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Conditions for Cooperation between Rats

in the Prisoner's Dilemma Model

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Abstract

Reciprocal cooperation is the act of working together with another individual to increase the

likelihood that the other individual will continue to work together during future encounters.

Reciprocal cooperation can be explained evolutionarily because it promotes the fitness of

individuals in certain conditions. Cooperation is most commonly studied in humans. However

less complex mammals such as rats display cooperative behaviors in certain conditions. This

study examines the necessary conditions for cooperation in rats by testing the significance of

housing conditions and prior interactions between cooperating rats. We found that rats did not

cooperate at levels greater than chance.

Cooperation is defined as one organism working together with another organism and may potentially entail an immediate cost to the helping individual (Dawkins, 1976). Cooperation is important for two main reasons. First, it is an important strategy for natural selection. Secondly, cooperation is important because as people, we greatly value cooperation in the workplace, in schools, and in society. Studying cooperation is important because if we better understand what factors influence it, then we can maximize the amount of cooperation that naturally occurs in everyday life.

Cooperation becomes a beneficial strategy for enhancing survival ability when interactions between individuals are likely to reoccur. In situations where interactions between individuals are unlikely to reoccur, cooperation becomes a less powerful strategy and competition is emphasized (Axelrod & Hamilton, 1981). According to Dawkins (1976), vampire bats display cooperative behavior amongst individuals they frequently interact with. Vampire bats commonly regurgitate blood to bats that have not fed that night. While this comes at an immediate cost to the regurgitater, it helps to ensure the reciprocity of the other bat in case the regurgitater does not find food on a future night (Dawkins, 1976).

Cooperation is routinely assessed in many forms, the most salient example being the Prisoner's Dilemma. The Prisoner's Dilemma is a game between two individuals (Axelrod & Hamilton, 1981). This situation goes as follows: two people are charged with a crime. They are interrogated separately and can either confess or deny committing the crime, and the level of punishment varies based upon degree of cooperation. Axelrod and Hamilton set out to determine whether cooperation was an evolutionarily plausible strategy in the presence of competition (1981). They used the Iterated Prisoner's Dilemma model to create a situation to test different

strategies of competition and cooperation. The Iterated Prisoner's Dilemma (IPD) is simply the Prisoner's Dilemma game played multiple times with the same partner. In Axelrod and Hamilton's experiment, the game was simulated on computers. Programmers and mathematicians submitted their different strategies to compete against each other. The two "individuals" each simultaneously have the option to either cooperate or defect. If both choose to cooperate, then the players each receive three points. If both players defect, then each player receives one point. However, if one player defects and the other cooperates, then the defecting player gets a greater reward of five points and the cooperating player gets zero points. Analogously, if both prisoners in our human scenario choose cooperation, they avoid prison.

Likewise, in the iterated Prisoner's Dilemma, the best outcome for *both* players combined is if both players cooperate throughout the game. However, from the *individual's* perspective, if one can be assured that the other player will always cooperate, or if it is the last trial of the game, the individual fares best by defecting. Additionally, if both players defect continuously, the situation is optimal for neither player.

Among all the strategies in Axelrod and Hamilton's (1981) competition , one of the simplest strategies, Tit-for-Tat proved itself to be the strongest. The Tit-for-Tat strategy is simply to do exactly what the opposing member did in the previous trial. On the first trial, the Tit-for-Tat strategy begins with the assumption of cooperation. For example, let player one be using the Tit-for-Tat strategy. According to the traditional Tit-for-Tat strategy, player one should cooperate on the first trial. After that, the Tit-for-Tat player simply copies the last move of the opposing player.

After Tit-for-Tat won in the IPD game against all other competing strategies, Axelrod and Hamilton (1981) showed that the Tit-for-Tat strategy was "robust" because it survived by earning

a certain number of points per set of games among a variety of different strategies. After thousands of trials were run, the Tit-for-Tat programs were "surviving" above a certain level for the program to be declared "evolutionarily stable" in a situation where the majority of members use the Tit-for-Tat strategy. In real life, this means that in a population of individuals where resource patterns create a situation similar to the Prisoner's Dilemma, a likely pattern in behavior that might arise is the Tit-for-Tat version of cooperation regarding shared resources.

