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Male rats play a repeated donation game

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HIGHLIGHTS

- Unrelated male Long-Evans rats will work for a partner in a repeated donation game.
- Rats make more responses for a cagemate vs another partner.
- After pairing with a cagemate partner, rats fail to take advantage of generous responses by a good stooge.

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ABSTRACT

While previous studies have demonstrated direct and generalized reciprocity in female Norway rats [26], the present study determined if unrelated male laboratory rats respond on behalf of a partner in an iterated sequential game. Pairs of rats worked for food reward in an operant chamber, where participants alternated as Donor and Responder in successive trials. In each trial, the Donor chose between variable and constant reward levers, where the constant reward lever delivered 1 pellet, and the variable reward lever triggered insertion of Responder lever(s); the Donor received 2 pellets when the Responder made any response. In forced-choice constant (FC) trials, the Responder also received 1 pellet for responding on the constant reward lever. In forced-choice variable (FV) trials, the Responder received no pellets for responding on the variable reward lever. In free-choice (FR) trials, the Responder chose between constant (1 pellet) and variable reward levers (0 pellets). With their cagemate, rats earned 61.4 ± 2.0 pellets ($64.0 \pm 2.1\%$ of 96 possible pellets). As Donor in FC trials, rats preferred the variable reward lever, and the Responder responded frequently. In FV trials, Donor preference for the variable reward lever declined as Responder lever responses decreased. In FR trials, rats alternated responding on variable and constant reward levers as Donor and Responder, respectively. When paired with a new partner, there was no effect on Donor responses, but responses by the Responder decreased in the FV block. Similar effects were observed when paired with a maximally-cooperative stooge. Importantly, rats did not adjust their behavior as Donor to receive more pellets. Results suggest that unrelated male rats will work on behalf of a partner, and that their behavior is sensitive to familiarity, and to cooperative responses by their partner.

1. Introduction

Life in a complex environment presents frequent opportunities to choose among options with varying amounts of risk and reward. Financial investors use the risk/reward ratio to estimate monetary gains from a particular investment relative to the likelihood of realizing those gains. Animals make similar decisions about food. Studies in laboratory animals have elaborated the brain circuits and signals that shape decision-making for food under conditions of uncertainty, punishment and delay [11]. Although laboratory animal tests of decision-making do not typically incorporate social interactions, some risks involve a social dimension. Animals may compete with conspecifics for access to scarce resources (food, sexual partners), risking injury from aggressive encounters. In other settings, they may benefit from cooperation, either for food (cooperative hunting in carnivores) or defense from predators (mobbing in birds [4]). Kin selection and reciprocal altruism have been proposed to explain how cooperation develops (see Ale et al. [2]). Kinship can promote cooperation when the benefit to the recipient increases the evolutionary fitness of the donor [13]. Reciprocal altruism can promote cooperation when long-term benefits accrue to partners interacting repeatedly [34]. The present study tests cooperation in pairs of rats working for food reward in a repeated donation game [14].

Laboratory investigations often simplify social risk-taking to pairs of conspecifics [3]. Prisoner's Dilemma is a classic pair-wise game that is symmetric and simultaneous, where players always play the same

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role, and do not have knowledge of the actions of their partner [19]. The iterated Prisoner's Dilemma (IPD) tests participants in repeated multiple rounds with the same partners [24], to allow for development and expression of cooperative responses. We recently used an operant model of IPD to test cooperation in pairs of rats [39]. In our study, cooperative responses varied with food availability, and among pairs of rats. However, sustained mutual cooperation in animal models of IPD is challenging because participants learn the payoffs from mutual cooperation, mutual defection, and unilateral defection through trial-and-error in successive rounds, and each participant responds without knowledge of their partner's decision in that round. Furthermore, defection is a tempting choice because unilateral defection offers the largest individual payoff. Accordingly, using calculated reciprocity as a successful IPD strategy requires that participants infer the payoff matrix and choose a response based on an expectation of their partner's decision. In this regard, our rats did not appear to follow strategies such as tit-for-tat [3] or win-stay, lose-shift [22]. Similar results have been obtained in previous IPD studies of birds [33].

Not all cooperative games are simultaneous. Cooperation may also be expressed over a 2-turn cycle. This is relevant to mutual grooming practiced in many species [10], and implied in the popular saying, “you scratch my back, and I'll scratch yours”. When a sequential game is played in repeated trials, participants can observe their partner's decision in the previous round, and adjust their behavior accordingly [36]. Direct reciprocity, where participants take turns responding to deliver a reward to their partner, is a simple form of sequential cooperative behavior. Direct reciprocity has been demonstrated in female Norway rats working to deliver food reward to a partner [26]. Female rats also show generalized reciprocity, where a participant who has previously received assistance works to deliver food reward to an unfamiliar partner [26].

