Cooperation in rats playing the iterated Prisoner's Dilemma game

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Humans and animals show cooperative behaviour, but our understanding of cooperation among unrelated laboratory animals is limited. A classic test of cooperation is the iterated Prisoner's Dilemma (IPD) game, where two players receive varying payoffs for cooperation or defection in repeated trials. To determine whether unrelated rats cooperate in the IPD, we tested pairs of rats making operant responses to earn food reward in 25 trials/day. The operant chamber was bisected by a metal screen with a retractable lever and pellet dispenser on each side. When levers extended, rats had 2 s to respond. Mutual cooperation (Reward) delivered three pellets each, mutual defection (Punishment) provided no pellets, and unilateral defection (Temptation) gave five pellets to the defector, while the partner (Sucker) received none. In eight pairs of males (RM−) and females (RF−), cooperation was defined by withholding a response. In seven pairs of RM+ males, cooperation was defined by responding on the lever. In males, food restriction significantly inhibited both cooperation and pellets received. There was no effect of dominance status. Males and females made similar numbers of responses under ad libitum feeding. However, neither food restriction nor dominance status affected responses in females. Rats were subsequently tested for reciprocity in 24 alternating trials/day. A response on the lever within 5 s delivered three pellets to the partner. Females made significantly more responses for their cage-mate than males. Responses within pairs were significantly correlated for males, but not for females. For both sexes, responses declined significantly when paired with an unfamiliar partner who never reciprocated ('bad stooge'). These results demonstrate that rats working for food show cooperation in IPD and direct reciprocity. Their responses depend on food availability and responses of their partner.
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There is a long history of efforts to understand cooperative behaviour, because cooperation is an important dimension of social interactions in humans and animals. Cooperation can be understood from an economic perspective, where benefits to participants are measured in terms of resources gained or evolutionary fitness (see Schuster & Perelberg, 2004). Cooperation can also involve cognitive and emotional elements, including responses to risk and reward (Rilling, 2011). To explore neural mechanisms underlying cooperative behaviour in laboratory animals, new experimental models must be developed. Studies in laboratory animals have already elaborated brain circuits and signals that shape decision making under conditions of uncertainty, punishment and delay (Floresco, St Onge, Ghods-Sharifi, Winstanley, 2008). Although laboratory animal tests of decision making do not typically incorporate social interactions, social decision making is an important

component of cooperative behaviour. In particular, individual participants can increase their benefit or reduce their risks by 'gaming' the system. Thus, game theory has been used to model interactions among participants (humans, animals, organizations, governments) in potential cooperative interactions (Axelrod, 2006). The present study tested cooperation in pairs of unrelated rats in an operant model of the iterated Prisoner's Dilemma (IPD) game and in a test of direct reciprocity.

Kin selection and reciprocal altruism have been proposed to explain how cooperation develops (see Ale, Brown, & Sullivan, 2013). Kinship can promote cooperation when the benefit to the recipient increases the evolutionary fitness of the donor (Hamilton, 1964). Reciprocal altruism can promote cooperation when long-term benefits accrue to partners interacting repeatedly (Trivers, 1971). Field studies describe the flexible interplay of multiple partners working for rewards and punishments among social animals living in complex environments. However, the sheer complexity of such interactions makes it difficult to resolve the relative roles of kin selection and reciprocal altruism in understanding cooperative behaviour (Raihani & Bshary, 2011).

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Laboratory investigations of cooperation often simplify the interactions to pairs of conspecifics (Axelrod, 2006). Pairwise games include the Prisoner's Dilemma, Hawk–Dove, and stag hunt. In their classic form, each of these games is both symmetric and simultaneous, where each player does not have knowledge of the actions of their partner. The games may be played in a single round, or may be repeated in multiple rounds with same partners, as in the IPD (Raihani & Bshary, 2011). While cooperation has been extensively studied in human laboratory tests (Melis & Semmann, 2010), there currently exist only a handful of laboratory studies of IPD in animals, and these differ in terms of animal species and experimental design. Additional studies will help to refine methods to test IPD in laboratory animals and provide insight into the limits of cooperative behaviour in animals. IPD tests reciprocal altruism, where a cooperative response by each participant benefits the recipient, while reducing the immediate benefit to the donor (Trivers, 1971). Like IPD, direct reciprocity is a dyadic interaction, representing the repeated reciprocal exchange of equivalent benefits between two parties. When delivering a benefit to their partner, each participant experiences a temporary net cost, which is exceeded by the benefit they subsequently receive from a partner working on their behalf (Nowak, 2006). Direct reciprocity is distinguished from generalized reciprocity, where one party offers benefits without expectation of return, or pseudoreciprocity, where actions initiated by one party produce self-interested behaviour by the other party that conveys benefits to initiator (Connor, 2010).