Evolutionary Stability means that the program can continue to survive and succeed in remaining the dominant strategy when other, non-Tit-For-Tat strategies emerge. Finally, Axelrod and Hamilton (1981) demonstrate that the Tit-For-Tat strategy is "initially viable", or able to succeed when introduced into a population of non-Tit-For-Tat strategies. These three factors, robustness, stability, and initial viability make the Tit-For-Tat strategy a legitimate possibility for a model of cooperation. Furthermore, the Tit-for-Tat strategy is the most well studied strategy relating to the social sciences for the Iterated Prisoner's Dilemma. It is also currently the strategy best studied in people and one of the two only Prisoner's Dilemma strategies studied in rodents. For these reasons, the Tit-for-Tat strategy is used for this study.

There is some evidence that rats are more likely to cooperate with individuals they have previously interacted with in a cooperative manner. Rutte and Taborsky (2008) had rats pull a stick to gain food access for another rat. They found that rats whose cage-mate pulled the stick to feed others were more likely to reciprocate the behavior than were rats whose non-cage-mate did not pull the stick. Furthermore, rats whose cage-mate pulled the stick were more likely to pull the stick for other unfamiliar rats, which is an example of generalized cooperation.

This current study aims to replicate and extend upon results from Viana (2010) by

demonstrating that under the specifications set by the Prisoner's Dilemma paradigm, test rats cooperate with an experimenter-controlled "dummy" rat playing according to the Tit-for-Tat strategy, at a level greater than would be expected by chance as was found by Viana (2010). Secondly, it is predicted, based on previous non-Prisoner's Dilemma research, that rats which are paired with cage-matess as opposing partner, will cooperate at higher levels than rats that have never met the opposing player (Rutte & Taborsky, 2008).

Methods

The basic design of this experiment is highly congruent to the previous prisoner dilemma studies using rats, particularly the Viana study (2010). Test rats were run through a double t-maze against a "dummy" rat. In a true prisoner's dilemma test, the rat would not be able to determine the location of the "dummy" rat before choosing an arm in the testing phase. In the Viana study, however, test rats could potentially see the arm occupied by the dummy rat through a clear door. To address this potential issue, the entry arm of the t-maze was lengthened and two sliding doors installed to prevent the rat from using the "dummy" rat's location as a visual cue to choose an arm. Scent cues were eliminated by thoroughly spraying and wiping down the maze in between animals with Nolvasan solution. Sound cues were minimized by playing a computerized soundtrack of white noise during all trials. One arm represents the choice to cooperate, the other arm of the maze represents the choice to defect. The arms were randomly assigned to pairs of rats so as to prevent side biases. The payoff matrix (Figure 1) shows the numbers of reinforcements or punishments given to the rat depending on which arm is chosen. Rewards were in the form of Fruit Loop segments. Aversive stimuli were in the form of short puffs of compressed air from a canister. A small pilot study with rats was run prior to the current study to

determine that using less aversive stimuli like puffs of air remain aversive for a period of several weeks. This is important because the Viana study used a much more aversive stimulus, tail-pinching.

Subjects:

The subjects were 15 male Sprague-Dawleys housed in pairs and given free access to food and water. The rats were housed in pairs because previous studies have found that rats are more likely to cooperate with each other and be less aggressive if housed together (Schuster, Berger, & Swanson, 1993). Rats were given free access to food and water, as satiation affects motivation in that food deprivation decreases the likelihood for rats to cooperate (Viana, Gordo, Sucena & Moita, 2010). All subjects were completely naive to conditions of the experiment. Five additional rats were assigned to the study as "dummy" rats. The dummy rat is placed by the experimenter in the cooperate or defect box according to the Tit-for-Tat strategy and the test rat's arm choices. Dummy rats were not reused as experimental rats in order to ensure that experimental rats did not develop learned helplessness during the "dummy" trials.

Out of the 15 initial experimental rats, three subjects were excluded based on failure to eat the Fruit Loops during trials after the acclimation phase.

Analyses:

Independent groups t-tests were used to compare the final stabilized cooperation level for rats in the *familiarity* versus *unfamiliarity* groups. The cooperation level will simply be the portion of the trials the experimental rat cooperates per set of trials. In addition to overall level of cooperation, levels of mutual cooperation, overall defection, and mutual defection were

compared. A Bonferroni correction (N = 32 tests) was employed to control for the amount of comparisons being performed.

