consisted of two computer-controlled operant panels (44 × 30 × 15 cm; “HOPs”, PRS Italia, Rome, Italy; [29,30]) placed, one opposite the other, in a black PVC box (66 × 44 × 30 cm) equipped with a transparent cover. Each panel occupied four-tenths of the total living area. Each operant panel was provided with two nose-poking holes (one on each side), two purple hole lights above them, a single white house-light placed in the top middle of the panel, a feeder device, two food magazines (next to each hole, with magazine lights) where palatable pellets (45 mg, F0021, BioServ, Frenchtown, NJ, USA) were delivered. The panels were connected through an interface to a computer, where a software (“SK020”, PRS Italia, Rome, Italy) controlled and recorded all events. Additionally, a SONY video camera (DCR-SX21E) was positioned above and at approximately 90° to the apparatus to allow for video recording of subjects’ behaviour.
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