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THE ROLE OF AUTOSHAPING IN COOPERATIVE TWO-PLAYER GAMES BETWEEN STARLINGS

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We report a study of the behavior of starlings in laboratory situations inspired by the "prisoner's dilemma." Our purpose is to investigate some possible mechanisms for the maintenance of cooperation by reciprocity and to investigate the process of autoshaping at a trial-by-trial level. In Experiment 1, pairs of starlings housed in adjacent cages played a discrete-trial "game" in which food could be obtained only by "cooperation." In this game, pecking at a response key eliminated the opportunity to obtain food but produced food for the partner. If neither bird pecked, neither had the opportunity to obtain food in that trial. Some level of cooperation persisted for several sessions whether the birds had been pretrained for a high or low probability of pecking at the key. The probability of a cooperative response was higher after trials in which the partner responded (and a reward was obtained) than after trials in which neither bird responded (and no reward was obtained), but the probability of a response was even higher after trials in which the same bird had responded, even though no reward was obtained by the actor in these trials. This behavior did not require visual presence of another player, because similar results were obtained in Experiment 2 (a replicate of Experiment 1 in which the members of the pair could not see each other) and in Experiment 3, a game in which each starling played with a computer responding with "tit for tat." Using an omission schedule, in which food was given in all trials in which the bird did not peck, Experiment 4 showed that pecking could be maintained by autoshaping. In this experiment, overall probability of pecking decreased with experience, due to a drop in the tendency to peck in consecutive trials. The probability of pecking in trials following a reinforced trial did not decrease with experience. An implementation of the Rescorla–Wagner model for this situation was capable of reproducing molar, but not molecular, aspects of our results. The results violate the predictions of several game-theoretical models for the evolution of cooperation, including tit for tat, generous tit for tat, and the superior win-stay-lose-shift.

Key words: autoshaping, cooperation, prisoner's dilemma, Rescorla–Wagner model, two-player games, tit for tat, key peck, starlings

Some actions result in benefits to individuals other than the actor. In a very general sense, these actions may be called "cooperative," without intending any attribution of further properties normally associated with cooperation. Among cooperative actions some also carry benefit to the actor (Type I), whereas others, at least prima facie, appear to benefit only other subjects (Type II). Although most cooperative actions in the real world are probably of Type I, these actions are unproblematic from an individual perspective, because their cooperative nature is normally interpreted as secondary to the reward to the actor. Type II actions are problematic and thus especially interesting, because without further elaboration they appear to be unaccounted for both in terms of the law of effect and in terms of natural selection.

In cooperative hunting, for example, a chimpanzee may surreptitiously approach a group of foraging colobus monkeys and suddenly switch to a conspicuous behavior that flushes a monkey towards a site where a second chimpanzee waits in ambush. The second animal may catch, kill, and start eating the prey (Boesch, 1990). This behavior would be biologically unaccounted for unless one could find that the first chimpanzee got a share of the prey, that it got a piece of another prey later on, that it got some other nonforaging benefit, or that both individuals are related. In all these cases the action is transformed into a Type I action, although when kinship is invoked it is not required that the actor receive any benefit: The genes that favor the inclination of the actor to behave cooperatively may be present in the

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receiver, and thus cooperative behavior may be sustained at the phylogenetic level.

Given their problematic nature, it is not surprising that there is a plethora of theoretical models that can transform the interpretation of Type II actions so as to place them in the Type I category and preserve theoretical consistency. These models have been expressed at ontogenetic and evolutionary levels (Axelrod & Hamilton, 1981; Godfray, 1992; Hamilton, 1964; Nowak, 1990; Nowak & Sigmund, 1992; Trivers, 1971), but little work has been done on psychological mechanisms that can account for the presence of behavior that, at least in the short term, benefits others at a cost to the actor.

We use a technical setting inspired by (but not identical to) the classical game known as the prisoner's dilemma (Rapoport & Chummah, 1965). In this game, each player has two options: cooperate or defect. If both cooperate, both do better than if they defect. But if one player defects while the other cooperates, the defector gets more than if both had cooperated, and the cooperator gets less than if both had defected. This scheme is interesting because of the conflict between behavior that leads to maximal average long-term payoff (mutual cooperation) and behavior that gives the chance of maximal short-term payoff (defecting gives higher immediate gains whether the partner cooperates or defects).

Axelrod and Hamilton (1981) claimed that if there is a constant probability *w* of a further game with the same opponent, then a strategy called tit for tat (TFT), defined as "cooperate in the first game and from then on do whatever the other player did in the preceding game," can be an evolutionarily stable strategy (ESS) (Maynard Smith, 1982), provided that *w* is large enough. This statement has led to a number of empirical studies claiming to demonstrate TFT in real animals. There are various problems with these tests. Firstly, the real prisoner's dilemma is one in which both players act at once and not in alternation, as in most laboratory tests. Second, it is not strictly true that TFT is an ESS. This is especially so if there are occasional "mistakes," as is surely the case in all biological systems. In a population of players playing TFT, the strategy "always cooperate" does better than TFT because "it brings the best out of people." TFT instead gets locked in mutual defection after mistakes. Actually, Nowak (1990) showed that TFT could be invaded by a more benign strategy, called "generous tit for tat" (GTFT), in which a player occasionally cooperated after a defection by the partner. More recently, Nowak and Sigmund (in press) have demonstrated that another strategy, called "simpleton" by Rapoport and Chummah (1965), "Pavlov" by Kraines and Kraines (1989), and "win stay lose shift" (WSLS) by Nowak and Sigmund, outperforms both TFT and GTFT. A WSLS player cooperates if and only if both players opted for the same alternative in the previous move. In other words, a WSLS player repeats its move if both players cooperated or if the first player defected while the opponent cooperated, but switches to the alternative if both defected or if the first player cooperated and the opponent defected. WSLS is psychologically realistic: It is controlled by the contingency of its own behavior and rewards, rather than by the partner's behavior alone (as in TFT). WSLS does not recognize partners, nor does it build up trust. It invades TFT or GTFT populations because it handles mistakes efficiently and because it defeats all-out cooperators. In Nowak and Sigmund's words, "Pavlov (WSLS) has no qualms in exploiting a sucker, once it has been discovered (after an accidental mistake) that it need not fear retaliation. Softies cannot subvert a Pavlov population." All these strategies (TFT, GTFT, and WSLS) are based on single-trial memory, but the significance of this unsound assumption is not yet fully known.

Although there are numerous demonstrations of Type II cooperative behavior solved by reciprocal altruism under natural circumstances (Packer, 1977; Seyfarth & Cheney, 1984; Wilkinson, 1984), there is no convincing example of actual use of TFT or any of the superior alternatives by nonhuman subjects. Even though TFT, GTFT, and WSLS are specified on an encounter-by-encounter basis, most analyses of cooperative behavior have looked at aggregates of events, without paying attention to the sequences of individual actions and thus providing no direct evidence for or against the use of single-trial memory rules such as these. In particular, we do not know of evidence for an increased probability of a cooperative response after a cooperation from the partner and a decrease after either defection by the partner or cooperation by the subject itself. We suspect that memory of actual players will often (or always) span more than one move.

