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THE PRISONER'S DILEMMA GAME AND COOPERATION IN THE RAT[1]

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Summary.—Cooperation in pairs of rats playing the prisoner's dilemma game was investigated. Six pairs of animals were taught to make either cooperative or uncooperative responses by running to one or the other end of a T-maze. Two T-mazes were joined together such that animals could respond simultaneously. Animals were run under conditions in which visual communication was present and absent. Mutually uncooperative responses were the most common and mutually cooperative behaviors the least preferred. Introduction of a barrier between the mazes, which removed visual communication between pairs, sharply accentuated uncooperative behavior. Similarities of the present findings to results with human subjects and the implications of using game theory for studying cooperative behavior in animals are discussed.

Much of the research on cooperative behaviors in rats has traditionally involved a task in which two animals must coordinate their behaviors to obtain a food reward. Despite the lack of evidence that rats cooperate in food gathering in the wild (Barnett & Spencer, 1951) several studies have purported to show that rats can learn to cooperate under special laboratory conditions. The most commonly cited research is that by Daniel (1942, 1947) in which rats learned to take turns at sitting on a platform so another rat could feed without being shocked. Mowrer (1940) has shown that one rat will work so both it and other rats may feed.

Other research has indicated the development of a worker-parasite relationship in tasks where in two hungry rats are placed in an operant situation with only one lever and one food trough separated at a distance such that the animal could not lever press and feed simultaneously (Mowrer, 1960; Baron & Littman, 1961; Oldfield-Box, 1967). The most common findings in these studies are that one rat does most of the work in pressing the lever while the other rat consumes the fruits of the labor. Some evidence exists that group-trained rats display more cooperation on such a task (Oldfield-Box, 1967).

It is unlikely that rats in a more natural setting are often in such an all-or-none situation. More likely cooperative behavior will sometimes lead to in-

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creased rewards and at other times will not. The outcome of cooperative response for rats, as with humans, is usually dependent upon the actions of the other animal as well. Cooperative behavior may sometimes lead to a smaller reward if the cooperation is not reciprocated by another subject. This fact has been clearly recognized in research on cooperation in human behavior and has led to the development of several games whereby each subject can make either cooperative or uncooperative responses with rewards dispensed according to both subjects' responses. Research with the prisoner's dilemma game typifies this approach.

The prisoner's dilemma is a game involving two people in which both stand to gain moderately if they trust each other to cooperate; on the other hand, if one of them makes the trusting response the other may gain a relatively large reward and simultaneously penalize his opponent by choosing an alternative, exploitative, or competitive response. Finally, if they both are competitive, they will both lose.

Game theory has been used extensively in studying cooperative/competitive aspects of human behavior. Colman (1982) reviews much of this research. There is growing recognition that game theory is also a useful model for studying cooperation and competition in animals. Maynard-Smith (1972) originally examined how game theory could be applied to the evolution of animal behavior. Maynard-Smith uses payoff matrices showing outcomes of various behavioral strategies, although he emphasizes that these strategies need not imply that animals are making rational decisions about what they do. The costs and benefits of each strategy are defined depending on what the other animal does. Many of the predictions arising from Maynard-Smith's models are borne out quite well in real life (Huntingford, 1982). This approach has now been fruitfully applied to a number of questions about competition (Maynard-Smith, 1979), the results of which are reviewed by Lazarus (1982). Lazarus concludes that the game theory approach is clearly an appropriate one, being a direct extension of the neo-Darwinian theory of natural selection. Lazarus further concludes further application of the approach to various aspects of competition as well as other types of social interaction is appropriate.

The present research utilizes a game-theory methodology to investigate cooperative/competitive tendencies in pairs of rats playing the prisoner's dilemma game during which both animals must cooperate to maximize their joint payoffs but where they may increase their own gains at the other animal's expense by being uncooperative. The situation was further structured such that if both animals were uncooperative their joint payoff would be less than if both had cooperated. The role of visual communication in cooperation was also investigated.

METHOD

Subjects

Twelve female albino rats weighing between 180 and 215 gm. were used. All subjects had been reduced to approximately 80% body weight prior to the experiment and were maintained at this weight throughout the experiment.

Apparatus

Fig. 1 illustrates the maze used in the present study. All components are of wood except the Plexiglas partition separating the two T-mazes and the Plexiglas sliding doors. The interior of the maze was painted flat gray. The maze consisted of a pair of start boxes (S), holding boxes (H), and goal boxes (G).