Testing participants in repeated trials, as with IPD, allows for development and expression of cooperative responses. Cooperation in a symmetric and simultaneous game such as IPD is limited by the cognitive abilities of the participants. The specific cognitive requirements for cooperation are not yet established. At a minimum, they include individual recognition, communication (Lopuch & Popik, 2011), as well as elements of cognitive flexibility (Floresco, 2013). Rats are social animals that possess these basic capabilities (Schuster & Perelberg, 2004). Unlike other recent animal models of IPD (St-Pierre, Larose, & Dubois, 2009; Stevens & Stephens, 2004; Viana, Gordo, Sucena, & Moita, 2010), the model used here requires that the participants make a decision quickly without information about their partner's choice, and the model can be repeated in multiple trials per session. We tested cooperation in male and female rats working for food reward, under both food restriction and ad libitum feeding. The hypothesis was that cooperative responses by pairs of rats playing IPD and direct reciprocity vary according to the sex, dominance status, familiarity and satiety of the participants. Specifically, we predicted that cooperation would be greater in females, in subordinate rats and among well-fed, familiar partners. We compared responses of individual rats in repeated trials against successful strategies, such as Tit for tat (Axelrod, 2006) and Pavlov (Nowak & Sigmund, 1993). We also measured the effects of dominance status and partner familiarity on cooperative responses.

METHODS

Animals

Adolescent male ($N = 32$) and female ($N = 16$) Long–Evans rats (6 weeks of age; ca. 200 g body weight at the start of the study; Charles River Laboratories, Wilmington, MA, U.S.A.) were pair-housed with a same-sex conspecific under a reversed 14:10 h light:dark cycle. To facilitate operant responding, male rats were maintained on a slow rate of growth (3–4 g/day) during training, as in Cooper, Goings, Kim, and Wood (2014). To eliminate cyclic fluctuations in ovarian steroid hormones and maintain chronic physiologic levels of oestrogen, female rats were ovariectomized via

bilateral dorsal flank incision, and received a subcutaneous 4 mm Silastic oestradiol implant (inner diameter: 1.98 mm; outer diameter: 3.18 mm; Dow Corning, Midland, MI, U.S.A.; Bridges, 1984). Behaviour was tested under dim light during the first 4 h of the dark phase when activity peaks. Experimental procedures were approved by the University of Southern California's Institutional Animal Care and Use Committee (protocol number 11773) and were conducted in accordance with the animal care guidelines of the National Research Council (2011).

Operant Chambers

Training and testing were conducted in operant conditioning chambers controlled by WMPC software (Med Associates, Fairfax, VT, U.S.A.), and enclosed in sound-attenuating boxes with fans for ventilation. Operant chambers were divided in half by a removable mesh screen. Each side of the chamber was equipped with a retractable lever and stimulus light adjacent to a food trough connected to a pellet dispenser. A house light and clicker were mounted in the centre of the ceiling.

Training

Rats were trained individually to respond on the lever to receive 45 mg sucrose pellets (Bio-Serv Inc., Frenchtown, NJ, U.S.A.). They were habituated to lever insertion in daily 20 min sessions. Each trial began in darkness with the lever retracted in the intertrial interval (ITI) state. The stimulus light was illuminated 2 s before the lever was inserted into the chamber. Rats were required to press the lever within 10 s to receive a sucrose pellet, after which the lever retracted, the stimulus light turned off and the house-light was illuminated for 30 s. If a rat failed to respond within 10 s, the chamber reverted to ITI and the trial was counted as an omission. The response time was gradually decreased to 5 s, and then to 2 s. Final trial duration was 34 s. All rats met a criterion of 25 responses per 20 min session (35 trials) for 2 consecutive days before behavioural testing began.

Iterated Prisoner's Dilemma

Once both cage-mates were trained, they were tested as pairs in daily sessions of 25 trials each. At the start of each trial, stimulus lights were illuminated for 2 s before levers were inserted on both sides of the chamber. Rats had 2 s to respond before the levers retracted, and the house-light was illuminated for 30 s. For trial outcomes where pellets were delivered (mutual cooperation, unilateral defection), pellets were dispensed every 0.5 s, and an audible clicker on the cage top signified each pellet entry into a food trough so that both rats could recognize when pellets were delivered.

On every trial, each rat chooses to cooperate or defect. As defined by Rapoport and Chammah (1965), mutual cooperation is represented as Reward, unilateral defection is Temptation/Sucker and mutual defection is Punishment. For RM– male and RF– female rats ($N = 8$ pairs each), cooperation was signified by withholding a lever response (Reward–; Fig. 1a, left). Each rat received three pellets (Reward) on trials when both rats refrained from pressing their lever. They received no pellets on trials when both pressed their levers (Punishment). When one rat pressed a lever (Temptation) while the cage-mate refrained (Sucker), the Temptation rat received five pellets and the Sucker received none. In terms of pellets earned, Temptation > Reward > Punishment = Sucker. Because rats receive equal numbers of pellets with Punishment or Sucker, the payoff matrix is a weak Prisoner's Dilemma (Kuhn, 2014). However, the Sucker could hear and see the Temptation