The literature on experimental analyses of behavior presents several studies that are potentially relevant. For example, Skinner (1962) succeeded in producing a form of primitive cooperation in which pairs of pigeons obtained food only if they pecked at their respective keys within a 10th of a second of each other. More relevantly, Boakes and Gaertner (1977) showed that an apparently complex form of cooperative communication could be established between pairs of pigeons by a combination of autoshaping and operant conditioning. In their experiment, a pigeon (sender) was exposed to a key that could be illuminated with either red or green. A 2nd pigeon (receiver) could not see the sender's key but could see and hear its general behavior, and had access to two response keys. Both sender and receiver received a food reward if the receiver pecked at the correct key in each trial. "Correct" meant either left or right depending on the color shown to the sender in that trial. The pigeons learned to behave cooperatively and obtained rewards in a large proportion of the trials. Further, Boakes and Gaertner's careful analysis of the behavioral details showed that this emergent cooperation was produced by each pigeon attending to its own contingencies, including the behavior of the other pigeon as a discriminative stimulus. Autoshaping played a major role in this system. Because recent interest on cooperation in the behavioral ecology literature has been concerned with the consequences and selective history of this kind of behavior rather than with its mechanisms, studies on the dynamics of cooperative behavior have lacked similar analytical strength. In some cases, experimental results are described as "partners build up trust" (Milinski, Külling, & Kettler, 1990) without reference to plausible psychological principles that may cause this behavior. We favor greater emphasis on testing the predictions of the proposed underlying rules at the level at which the rules are formulated (for example event by event for TFT). In this paper we make an attempt to establish a link between pairwise cooperation and individuals' responses to their contingencies.

We studied the dynamics of behavior of pairs of starlings subject to pairwise interactions, or "games," in the laboratory. In the main game, food could be obtained on each trial only by cooperation of Type II. Each subject had the possibility of making food available to its partner but not to itself, and further, the action of making food available to a partner precluded obtaining food in a particular trial. The short-term advantage is to restrain in order to have the chance of an action by the partner, but this leads towards mutual defection. We have the double objective of examining possible mechanisms for special forms of cooperation and to analyze trial-by-trial effects of reinforcement.

GENERAL METHOD

Subjects

The subjects in the four experiments were 4 male (Birds 7, 9, 10, and 12) and 8 female (Birds 1, 2, 3, 4, 5, 6, 8, and 11) starlings (*Sturnus vulgaris*) caught in the wild. After capture, the birds were housed in an outdoor aviary for 4 weeks. During this period they were provided with water and food (starter turkey crumbs) ad libitum supplemented by mealworms (*Tenebrio* sp.) twice a week. They were then moved indoors to individual cages (0.9 m long by 0.45 m wide by 0.5 m high). The birds were divided into two groups of 6 and were housed in separate rooms at 20 ± 2 °C with a 12:12 hr light-dark cycle. They were deprived of food for 16 hr before each experimental session and received a complement of food 30 min after its completion, so that the total daily ration totaled 20 g.

Apparatus

The experiments were conducted in the house cages. Each cage had a removable panel with a centrally mounted food hopper and a response key (2.5 cm diameter) 8 cm to the right of the food hopper. In front of the panel, there was a perch 1 cm in diameter placed 16 cm below the center of the pecking key. A BBC Master microcomputer using SPIDER experimental control language (Paul Fray Ltd.) controlled the stimulus events and response contingencies and recorded the data.

EXPERIMENT 1

The aim of this experiment was to determine whether cooperation was maintained in our game design. There were three phases, the first and second for training and the third as

Table 1

Number of trials received and proportion of responses in positive ($X^+ \rightarrow$ FOOD) and negative ($Y^- \rightarrow$ ITI) trials during the last session of Phases 1 and 2 in Experiment 1. In Phase 2, Birds 1 to 6 received S associated with Y^- (Group I), whereas Birds 7 to 12 received S associated with X^+ (Group II).

	Phase 1		Phase 2		
Bird	% of trials X^+ with peck (*n*)	% of trials Y^- with peck (*n*)	% of trials X^+ with peck (*n*)	% of trials Y^- with peck (*n*)	% of trials (X^+ or Y^-) with peck in S
B1	100 (30)	0 (30)	100 (30)	0 (30)	0
B2	64.4 (45)	0 (45)	69.8 (43)	0 (40)	0
B3	100 (30)	7.14 (30)	100 (30)	3.23 (31)	3.23
B4	76.9 (39)	2.5 (40)	96.8 (31)	3.57 (29)	7.14
B5	47.8 (46)	0 (44)	50 (44)	2.17 (46)	8.7
B6	31.8 (44)	0 (46)	40.9 (44)	0 (46)	6.52
B7	96.8 (31)	3.03 (33)	96.8 (31)	0 (33)	80.6
B8	100 (30)	0 (30)	41.3 (46)	0 (44)	17.4
B9	66.7 (45)	0 (43)	83.3 (36)	0 (37)	55.6
B10	96.8 (31)	0 (32)	73.2 (41)	0 (40)	12.2
B11	100 (30)	3.23 (31)	100 (30)	0 (30)	100
B12	100 (30)	6.67 (30)	100 (30)	0 (30)	96.7

the game itself. In the game, the birds were not rewarded in trials in which they pecked at the initial stimulus of each trial, but they could obtain rewards in trials when they restrained from pecking if the partner did peck. Cooperative equilibrium could be maintained if both subjects behaved as expected from TFT or some approximation of it. At a trial-by-trial level, this implies that cooperative responses (pecking at the start of a trial) should become more likely after cooperative actions by the partner.

METHOD

Procedure

The birds were arranged as six pairs. The members of each pair were in adjacent cages, with partners being separated by wire mesh and visually exposed to each other's cage (including the working panel). Pairs were visually isolated from other pairs. The six pairs were tested as two three-pair groups, which differed in their training before entering the game. The two groups were used to test whether the persistence of cooperative performance depended on initial readiness to respond.

Phase 1

During this phase, the birds learned the discrimination between a stimulus predicting food (X^+) and one predicting no food (Y^-). The birds received, in a pseudorandom order, two different types of trials, positive and negative. In positive trials the response key was transilluminated with a color (X^+), and after 6 s there was an opportunity to gain 3 s of access to food. Delivery of food was conditional on at least one key peck during X^+. If no key peck occurred, the schedule advanced to the intertrial interval (ITI). In negative trials the response key was transilluminated with a different color (Y^-), and after 6 s the key went dark and the schedule went straight into the ITI. Trials were separated by ITIs of 45-s average duration (range, 30 to 60 s). For half of the pairs, X^+ was red and Y^- was green; for the remaining pairs, this was reversed. Each experimental session ended after 30 reward trials or 90 reward plus no-reward trials, whichever was reached first. No-reward trials included negative trials and trials programmed to be positive but in which the bird missed a reinforcement by not pecking at the key during X^+. Phase 1 ended after 11 sessions. All birds reached asymptotic levels of responding in X^+ and Y^-. Table 1 shows individual responding and discrimination at the end of training.