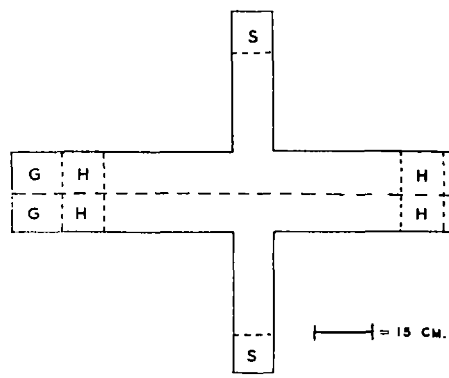

FIG. 1. Double T-mazes with start boxes (S), holding boxes (H), and goal boxes (G)

Procedure

The animals were taught to play a variation of the prisoner's dilemma game in which pairs of animals were run simultaneously with each animal having the capability of making a cooperative (C) or uncooperative (U) response, depending upon which goal box the animal ran to. If both animals made a cooperative response (CC) each received three 45-mg. Noyes food pellets in the goal box. If both made an uncooperative response (UU) only one pellet was delivered to each. In the event that one animal made a cooperative response while the other made an uncooperative response (CU or UC) the cooperative respondent received no pellets while the uncooperative animal received five pellets. The payoff contingencies are summarized in Table 1.

Three training procedures were used for each animal: maze familiarization, matrix training, and cooperation testing.

TABLE 1

PAYOFFS IN 45-MG. FOOD PELLETS FOR ALL COMBINATIONS OF COOPERATIVE AND UNCOOPERATIVE RESPONSES

Animal 1	Animal 2
C	C
+3	+3
C	U
0	+5
U	C
+5	0
U	U
+1	+1

Maze familiarization.—Animals were run singularly in one of the T-mazes constituting the maze. Each animal was run for 24 trials per day for 2 days. All doors leading to the goal boxes were open and animals were allowed to choose right or left running responses. The animals were randomly reinforced with three 45-mg. pellets for left- and right-running responses on a 50% schedule of reinforcement. This procedure served to familiarize the animals with the apparatus without differentially reinforcing right- or left-running behavior.

Matrix training.—The animals were taught the payoffs that occurred when all possible combinations of cooperative and uncooperative responses occurred (see Table 1). For one-half the animals running to the right-hand alley corresponded to a cooperative response and running to the left represented an uncooperative response. For the remaining one-half of the animals these designations were reversed. This procedure was designed to counterbalance the effects of any position preferences during cooperation testing. In addition, animals were paired such that for one-half the pairs running to contiguous goal boxes corresponded to either a CC or UU response while for the remaining one-half of the pairs such a response corresponded to a CU or UC response. Such a procedure controls for the tendency for the animals to follow one another into one or the other end of the maze during cooperation testing. Animals were run in pairs with animals being released simultaneously from their respective start boxes. The door to one of the holding boxes was left open while the other was closed, which forced each animal to make a right- or left-turning response of the experimenter's choosing. The doors to the holding boxes were arranged such that the pairs of animals were made to respond CC, UU, UC, and CU an equal number of times. As soon as both animals had entered the holding box, the appropriate reward was dispensed into the goal box and the animals were simultaneously released from the holding boxes into the goal boxes. Animals were simultaneously removed from the goal boxes upon consuming the pellets. Each pair of animals received three days of 24 trials of this matrix training procedure.

Cooperation testing.—The doors into both holding compartments remained open. Both animals were released simultaneously from the start box. The first respondent remained in its holding box until the other animal also entered a holding box at which time the appropriate number of food pellets was dispensed into the goal boxes. The animals were then simultaneously released from the holding boxes into the goal boxes. Each pair was run for 24 trials per day for 10 days at which time the Plexiglas partition separating the alleys was replaced with a cardboard barrier which extended between the entrances into each goal box. This barrier prevented an animal from observing the response of its partner until after the goal box had been entered. The animals were run an additional 10 days at 24 trials per day with this barrier in place.

RESULTS

Data were initially analyzed in terms of the responses made by each pair of rats and not by individual responses. On a given trial a pair could make a CC, UU, or CU/UC response. Fig. 2 illustrates the mean number of responses made in each of these three categories over days. Response categories CU and UC are essentially identical kinds of behaviors and have thus been com-