The present study extends these earlier findings to evaluate reciprocity in male laboratory rats in a repeated donation game. Compared with females, male rats show more territorial aggression [1], which could reduce cooperative behavior. Compared with wild rats, laboratory rats show more proximity and play behavior as juveniles [16], but spatial memory is similar (Harker and Whishaw, 2013). Our model is a game because the first participant (Donor) chooses between two levers, and maximizes his reward by anticipating the response of his partner (Responder). Initially, we tested pairs of rats with their cagemate to determine if they could make appropriate responses to obtain pellets under 3 experimental blocks offering different Responder lever choices. Subsequently, each rat was tested either with another trained rat or with a maximally-cooperative partner (good stooge). We predicted that rats would show more cooperative responses when paired with their cagemate vs a non-cagemate partner. In particular, rats should show greater sensitivity to trial losses and partner omissions with a non-cagemate partner. When paired with a good stooge, we further predicted that rats would change their responses to maximize pellets gained.

2. Materials and methods

2.1. Animals

Thirteen pairs of adult male Long-Evans rats ($n = 26$; 200 g BW at the start of the study) were purchased from a commercial supplier (Charles River Laboratories, MA) and pair-housed randomly under a reversed 14L:10D photoperiod. Rats were maintained on a slow rate of growth (3–4 g/day) during training, as in Cooper et al. [6]. Behavior was tested under dim light during the first 4 h of the dark phase. Experimental procedures were approved by USC's Institutional Animal Care and Use Committee and were conducted in accordance with the Guide for the Care and Use of Laboratory Animals, 8th Ed (National Research Council, National Academies Press, Washington DC; 2011).

2.2. Operant chambers

Training and testing were conducted in operant conditioning chambers controlled by WMPC software (Med Associates, VT), and enclosed in sound-attenuating boxes with fans for ventilation. As in Wood et al. [39], operant chambers were divided in half by a mesh screen. Each side of the chamber was equipped with two retractable levers and stimulus lights flanking a food trough connected to a pellet dispenser (Fig. 1A). A house light and clicker were mounted in the center of the ceiling.

2.3. The repeated donation game

2.3.1. Cagemates

Initially, rats were trained individually in reward discrimination, as in Wood et al. [39]. Stimulus lights above each lever were illuminated for 2 s before the levers were inserted. Rats had 5 s to respond before the levers retracted, stimulus lights were extinguished, and the trial was scored as an omission. A response on the constant reward lever (constant lever) delivered one 45-mg sucrose pellet (Bio-Serv, Flemington, NJ), while a response on the variable reward lever (variable lever) delivered 2 pellets. Pellets were dispensed every 0.5 s, and an audible clicker on the cage top signified each pellet entry into a food trough. The house light was illuminated while pellets were delivered, and remained lit during the 30-sec intertrial interval (ITI). Training included 24 trials/day, and continued until rats selected the variable

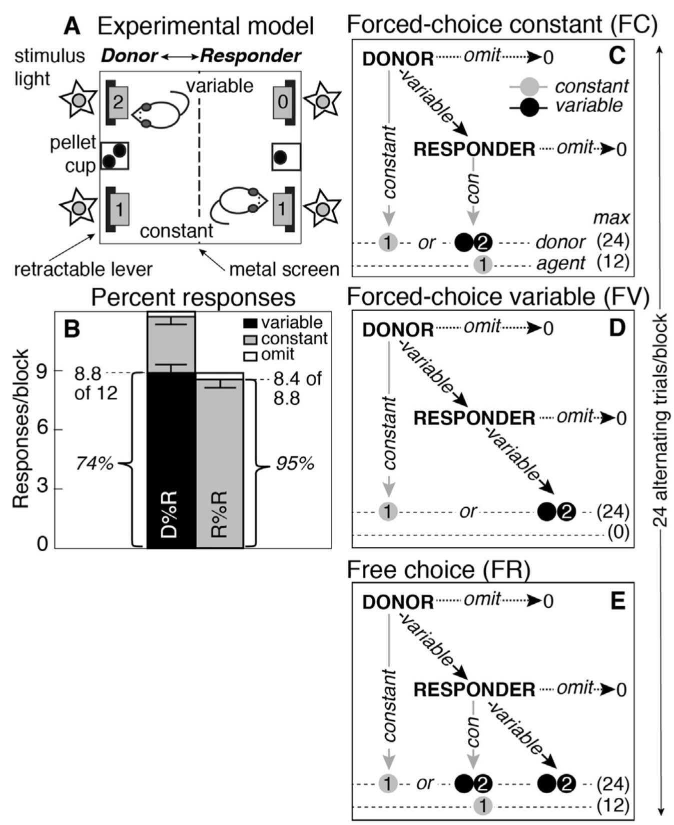

Fig. 1. A: The repeated donation game tests 2 rats in an operant chamber separated by a metal screen, with 2 retractable levers and stimulus lights flanking a pellet cup on each side. Pairs of rats are tested in 3 blocks of 24 trials each, serving as Donor and Responder in alternate trials. See Materials and methods for details. B: Percent responses by Donor and Responder calculated from responses in forced-choice constant (FC) trials with a cagemate. *Closed bars* indicate responses on the variable reward lever, *shaded bars* indicate responses on the constant reward lever, and *open bars* indicate response omissions. C–E: Lever options and pellets delivered for forced-choice constant (C; FC), forced-choice variable (D; FV), and free-choice (E; FR) blocks. Pellets delivered to Donor from a response on the variable lever are in *closed circles*; pellets delivered from a response on the constant lever are in *shaded circles*.