Phase 2

This phase introduced a difference between groups and a new stimulus (S). S consisted of the transillumination of the response key with amber light during the 6 s preceding either Y^- or X^+. In 6 of the birds, S preceded Y^- (Group I), and in the other 6 S preceded X^+ (Group II). Thus, subjects of Group I received, with equal frequency, trials with the sequence S → Y^- → ITI and trials with the sequence X^+ → food → ITI, whereas subjects of Group II received, with equal frequency, trials with the sequences S → X^+ → food → ITI and Y^- → ITI. The transition X^+ → food was conditional to a peck. Phase 2 ended after five sessions, and each session finished after 30 reward trials or 90 reward plus no-reward trials, whichever was reached first.

At the end of this phase, the birds of Group I responded to S on 4.26 ± 1.53% of trials, whereas the birds in Group II responded to S on 60.4 ± 15.8% of trials. All the birds maintained a high level of response in X^+ (76.2 ± 10.8%) and a low level of response in Y^- (1.5 ± 0.69%). A two-way repeated measures ANOVA (Group and Session) for the percentage of responses in S showed statistically significant differences between groups, $F(1, 10) = 26.16$, $p < .001$, and sessions, $F(4, 40) = 3.48$, $p < .01$. Thus, at the beginning of Phase 3, the response probability in S was low for the birds of Group I and high for the birds of Group II, and all birds discriminated between X^+ and Y^-.

Phase 3 (Game)

During this phase, both groups had the same schedule. Trials began with the transillumination of the response key with S for both members of each pair. The first peck by either bird extinguished S and turned the keys of both birds for up to 6 s to a new color: Y^- for the bird who pecked and X^+ for its partner. Pecking in X^+ produced 3-s access to food, whereas Y^- was always followed by an ITI. If neither bird responded in S after 6 s, the keys of both cages went dark and a new ITI started. The stimulus sequences thus were S → Y^- → ITI and S → X^+ → food → ITI for a bird that pecked in S and its partner, respectively, and S → ITI for both birds when neither pecked. The transition X^+ → food was conditional on a peck by the partner.

The summary of changes in schedule between Phases 2 and 3 is as follows. The sequence S → ITI was new for both groups. The sequence S → X^+ → food → ITI was new for Group I and familiar for Group II. The sequence S → Y^- → ITI was new for Group II and familiar for Group I. No trials started without S. In each trial no more than 1 bird could obtain food: A bird received food when it did not peck in S, given that its partner did peck. But both birds lost the reward if neither pecked during S. Each pair received one daily session on each of 12 days. For each pair, the sessions ended after 60 reward trials or 90 reward plus no-reward trials, whichever was reached first.

RESULTS

Molar Analysis

Cooperation was not stable and was very variable between and within pairs, but it was present and persisted for several sessions (Figure 1 and Table 2). The differences between groups in the level of responding to S established during Phase 2 were not present in Phase 3.

We conducted a two-way repeated measures ANOVA (Group and Session) for the percentage of responses in S during the game. The differences between groups in the level of responding to S established during Phase 2 were not significant in Phase 3, $F(1, 10) = 0.094$, ns. There was a decline in the probability of responses in S during the experiment, $F(11, 110) = 2.11$, $p < .05$, but a posteriori analysis (one-way repeated measures ANOVA) showed that this decrease was statistically significant in Group I, $F(11, 55) = 2.02$, $p < .05$, but not in Group II, $F(11, 55) = 0.6$, ns. Pairwise comparisons between sessions showed that the decline observed in Group I was due to an initial drop in pecking (the only significant contrasts were found between Sessions 1, 2, and 3 vs. Sessions 8 to 12; Fisher PLSD test). Thus, in neither group were there statistically significant declines in responding after Session 4, indicating that the level of responding may have reached equilibrium, or at least a very slow decline.

Molecular (Trial-by-Trial) Analysis

The detection of reciprocity rules such as TFT requires attention to individual actions as a function of its precedents. In order to evaluate the presence of reciprocity between members of pairs, for each bird we calculated the probability of responding in a trial given that "self," "partner," or "neither" had re-