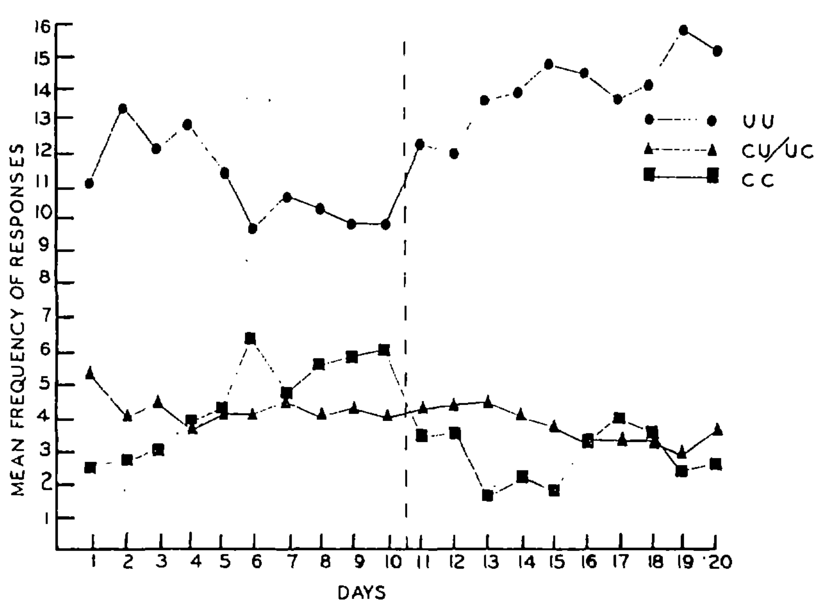

FIG. 2. Mean frequency of mutually uncooperative (UU), mutually cooperative (CC) responses. Visual communication between pairs was blocked on Days 11 to 20.

bined and averaged in Fig. 2. Inspection of Fig. 2 shows that the predominate mode of responding was the mutually uncooperative response. An analysis of variance indicated a significant difference between UU and CC responses on Days 1 to 10 ($F_{1,5} = 18.00$, $p < .01$) while no significant differences were obtained over days or in the interaction. A similar analysis between combined CU/UC responses and UU responses also indicated a significant difference ($F_{1,5} = 19.81$, $p < .01$) and a significant interaction ($F_{9,45} = 7.88$, $p < .01$) while no significant difference was obtained over days. Prior to introduction of the barrier, the preferred mode of responding was mutually uncooperative. An analysis of differences between CU/UC and CC responses indicated no significant differences in the main effects or interaction term.

On Days 11 to 20 a cardboard barrier separated the runways eliminating visual communication. Fig. 2 shows that the incidence of UU responses became accentuated with the introduction of the barrier while a concomitant decrease in CC responses is observed. The incidence of CU/UC behaviors appears little changed by the introduction of the barrier. An analysis of variance again indicated a significant difference between CC and UU responses ($F_{1,5} = 16.07$, $p < .02$) and between CU/UC and UU responses ($F_{1,5} = 35.82$, $p < .002$). In both cases there were significantly more mutually uncooperative (UU) responses. No significant differences were obtained between CU/UC and CC and no differences over days or interactions were significant.

A definitive statement regarding the effects of the barrier cannot be made without the relevant control group as the observed changes may merely be a reflection of changes in strategy over time. Nevertheless, the trend of UU responses from Days 1 to 10 shows a clear and fairly consistent decrease with a slope of $-.315$ while Days 11 to 20 show an increase in such responses with a slope of .272. A test of the difference between these two trends (Crow, Davis, & Maxfield, 1960) yielded a significant difference ($t_{116} = 2.19$, $p < .05$). A significant difference in trends is observed with and without visual communication capabilities. A similar analysis for both CC responses and CU/UC responses gave no significant differences between trends on the first and last 10 days, although the differences in trends of the CC data approached significance ($t_{116} = 1.66$, $p < .10$).

For each animal the latencies between leaving the start box and entering the holding box were recorded. For all pairs on all trials a record was made of which of the pairs responded, i.e., entered a holding box, first and what effects this had on the animal responding second. If the first animal makes a U response, the second animal has little choice but to respond the same way if he wishes to receive any reinforcement (Table 1). It is clear that, if the animals are affected by the payoff matrix, the animal responding second will avoid responding C after a U response by the animal responding first (U_1C)