Results

A paired t-test for percent of cooperative responses during the first and the last set of trials showed no significant difference ($p = 0.45$). While not significant, the later trials were slightly higher in cooperation than the initial trials. A paired t-test for cooperation levels across day one to day two shows no significant difference ($p = 0.18$). However, there is a greater increase across the two days than between the first day and the second day. Additionally, a paired t-test between the percent of cooperative responses during the first day and during the sum of the rest of the days is also not significant ($p = 0.23$). Furthermore, the decrease in mutual defection seen between the first and second day of testing and the first through the final day of testing were not significant ($p = 0.65$). To test the hypothesis that rats paired with cage-mates would cooperate more than rats cooperating with unfamiliar rats, unpaired t-tests were done and showed that there was no difference between groups on the final day of training or on the first day of training, ($p = 0.81$, $p = 0.76$). Additionally, it is interesting to note that rats did not mutually defect at levels greater than would be expected by chance ($p > .05$). This means that rats did not enter into what is know as a "defection loop", or a pattern of continually defecting. A Bonferroni correction was made (N = 32 tests) to account for multiple t-tests. Both with and without the correction, results were nonsignificant.

Discussion

These results suggest that there was no impact of familiarity on rats' level of cooperation in the Prisoner's Dilemma. Compared to Viana study (2010), the current experiment design differed in several important aspects. First, it was done over a more prolonged period; rats were trained and drug-tested over a period of two and a half months. The Viana study had a much smaller sample size, five rats, whereas the current study began with fifteen test rats. The sample size reduced to twelve after three rats were eliminated for failing to eat the reinforcements by the end of the first training day. While the larger sample size allowed for the potential for more power to detect results, it also led to the rats being tested every second to fourth day due to time constraints. Nonconsecutive test days may have led to decreased learning of the task in the test rats.

Additionally, unlike the Viana study, the test rats were trained to pass through a double-walled chamber before reaching the goal box of the double t-maze. This eliminated any visual cues a rat might utilize in choosing an arm. In the Viana study (2010), rats were run through a plexiglass maze that enabled rats to potentially see into the end box and determine placement of the dummy rat before choosing an arm to enter. In a true Prisoner's Dilemma task, players should have no interaction or cues from the opposing player between trials. Introducing additional information, such as visual cues regarding the dummy rat's cooperation status, changes the task from the Prisoner's Dilemma to a four category discrimination task.

Another element that is different is that the current study used adult rats slightly over one year old, whereas the Viana study used younger adolescent rats. Future studies need to be done to determine whether age is a significant variable in determining rats' willingness to cooperate in a

Prisoner's Dilemma type situation. It is possible that there is a critical period for learning cooperative tasks, and that the rats in the current study had passed that period. Specifically, research demonstrates that as rats age, they lose a significant amount of frontal cortical functioning (Barense, Fox, & Baxter, 2002). The Prisoner's Dilemma task is heavily dependent upon frontal lobe function for the initial acquisition of the task, and minor frontal lobe impairment may account for why the rats did not successfully learn to cooperate in the present study (Barense, Fox, & Baxter, 2002).

One difference between the Viana study and this current study that is not likely to have any impact is the type of punishment used. The Viana study used tail pinches with a forceps. Puffs of air from a compressed air canister was adopted as a less painful and more humane option than tail pinches. After a brief pilot study, it was determined that puffs of air from a compressed air canister were avoided and remained avoided for a period of several weeks. Rats continued to consider the air puffs as aversive as evidenced by increased sudden movement away from the puff of air and occasional defecation.

Limitations of the model:

The current study demonstrates some significant limitations of the rodent Iterated Prisoner's Dilemma model. First, testing may need to be done on consecutive days for cooperation to occur. Second, the role of visual cues in arm choice needs to be further investigated. Third, further testing needs to be done to determine if there is indeed an age effect on cooperative behavior in rats. Finally, it is not necessary to assume that because this study did not find rats to cooperate at levels greater than would be expected by chance, that rats do not

cooperate in the Prisoner's Dilemma. Intervening factors, such as rat age and nonconsecutive testing days may likely have limited results. Additionally, it would be erroneous to state that because the particular study suggested null results, that cooperation does not exist in rats, especially since previous studies have found otherwise (Viana, Gordo, Sucena, & Moita, 2010; Gardner et al., 1984).

It is, however, important to establish the conditions under which the Prisoner's Dilemma Tit-for-Tat condition lead to cooperation in order to develop a reliable and easily reproducible model for measuring cooperation in rodents. Once such a standardized model, including all necessary behavioral conditions for cooperation to hold, is established, the specific neurological factors that influence cooperation in rodents can be discerned. Because rodent models are the most common animal model for behavioral testing, it would greatly benefit the behavioral neuroscience field to have a standardized rat test for measuring cooperation.