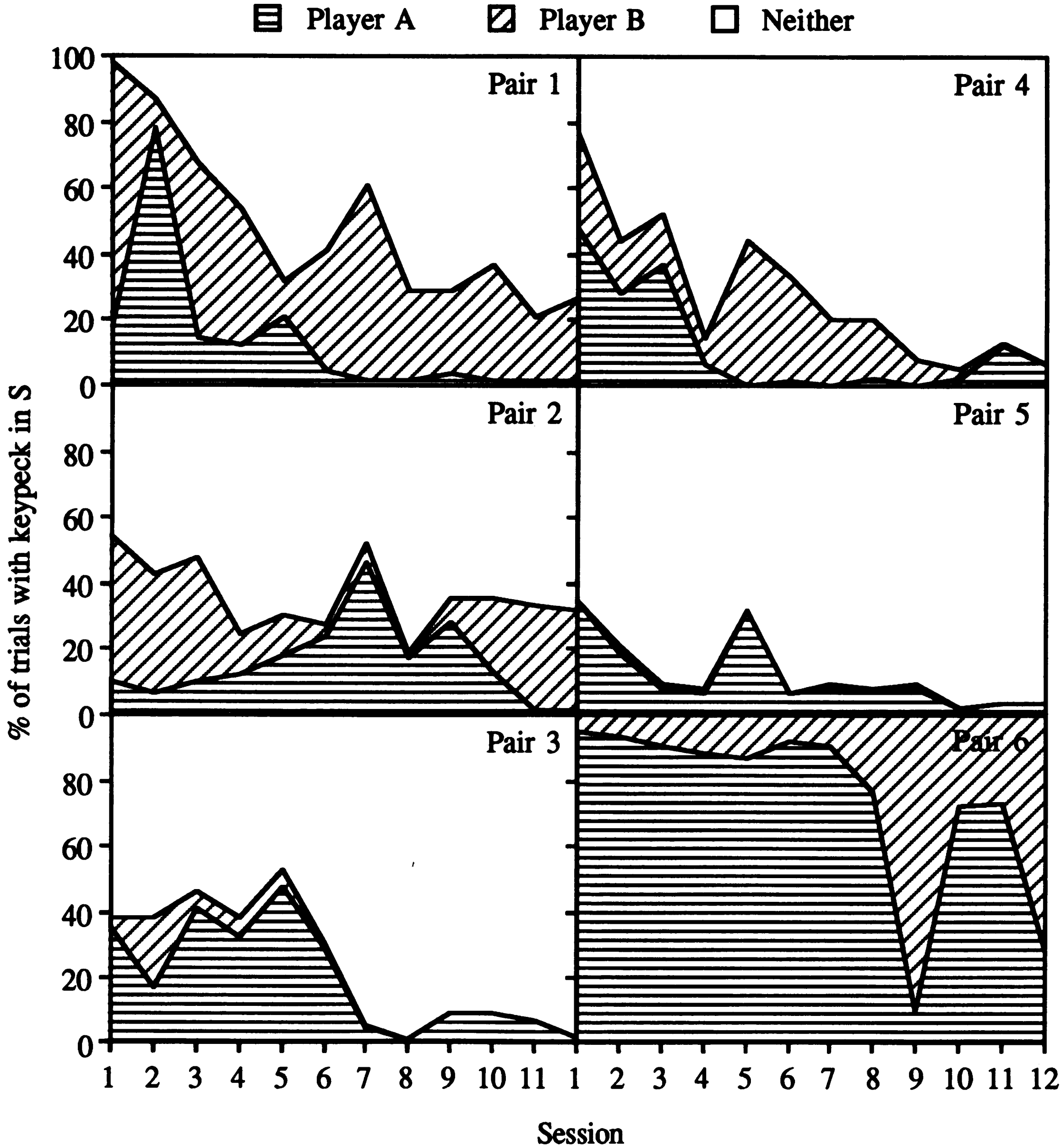

Fig. 1. Percentage of cooperative responses by members of six pairs in Experiment 1 (players can see each other). The shaded areas indicate the percentage of trials with a response in S, and the white areas are those trials with no pecking by either bird. Pairs 1 to 3 were pretrained for low pecking and Pairs 4 to 6 for high pecking. The values for Player A show its percentage, whereas the values for Player B are sums of the percentages for both players.

sponded in the previous trial. Trials in which self responded were labeled "A," those in which the partner responded were labeled "B," and trials in which neither bird responded were labeled "N." Events in the preceding trial are indicated by ′ (prime). The probability of responding in a trial given a self response in the previous trial ($p_{A|A'}$) equals the number of sequences A′ → A divided by the total number of A′, namely the sum of sequences A′ → x, with x representing A, B, or N in the current trial

$$P_{A|A'} = \frac{A' \rightarrow A}{A' \rightarrow x}.$$

Similarly, the probability of responding given

Table 2

Number of trials per session in which Player A (A), Player B (B), or neither bird (N) responded in S (Experiment 1). The composition of each pair (Player A/Player B) was Pair 1: Bird 1/Bird 2, Pair 2: Bird 3/Bird 4, Pair 3: Bird 5/Bird 6, Pair 4: Bird 7/Bird 8, Pair 5: Bird 9/Bird 10, Pair 6: Bird 11/Bird 12 (see Figure 1).

	Pair 1			Pair 2			Pair 3			Pair 4			Pair 5			Pair 6		
Session	A	B	N	A	B	N	A	B	N	A	B	N	A	B	N	A	B	N
1	11	49	1	9	40	41	32	2	56	37	23	18	31	0	59	57	3	0
2	54	6	9	6	32	52	15	19	56	25	15	50	17	2	71	56	4	0
3	13	47	29	9	34	47	37	4	49	33	14	43	7	1	82	54	6	0
4	11	37	42	11	11	68	29	5	56	6	7	77	6	1	83	53	7	0
5	19	10	61	16	11	63	43	4	43	0	40	50	29	0	61	52	8	0
6	4	33	53	21	4	65	26	1	63	1	29	60	6	0	84	55	5	0
7	1	54	35	42	5	43	4	1	85	0	18	72	7	1	82	54	6	0
8	1	25	64	15	2	73	1	0	89	2	16	72	7	0	83	46	14	0
9	3	23	64	25	7	58	8	0	82	0	7	83	7	1	82	6	54	0
10	1	32	57	12	20	58	8	0	82	2	3	85	2	0	88	43	17	0
11	1	18	71	1	29	60	6	0	84	11	1	78	3	0	87	44	16	0
12	1	23	66	1	28	61	2	0	88	6	0	84	3	0	87	17	43	0

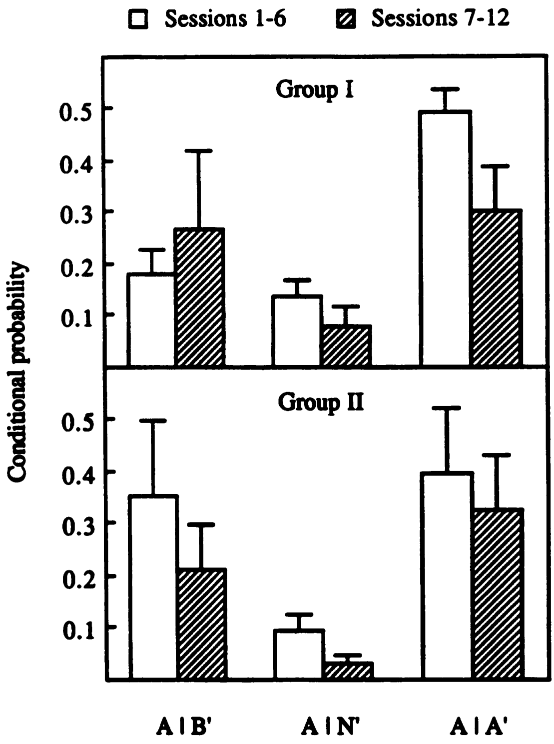

Fig. 2. Molecular analysis of the game phase in Experiment 1. The bars are the conditional probabilities (*M* ± *SEM*) of Player A responding in S in trial *n*, given that Player B (A|B'), Player A (A|A'), or neither (A|N') responded in S in trial $n - 1$. We conducted a three-way ANOVA with Group as the between-subjects factor and Session Block and Previous Trial as the within-subjects factors for the arcsine transformation of the probability of peck in S in a given trial. There were no statistically significant differences between groups, $F(1, 10) = 0.034$, ns; or between session blocks, $F(1, 10) = 2.89$, ns; but the probability of a peck in S was statistically significantly different depending on whether the subject, its partner, or neither pecked in S the previous trial, $F(2, 20) = 11.80$, $p < .001$. Pairwise comparisons (Tukey test) showed differences between A|B' and A|N' ($p < .05$), A|A' and A|N' ($p < .01$), and A|A' and A|B' ($p < .05$).

that the partner had responded on the preceding trial and the probability of responding given that neither bird had responded on the preceding trial were, respectively,

$$p_{A|B'} = \frac{B' \to A}{B' \to x} \text{ and } p_{A|N'} = \frac{N' \to A}{N' \to x}.$$

There were birds that did not experience some sequences in some sessions; therefore, the corresponding conditional probabilities could not be calculated. For that reason, to test if the difference in response probability between early and late sessions was accompanied by a