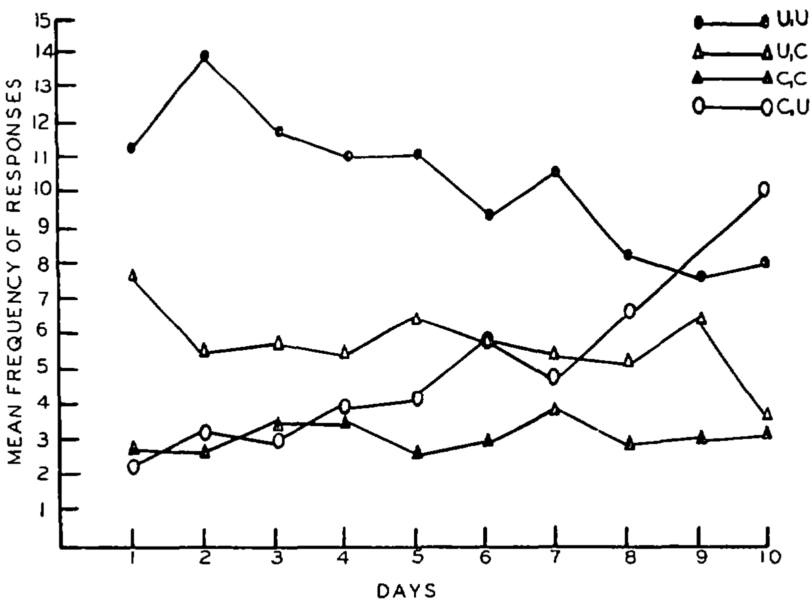

FIG. 3. Mean frequency of cooperative and uncooperative responses of second-responding animals following first-respondent's uncooperative (U_1C and U_1C) and cooperative (C_1C) responses

but would rather also respond uncooperatively (U_1U) to maximize the gain. Fig. 3 illustrates the mean frequencies of these two categories of responses as well as the case in which the first respondent makes a C response (C_1C and C_1U). Fig. 3 shows a consistently higher incidence of U_1U responses over U_1C responses as would be expected if the payoff was to be maximized. Chi-squared comparisons were made of the differences between these values for each of the first 10 days. If the animals were not affected by the payoff matrix or were not influenced by the other animal's response, then one would anticipate that it would make no difference how the first animal responded and one would expect an identical frequency of responding to both C and U. The chi-squared comparisons indicated that the tendency to respond U_1U over U_1C was significant on Days 2 ($\chi_1^2 = 13.84$, $p < .005$), 3 ($\chi_1^2 = 8.61$, $p < .005$), 4 ($\chi_1^2 = 7.04$, $p < .01$), 5 ($\chi_1^2 = 4.88$, $p < .05$), 7 ($\chi_1^2 = 6.11$, $p < .02$), and 10 ($\chi_1^2 = 4.08$, $p < .05$). Interestingly, the largest difference was obtained on Day 2 with differences being generally attenuated during the latter days of the experiment. Nevertheless, the relatively large and consistent differences in favor of U_1U responses is evidence that the animals were indeed influenced appropriately by the payoffs involved and responded to maximize their own payoff.

Fig. 3 also illustrates the effect of the first respondent making a C response.

In this situation the second respondent has the choice of also cooperating (C_1C—each will receive three pellets) or not cooperating (C_1U—the animal can maximize its own reward of five pellets while preventing the other animal any payoff). Fig. 3 shows that for the first four days both C_1C and C_1U occur equally frequently with an increasing tendency on later days to perform uncooperatively in such a situation. A significant difference was obtained on Day 8 only ($\chi_1^2 = 2.88, p < .02$).

Discussion

Several conclusions based on the present findings seem relevant. Perhaps of foremost importance is the demonstration that rats apparently possess the capability to respond appropriately in a fairly complex game-type situation in which the payoffs are affected not only by one's own responses but by responses of another animal as well. The data from the present study, specifically the first-choice data (Fig. 3) indicate the animals quickly begin responding appropriately according to the payoffs involved.

The findings suggest the rat is essentially an uncooperative organism. This finding is dissonant with some previous reseach findings (Daniel, 1942, 1947; Mowrer, 1940) which indicated that rats would cooperate for mutual gain. This discrepancy in findings can likely be accounted for by examination of payoff contingencies in the present research compared with previous work. In the earlier studies animals were in a situation in which if they did not cooperate with one another they would either receive no reward or would receive electric shock. The evidence seems conclusive that in such a situation animals will display cooperative behaviors. However, it seems such a contingency is rather artificial to the more naturalistic situation. Animals which hunt in packs are required to cooperate with one another although such cooperation may or may not lead to enhanced payoffs for a particular individual. An animal who helps in the kill may find the other animal(s) will reap the rewards and may not allow him to feed at all. This appears to parallel what happens in the present research when a C_1U response occurs. This may account for the fact that wild rats are not observed to cooperate in food-gathering activities in the wild (Barnett & Spencer, 1951).

Some interesting parallels are found in the way humans and rats play the prisoner's dilemma game. Scodel, Minas, Ratoosh, and Lipetz (1959) and Minas, Scodel, Marlowe, and Rawson (1960), among others, have shown that the level of cooperative responses in repeated prisoner dilemma games is low and decreasingly lower for later trials. A parallel finding exists in the present study, particularly on Days 11 to 20.