The Prisoner's Dilemma model is useful, but perhaps not the ideal model for studying cooperation in rats. The model is effective in that it utilizes rats' natural foraging behavior. Additionally, the Prisoner's Dilemma model requires less extensive training compared to other rat cooperation tasks, which require more complicated behaviors such as pulling a string to give another rat access to food (Rutte & Taborsky, 2008). However, the current Prisoner's Dilemma model does have potential criticisms. The classic Tit-for-Tat strategy is not ideal. In computer models (Axelrod & Hamilton, 1981) the Tit-for-Tat strategy can result in what is known as a defection loop. This is when individuals get stuck in a pattern of repeatedly defecting in retaliation to a previous player's defection. Since animals and people are not always perfect responders, mistakes in responding can trigger the first few defections, which if both players are

using the Tit-for-Tat strategy will result in a never-ending series of defection. These unintentional responses or errors in responding are known as noise (Wu & Axelrod, 1995). Noise that results in defection will further the cycle of defection among Tit-For-Tat players. However, in the current study mutual defection was not shown to be above the level expected by chance. This means that the experimental rat did not enter defection loops with the dummy rat. It is possible that the experimental rats did not enter defection loops because they also make errors in favor of cooperation, not just defection. It is likely that some extent of the rat's behavior is purely due to chance mistakes, but unlike in computer models, our animal behavioral model does not result in excessive noise or defection loops. Thus, in the real world noise may actually resolve the potential issue of defection loops in the computer model of Tit-for-Tat.

Future Directions:

Another computerized strategy, *Pavlov*, is even more successful than Tit-for-Tat (Kraines & Kraines, 1987). *Pavlov* is a program that starts out with an equal probability of defecting or cooperating. The program "learns" to behave in a manner similar to operant conditioning. If a response results in a favorable outcome such as gaining points in the Prisoner's Dilemma game-a reinforcing event-then the response will become more likely in the future. Additionally, because *Pavlov* can differentiate between individuals, it can easily develop different response preferences to each individual. Because of this increased flexibility, the *Pavlov* strategy is more robust, or able to take advantage of the varying strategies, than is Tit-for-Tat, which allows *Pavlov* to succeed in all populations. Kraines and Kraines (1989) hypothesize that this this additional property makes *Pavlov* more representative of real world applications of cooperation than

Tit-for-Tat.

Because the *Pavlov* strategy more closely represents the strategy that is thought to occur in nature, it would be beneficial to test rats against a partner using the *Pavlov* strategy. Kraines and Kraines (1989) found that programs both following the *Pavlov* strategy learned to cooperate in the Tit-for-Tat fashion in the shortest number of trials when playing against a partner using the *Pavlov* strategy. Since our rats did not learn the cooperation task, perhaps using the *Pavlov* strategy to determine placement of the dummy rats would increase learning even with nonconsecutive training days.

Biological Basis of Cooperation:

The biological basis of cooperation has only recently begun to be examined. For the scientific study of cooperation to progress, more research on an animal model needs to be done to determine the best method through which to measure cooperation. Human behavior as complex as gambling has an accepted animal model (Bos, Lasthuis, Heijer, Johanneke, & Spruijt, 2006). At the present time, the Iterated Prisoner's Dilemma provides the best lens through which to examine cooperation in both humans and non-humans. Human studies have found that cooperation during the IPD activates the pleasure centers in our brains which in itself is rewarding (Shinsuke, Kazuhisa, Syoken, Akiyama & Eizo, 2011). Whether people are wired to cooperate because it is biologically rewarding, or whether the brain changes to find cooperation rewarding as a result of experience, still remains unknown. A recent review on hormones affecting cooperation elaborates on this problem of causality regarding hormones (Soares, Bshary, Fusani, Goymann, Hau, Hirschenhauser, & Oliveira, 2011). The authors

conclude that while both situations potentially occur, fluctuations in levels of neurohormones may account for fluctuations in cooperativity. Other longer term fluctuations in hormones can either enhance or hinder an organism's ability to cooperate. Specifically, vasopressin, a neurohormone released in the hypothalamus, is necessary for the recognition of familiar individuals, a skill which is a precursor for cooperation. Other relevant hormones include testosterone, which increases aggression and therefore decreases cooperation, and oxytocin, which decreases amydala activation and increases trust in cooperative games. There are mixed results over the cognitive effect of estrogens, and whether or not there is an influence on cooperation (Soares, Bshary, Fusani, Goymann, Hau, Hirschenhauser, & Oliveira 2011).