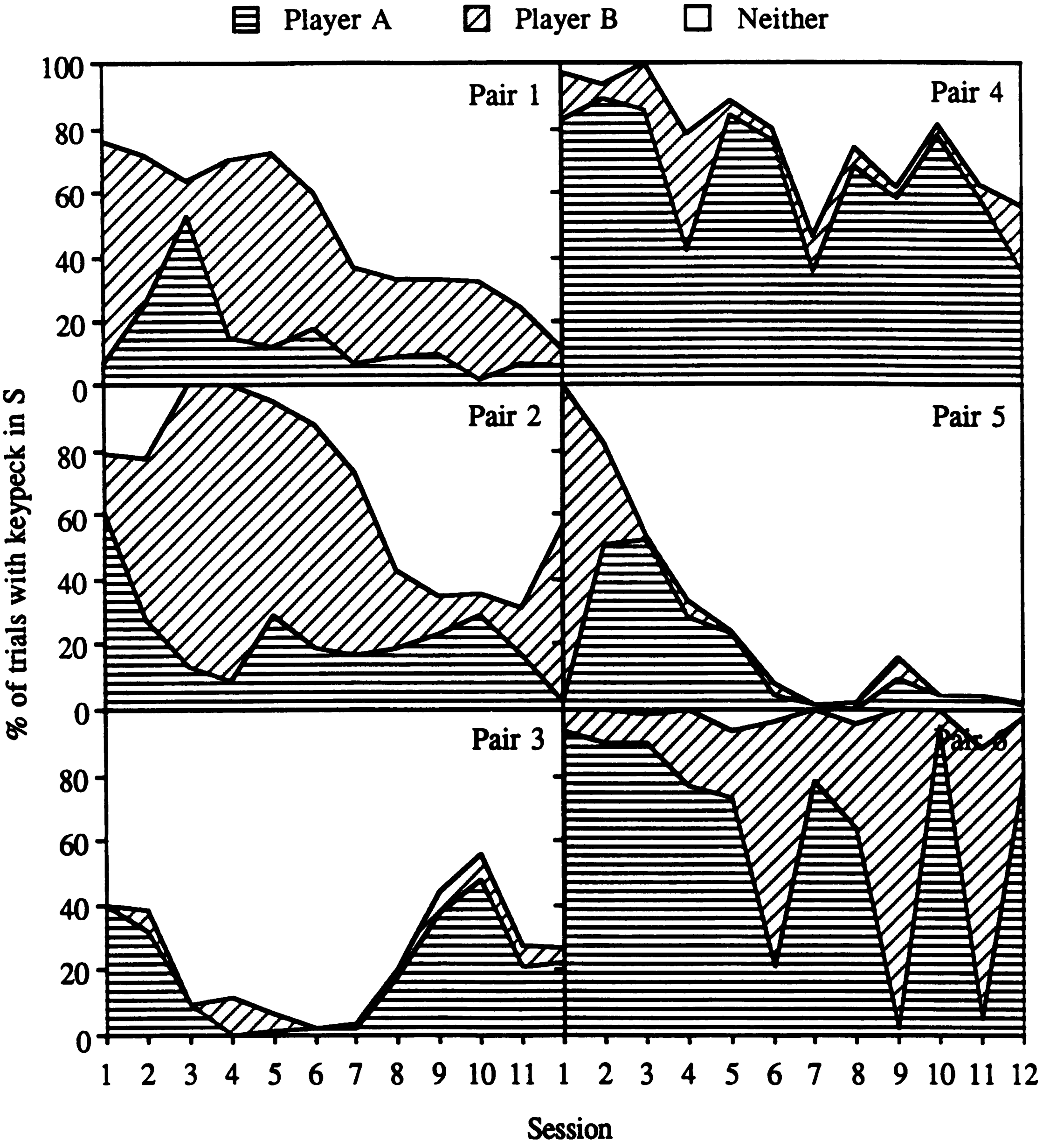

Fig. 3. Distribution of responses for the members of six pairs in Experiment 2 (players cannot see each other). Pretraining was as in Experiment 1.

change in conditional probabilities, we pooled the results of Sessions 1 to 6 and 7 to 12 and compared the transition probabilities in these two blocks of sessions.

Conditional probabilities are shown in Figure 2. The results satisfy some requirements of cooperation by reciprocity, because the probability of a pecking response was higher in trials preceded by a trial with a response of the partner (B′ → A) than in those preceded by a trial in which neither bird had responded (N′ → A). However, in contrast to the simple strategies discussed in the introduction, the probability of a pecking response was highest in trials preceded by a trial in which the same bird had responded (A′ → A) than in trials preceded by a trial with a response by the partner (B′ → A) or by neither bird (N′ → A).

Table 3

Number of trials received and proportion of responses in positive and negative trials during the last session of Phases 1 and 2 in Experiment 2. As in Experiment 1, during Phase 2 Birds 1 to 6 received S associated with Y^- (Group I), whereas Birds 7 to 12 received S associated with X^+ (Group II).

	Phase 1		Phase 2		
Bird	% of trials X^+ with peck (n)	% of trials Y^- with peck (n)	% of trials X^+ with peck (n)	% of trials Y^- with peck (n)	% of trials (X^+ or Y^-) with peck in S
B1	85.7 (35)	0 (36)	100 (31)	0 (29)	0
B2	90.9 (33)	0 (31)	96.8 (31)	3.45	3.45
B3	100 (30)	6.66 (30)	100 (32)	0 (28)	0
B4	81.1 (37)	0 (39)	93.8 (32)	0 (29)	3.45
B5	47.7 (44)	2.17 (46)	73.2 (41)	0 (38)	5.26
B6	45.7 (46)	0 (44)	45.7 (46)	0 (44)	2.27
B7	78.9 (38)	0 (40)	100 (30)	0 (31)	93.3
B8	93.8 (32)	0 (29)	90.9 (33)	0 (31)	51.5
B9	85.7 (35)	0 (35)	90.9 (33)	0 (30)	75.8
B10	93.8 (32)	0 (31)	100 (32)	0 (28)	63.3
B11	96.8 (31)	0 (33)	100 (30)	10 (30)	100
B12	100 (30)	0 (29)	100 (30)	3.23 (31)	96.7

This indicates that individuals engaged in multitrial bouts of either cooperation or defection, producing the paradoxical result that, on a trial-by-trial basis, the probability of responding is higher after nonreinforcement than after reinforcement. Notice that we are not analyzing rapid bursts of pecking but a longer term process, because each observation refers to the presence or absence of a single peck per trial and trials are separated by relatively long intertrial intervals.

Tendency towards cooperation may express itself in latency to respond as well as in probability of pecking. One might, for example, expect that a sophisticated player who has cooperated in the previous trial may wait some time for the reciprocation by its partner but may in the end respond to avoid losing the trial altogether. In game-theoretical terms, this may make sense if the cost of cooperating when the partner defects is low and if cooperating encourages the partner to cooperate later on, as expected from GTFT. To examine this possibility, we compared the latencies to the response in S given that self, partner, or neither had responded in the previous trial. Latency to peck in S was longer in trials preceded by a trial in which neither responded ($N' \rightarrow A$) than in trials preceded by a trial in which self ($A' \rightarrow A$) or the partner ($B' \rightarrow A$) responded. However, there were no differences in the latency to peck between sequences $A' \rightarrow A$ and $B' \rightarrow A$. A three-way ANOVA with Group as the between-subjects factor and Session Block and Previous Trial as within-subject factors found no statistically significant differences between groups or between session blocks.