Hoerl (1972), as well as several other researchers, has found that anything which decreases communication between human players leads to increased frequencies of uncooperative behaviors. This same tendency is clearly displayed in the present findings where the placement of the barrier apparently was correlated with a sharp increase in uncooperative responses. The level of mutually cooperative responses remained low throughout the duration of the experiment.

The most "interesting" behaviors we observed are not reflected in any of the tables or graphs but rather must be classified as anecdotal. For instance, on Days 1 to 10, with the Plexiglas barrier in place so the animals could observe each others' responses, it was observed that the animals would rush from the start box and meet face to face at the Plexiglas. There they would undertake an interesting "dance" whereby they appeared to feint left- and right-turning responses in what appeared to be an attempt to influence the other animal into making a desired response. Often 15 to 20 sec. of this mutual feinting behavior would occur before one animal would finally respond.

Interesting behaviors were also observed in the holding boxes. Here animals who had responded first and had made a cooperative response and observed the other animal making an uncooperative response would frequently turn around and attempt to open the door to escape the holding box. No such behaviors were observed when the animals made mutually cooperative responses.

When the animals were released from the holding box into the goal box, we observed that the animals who had no reward coming (CU/UC responses) often did not even check the food dish in the goal box. Furthermore, animals in this situation would very often attempt to jump over the barrier into the other goal box when the top to the maze was lifted. They consistently displayed aggressive tendencies toward their uncooperative compatriot in this situation. Again, this behavior was not observed following UU and CC responses.

The present study illustrates the efficacy of using game theory in a laboratory setting to study cooperative and competitive behaviors in animals. While previous research has mainly used game theory to explain the evolution of animal behavior (Huntingford, 1982), the present study illustrates its usefulness in laboratory studies of competition and cooperation.

REFERENCES

BARNETT, S. A., & SPENCER, A. H. Rat populations and control in two English villages. *Annals of Applied Biology*, 1951, 38, 444-463.

BARON, A., & LITTMAN, R. A. Studies of individual and paired interactional problems solving behavior of rats: II. Solitary and social controls. *Genetic Psychology Monographs*, 1961, 64, 129-209.

COLMAN, A. M. (Ed.) *Cooperation and competition in humans and animals.* Berkshire, UK: Van Nostrand Reinhold (UK), 1982.

CROW, E. L., DAVIS, F. A., & MAXFIELD, M. W. *Statistics manual.* New York: Dover, 1960.

DANIEL, W. J. Cooperative problem solving in rats. *Journal of Comparative Psychology*, 1942, 34, 361-368.

DANIEL, W. J. How cooperatively do individual rats solve a problem in a social situation? *American Psychologist*, 1947, 2, 316.

HOERL, R. T. Cooperation and competition as a function of communication and trust. *Dissertation Abtracts International*, 1972, 33(3-B), 1287-1288. (University Microfilms No. 72-73, 952)

HUNTINGFORD, F. The evolution of cooperation and altruism. In A. M. Colman (Ed.), *Cooperation and competition in humans and animals*. Berkshire, UK: Van Nostrand Reinhold (UK), 1982. Pp. 3-25.

LAZARUS, J. Competition and conflict in animals. In A. M. Colman (Ed.), *Cooperation and competition in humans and animals*. Berkshire, UK: Van Nostrand Reinhold (UK), 1982. Pp. 26-56.

MAYNARD-SMITH, J. Game theory and the evolution of fighting. In J. Maynard-Smith, *On evolution*. Edinburgh: Edinburgh University Press, 1972.

MAYNARD-SMITH, J. Game theory and the evolution of behavior. *Proceedings of the Royal Society of London B*, 1979, 205, 475-488.

MINAS, J. S., SCODEL, A., MARLOWE, D., & RAWSON, H. Some descriptive aspects of two-person non-zero sum games: Part II. *Journal of Conflict Resolution*, 1960, 4, 193-197.

MOWRER, O. H. Animal studies in the genesis of personality. *Transcripts of the New York Academy of Sciences*, 1940, 3, 8-11.

MOWRER, O. H. *Learning theory and the symbolic processes*. New York: Wiley, 1960.

OLDFIELD-BOX, H. Social organization of rats in a social problem situation. *Nature*, 1967, 213, 533-534.

SCODEL, A., MINAS, J., RATOOSH, P., & LIPETZ, M. E. Some descriptive aspects of two-person non-zero sum games. *Journal of Conflict Resolution*, 1959, 3, 114-119.

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