Conclusion:

This study's failure to show significant levels of reciprocity-based cooperation should not be construed as evidence that rats do not cooperate. Instead, it should be interpreted as possible limitations for cooperation among rats. Perhaps the frequency of training periods, or opportunities for cooperation, must be daily for rats to cooperate above chance. Further testing also needs to be done to determine if older rats show similar patterns of reciprocal cooperation both in natural and laboratory settings. After this basic research is done, it will be possible to interpret the impact of drugs and hormones on cooperative behavior, and the neurobiological mechanisms that control the behavior.

Overall, it is clear that standardized and easily replicable animal models of cooperation are currently lacking. Without these well-researched animal models for studying cooperation, there is still much about the field that remains unknown. This project sheds light on factors that

may influence the ability of animals to cooperate, and calls into question whether previous

studies are true examples of cooperation.

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	Dummy Cooperate	**Dummy Defect**
Test Rat Cooperate	Test: 2 Fruit Loops Dummy: 2 Fruit Loops	Test: 3 Puffs of Air Dummy: 3 Fruit Loops
Test Rat Defect	Test: 3 Fruit Loops Dummy: 3 Puffs of Air	Test: 1 Puff of Air Dummy: 1 Puff of Air

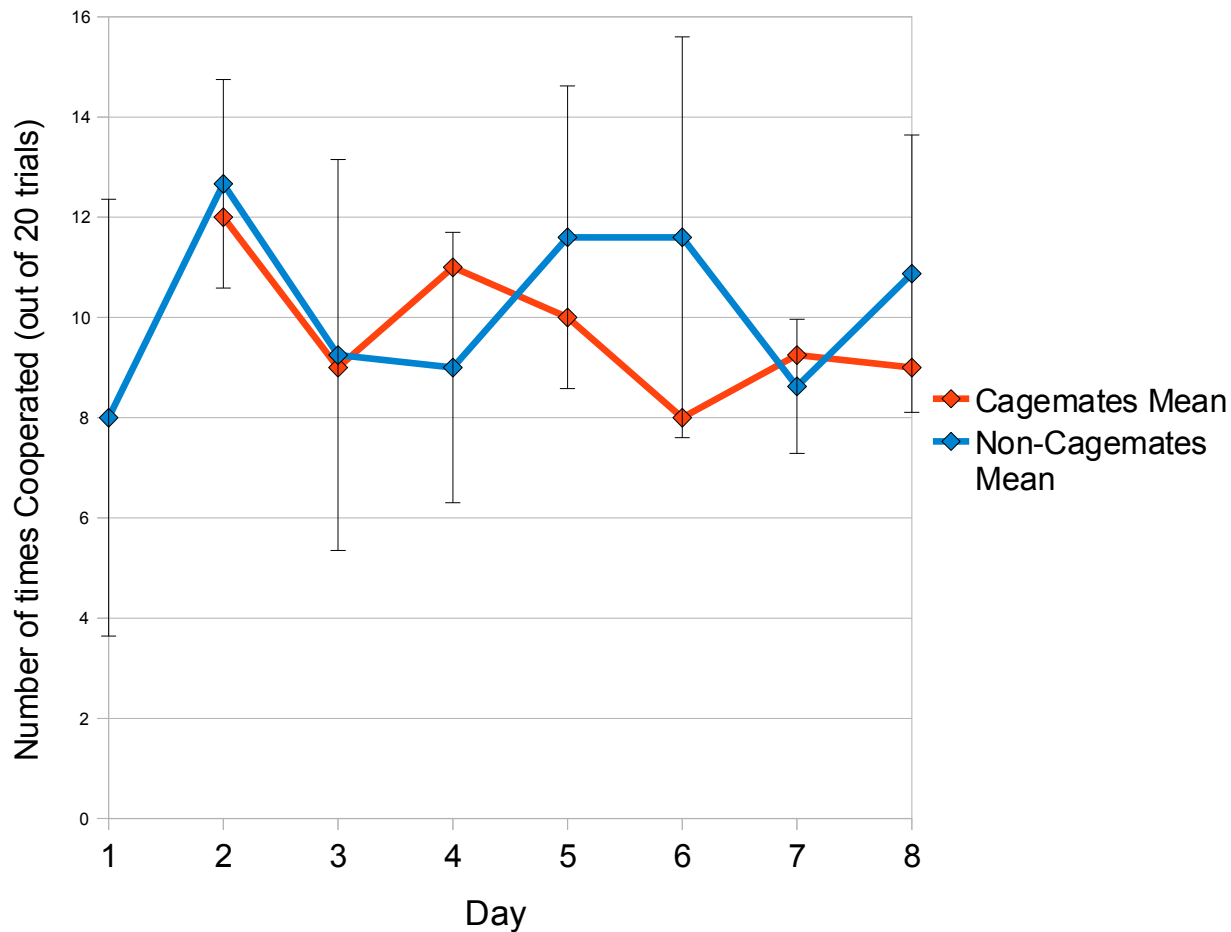Figure 1 shows the contingency matrix used for the rat Prisoner's Dilemma.