EXPERIMENT 2

METHOD

The purpose of this experiment was to control for the nature of the partner's influence. Birds could be responding to the sequence of reinforcing contingencies per se, or they could be somehow engaged in a dyadic cooperative interaction. To test for this, we replicated Experiment 1 with the same six pairs of birds using a partition that visually isolated the members of each pair. Because this experiment was performed after Experiment 1, we could not completely exclude order effects, but we tried to attenuate the problem by bringing the birds back to their baseline responding through a pretraining procedure. Pretraining (Phases 1 and 2) was as in Experiment 1. Phase 1 ended after 10 sessions, and Phase 2 ended after five sessions.

RESULTS

The asymptotic values of responding in X^+, Y^-, and S for the 12 birds at the end of Phases 1 and 2 are shown in Table 3. During Phase 2 the percentage of trials with a response in S

Table 4

Number of trials per session in which Player A (A), Player B (B), or neither bird (N) responded in S (Experiment 2). The composition of each pair was as in Experiment 1 (see Figure 3).

	Pair 1			Pair 2			Pair 3			Pair 4			Pair 5			Pair 6		
Session	A	B	N	A	B	N	A	B	N	A	B	N	A	B	N	A	B	N
1	5	55	19	46	14	16	36	0	54	51	9	2	2	58	0	56	4	0
2	21	39	24	21	39	17	29	6	55	57	3	4	37	23	13	54	6	0
3	47	10	33	8	52	0	8	0	82	51	9	0	47	1	42	55	5	1
4	13	47	26	5	55	0	0	10	80	32	28	17	25	5	60	46	14	0
5	10	50	23	18	42	3	1	5	84	57	3	8	21	1	68	47	13	4
6	16	38	36	13	47	8	2	0	88	57	3	15	4	3	83	13	47	2
7	6	27	57	14	46	22	2	1	87	32	10	48	1	0	89	47	13	0
8	8	22	60	17	22	51	16	2	72	55	5	21	0	2	88	40	20	3
9	9	21	60	21	10	59	34	6	50	52	3	35	8	6	76	1	59	0
10	2	27	61	26	6	58	43	7	40	57	3	14	4	0	86	57	3	0
11	6	16	68	15	13	62	19	6	65	52	4	34	4	0	86	3	57	8
12	5	5	80	2	49	39	20	4	66	32	18	40	1	1	88	49	11	1

differed significantly between groups, $F(1, 10) = 41.19$, $p < .001$. At the end of this phase, the percentage of trials with a response during S for Groups I and II were 4.08 and 89.9, respectively.

As in Experiment 1, during the game there was marked variability in the behavior of different pairs, both within and between groups (Figure 3 and Table 4). Notice that the performance of some pairs in Experiments 1 and 2 was very similar. Again, during the first session, the performance of pairs that had learned not to peck in S during Phase 2 (Group I) was similar to the performance of the pairs of Group II (which had learned to peck in S during Phase 2). Overall, the percentage of trials with a response in S was not significantly different between groups, $F(1, 11) = 0.49$, ns, or sessions, $F(11, 110) = 1.19$, ns, suggesting that a "cooperative" equilibrium may exist independently of initial pecking tendency. Although the stability of performance is suggested only by lack of significant decline across sessions and thus the evidence is weak, the presence of a substantial level of pecking at the end of the experiment is by itself a positive indication that the cooperation was not an ephemeral artifact of initial conditions.

The molecular analysis of conditional probabilities showed that, although reinforcement due to a partner's pecking increased the probability of responding with respect to a trial without any response, the probability of responding after a no-reward trial in which the same subject had pecked was highest (Figure 4). In a similar way, the analysis of the latencies to respond in S showed that these were longer in trials preceded by a trial in which neither responded than in trials preceded by a trial in which self or the partner responded, but there were no significant differences between these last ones.

Thus, the results of Experiment 2 were consistent with the results of Experiment 1 and show that performance in the game was insensitive to the visual perception of the partner. The order in which these experiments were carried out leaves open the possibility that presence of the partner might have had an effect during early stages of training but was not required later on.

EXPERIMENT 3

Given that the results of Experiments 1 and 2 indicate that cooperative performance in an approximation of the prisoner's dilemma game may be reached through the subjects' responses to their own reinforcement contingencies without influence of the visual perception of a partner, we conducted an experiment using a virtual partner that followed a consistent behavioral rule. The purpose of this experiment was to understand further the molecular details of the effects of reinforcement and nonreinforcement and to test if, as predicted by theoretical analysis of similar games, a strategy such as TFT could result in the maintenance

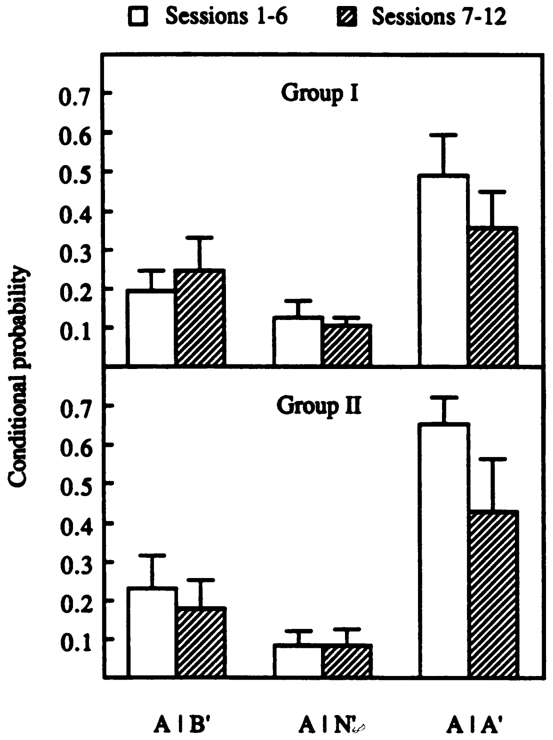

Fig. 4. Mean conditional probabilities for the game phase in Experiment 2. Notation as in Figure 2. There were no statistically significant differences between groups, $F(1, 10) = 0.1$, ns; or between session blocks, $F(1, 10) = 2.99$, ns; but the probability of a peck in S was significantly different depending on whether the subject, its partner, or neither pecked in S the previous trial, $F(2, 20) = 40.96$, $p < .001$. Pairwise comparisons (Tukey test) showed differences between A|B' and A|N' ($p < .01$), A|A' and A|N' ($p < .01$), and A|A' and A|B' ($p < .05$).

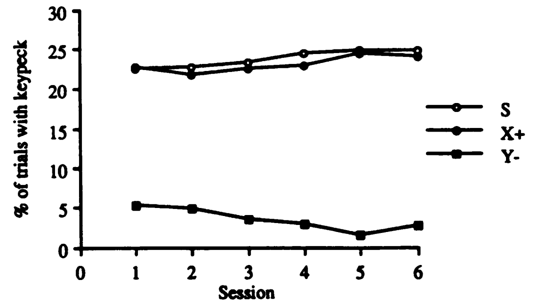

Fig. 5. Responding by subjects playing with a computer answering with tit for tat (Experiment 3). The figure shows the group mean percentage of responses in S, Y^- (trials in which the bird pecked during S), and X^+ (trials in which the computer reciprocated). There were no statistically significant differences within subjects, $F(5, 55) = 0.16$, ns; but the differences between subjects were significant, $F(11, 60) = 16.66$, $p < .001$).

of a cooperative equilibrium. The partner in this experiment was a computer programmed to use TFT.

In the first trial of each session S turned into X^+, giving the bird the opportunity to obtain food as if the partner had responded. From then on, the computer responded to the action of the bird in the preceding trial. When the subject pecked in S in a given trial, the sequence in that trial was S → Y^- → ITI, but on the following trial the sequence was S → X^+ → food → ITI, as if the partner had reciprocated in response to the subject's previous cooperative action. The duration of S in these reciprocation trials was half the duration of S in the preceding trial (i.e., half the latency to peck shown by the subject). The duration of S in reciprocation trials was shortened to decrease the probability of a bird responding in S in consecutive trials. When, instead, the bird did not peck in S in a trial in which the computer was not due to reciprocate, the sequence in that trial was S → ITI, and in the next trial food could not be obtained. In these retaliation trials, the sequence was S → ITI if the bird did not peck in S and S → Y^- → ITI if it did. Thus, food was never obtained in a trial in which the subject pecked in S, but could always be obtained in the following trial. The optimal strategy in this schedule was to alternate trials, responding in S and then collecting the food opportunity by pecking in X^+ in the following trial. The experiment lasted six sessions.

RESULTS

A cooperative equilibrium with the virtual TFT partner was quickly reached and maintained (Figure 5). Some of the birds had a considerable number of empty trials (did not respond when it was their turn), whereas others alternated responses with the computer. In some cases the subjects had short runs of progressively reduced latency to peck so that they actually managed to censor the cooperative response of the computer, responding in two or three consecutive trials. Overall, although the TFT virtual partner maintained responding in S, the birds obtained food in only 23.7% of the trials (maximum = 50%).

Discrimination between X^+ and Y^- was maintained throughout the experiment. In reciprocation trials (in which S turned into X^+)

the percentage of responses in X^+ ranged between 96.2 ± 0.63 and 99.1 ± 1.04, whereas in retaliation trials (in which S turned into Y^-) the percentage of responses in Y^- ranged between 7.4 ± 3.53 and 21.6 ± 6.23 (*M* ± *SEM*, *N* = 12).

As in Experiments 1 and 2, we calculated the probability of responding in a trial given that self (A), its virtual partner (B), or neither (N) had responded in the previous trial. However, because of the programmed behavior of the virtual partner, some sequences were either censored by the short duration of S when the computer reciprocated ($A' \rightarrow A$) or were not possible ($A' \rightarrow N$, $B' \rightarrow B$, $N' \rightarrow B$). The probability of responding was higher in trials preceded by a trial with a response by the partner than in trials preceded by a trial in which neither responded.

EXPERIMENT 4

The paradox exposed by the prisoner's dilemma for the maintenance of cooperation is present in the results of the three previous experiments. In Experiment 3, for example, the birds did produce a substantial number of cooperative responses (i.e., created trials in which they could not possibly be rewarded, but which primed the partner to respond cooperatively in the future). In the functional language of game theorists, the priming of the partner could be seen as the strategy of a GTFT player when facing a TFT partner. Nevertheless, in mechanistic terms, we need to explain this behavior in terms of its antecedents. Was it the reciprocation by the TFT partner that maintained responding, or is there a more parsimonious mechanistic interpretation? We suggest that cooperative responding was maintained by second-order autoshaping to X^+, with each partner (real or virtual) maintaining the level of response to S of the other partner by generating sequences $S \rightarrow X^+$. In classical Pavlovian terms, the occasional occurrence of a reward after a signal confers attractive properties to the latter, fostering a tendency to treat the signal as if it had properties of the reward that occasionally followed it. This Pavlovian effect could compete with the tendency not to make responses that lead to nonreinforcement, as expected from an operant conditioning process. In our setting, the effect of the sequences $S \rightarrow X^+$ could overwhelm the operant trend towards extinguishing pecking in S due to the contingency $S \rightarrow Y^- \rightarrow$ ITI experienced in those trials with a peck in S. Notice that this mechanistic account is compatible with a functional description: The generation of rewarded trials by the partner is necessary to maintain cooperation, but it differs in its additional predictions. The pairing of the signal and the outcome does not need to be related to the subject's own strategy.

To expose the contrast between these predictions, we ran an experiment using a negative-contingency (omission) procedure (Williams & Williams, 1969). In this experiment, the birds could obtain food in all trials provided that they refrained from pecking in S for 6 s. At that time, if no peck had occurred, S changed to X^+ and food could be obtained by a single peck. If the bird pecked during S, on completion of the 6 s, S changed to Y^- and 6 s later an ITI followed. In terms of the prisoner's dilemma, the subject could either obtain the "temptation" payoff in every trial (Maynard Smith, 1982) by refraining from pecking, the "sucker's" payoff by responding every time, or an alternation of both. The optimal strategy in this game is simply "always defect."

RESULTS

The averaged data shown in Figure 6A indicate that a substantial level of cooperative responding (32.3%) was maintained after several sessions, and it seemed to reach an overall equilibrium after no more than four sessions. That is, the average payoff in the population was reduced by the same amount simply because the birds responded according to the prediction of the conditioning account. However, the individual subjects showed marked differences in their tendency to decrease the probability of responding on S. Some birds reduced their number of responses after a few sessions, but others completely failed to solve the omission task, with no decrease at all (Figure 6B).

The discrimination between X^+ and Y^- was maintained throughout the experiment. The number of trials with a response in Y^- was only a small proportion of the trials with a response in S. At the same time, in most of the trials in which the birds did not respond in S, they responded in X^+.

Because the conditioning account is the result of two competing tendencies—an increase in responding due to the pairing of the signal with the reward and a decrease in responding due to learning that responding leads to no reward—the molecular analysis in this case is crucial to examine the presence of these tendencies. We calculated the conditional probabilities of pecking in S after having pecked in S in the preceding trial and of pecking in S after refraining from pecking in S and thus experiencing a positive contingency. For each subject we analyzed the changes in these probabilities between the first part (Sessions 1 through 6) and the second part (Sessions 7 through 12) of the experiment. Our expectation was that if these two effects were present, the probability of responding ought to increase after a trial with no response (i.e., with reward) and decrease after a trial with a response (i.e., without reward). The group mean probability of pecking in S after having pecked in S in the preceding trial decreased between the two halves of the experiment (paired *t* test, $t = 2.51$, $p < .03$), whereas the mean probability of pecking in S after refraining from pecking in S did not change (paired *t* test, $t = 0.134$, ns). Although the birds learned to react to a negative trial, their responding appeared to be maintained by the constant probability of responding to S in trials after sequences $S \rightarrow X^+ \rightarrow$ food. Throughout the experiment, the probability of a response during S after having responded in the preceding trial was higher than the probability of responding having refrained from responding in the preceding trial. One possible caveat is that our results may not show asymptotic performance, and it is possible that after long training the only responses maintained would be those after a trial with a sequence $S \rightarrow X^+ \rightarrow$ food. In any case, the results contradict the results of all simple rational strategies.