Figure 2 (above) shows the average levels of daily cooperation for cagemate pairs and non-cagemate pairs on the iterated Prisoner's Dilemma task
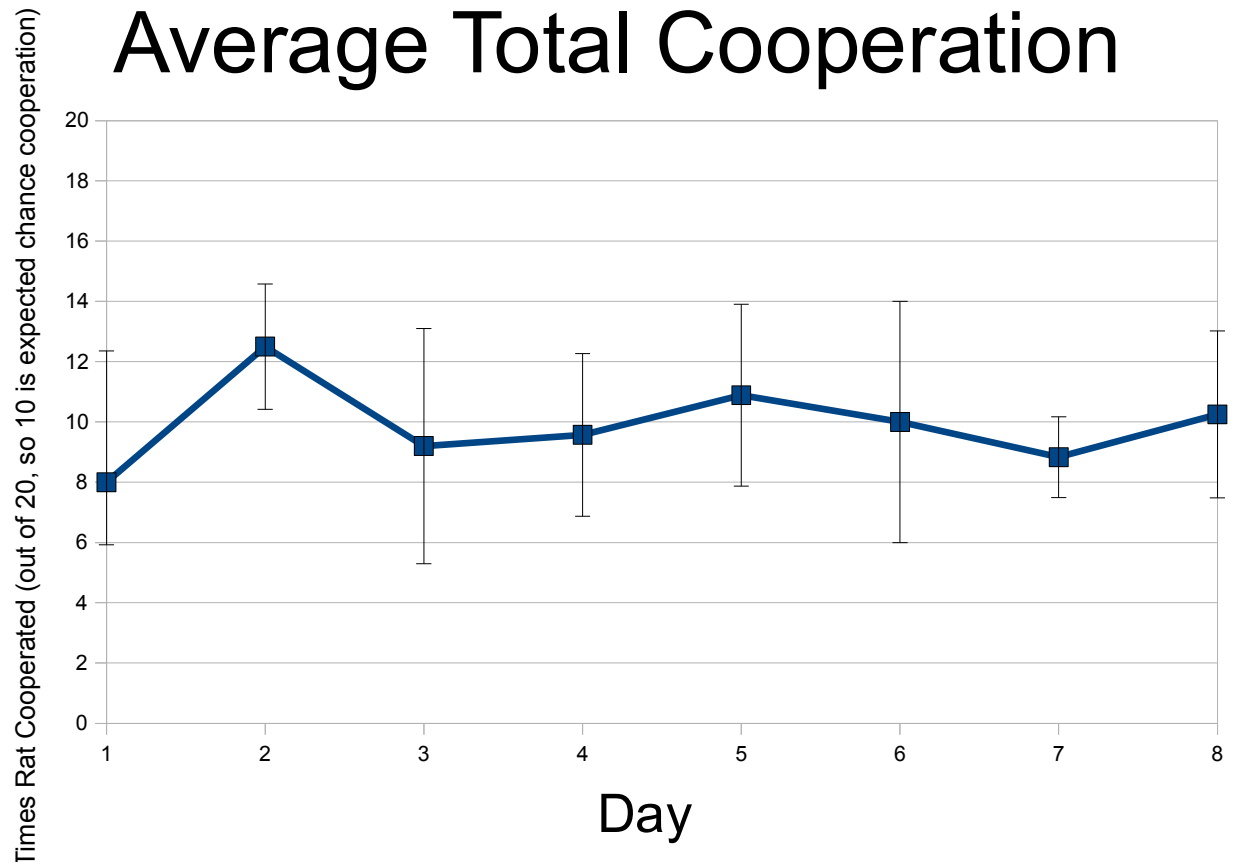
Figure 3 shows the average daily level of cooperation between all rat pairs. Rats cooperating ten times out of twenty are cooperating at levels expected by chance.