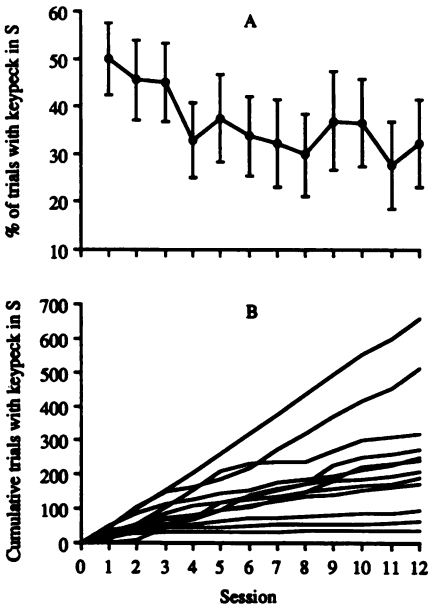

Fig. 6. (A) Percentage of trials with response in S (*M* ± *SEM*) during an omission task (Experiment 4). (B) Cumulative number of trials with a response in S for the 12 subjects. The curves correspond (from bottom to top on the right) to Birds 2, 10, 8, 6, 9, 4, 5, 1, 3, 12, 7, and 11.

GENERAL DISCUSSION

The results obtained in these four experiments are incompatible with a trial-by-trial application of the law of effect or proposed putative strategies based on single-trial memory, such as TFT, GTFT, or WSLS. In all experiments, trials with pecks in S ended in nonreinforcement and trials without pecks in S sometimes ended in reinforcement, but the birds responded in S and in some cases reached a stable performance. TFT does not match our results in the two-partner games, because the probability of a cooperative response was greatest after a cooperative response by the same subject, indicating that a greater-than-one-trial rule is necessary. Game-theoretical accounts in general fail to account for the results of Experiment 4, because here the subjects cooperated in a substantial proportion of the trials even when this led to a decline in reward in both the short and the long term.

The results are partly compatible with an interpretation in terms of classical conditioning and, in the case of the games between 2 subjects, in terms of coupled autoshaping of 1 subject by the other. Nevertheless, some aspects of the molecular analysis remain puzzling. As mentioned above, first-order sequential analysis showed a tendency to responding in runs, even though each response produced a short-term loss of food opportunity. A preliminary interpretation in terms of a delta rule based on the Rescorla–Wagner model (Rescorla & Wagner, 1972; Wagner & Rescorla, 1972) leads one to expect that the associative value of S and food in our experiments would increase after a trial with the sequence $S \rightarrow X^+ \rightarrow$ food and decrease after a trial with the

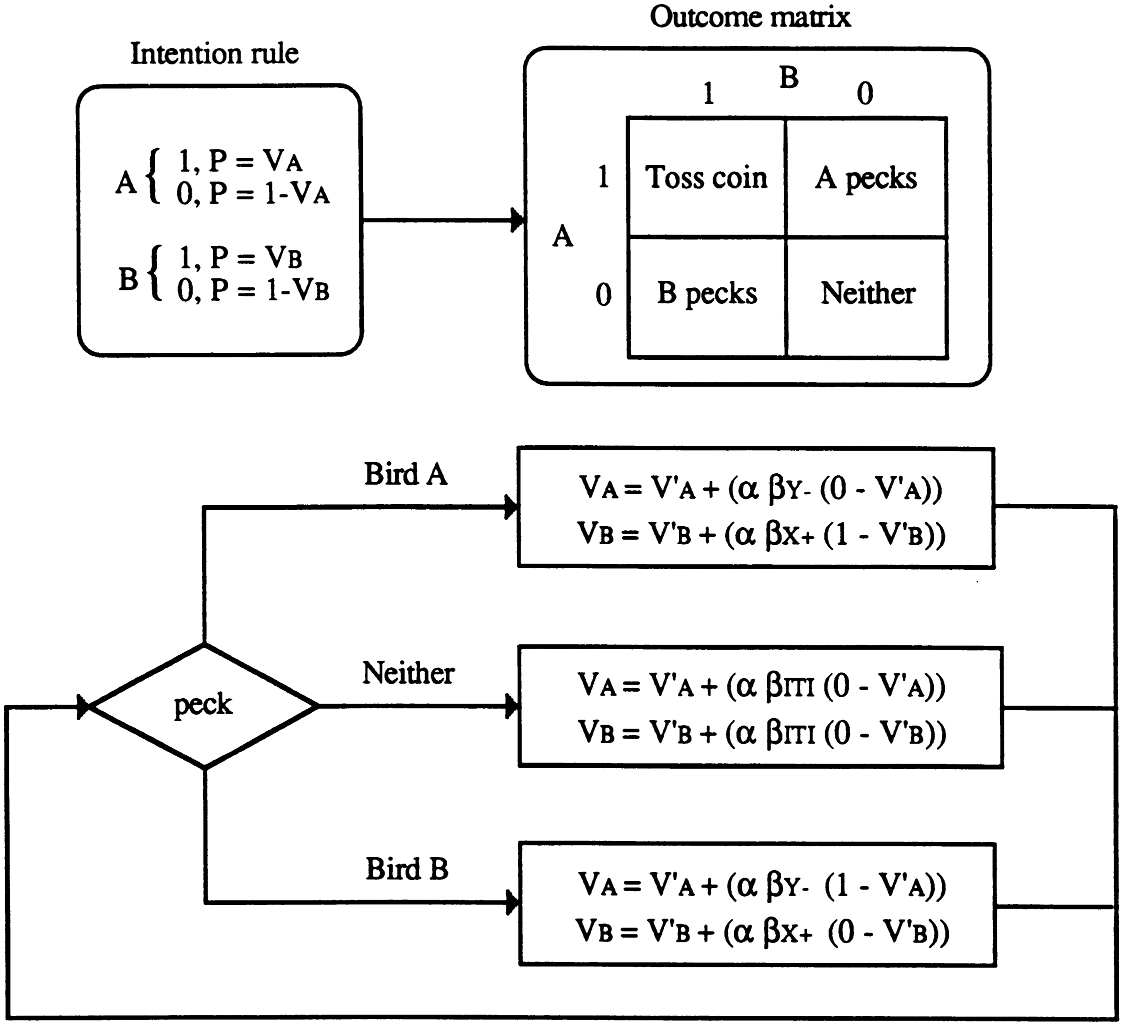

Fig. 7. Diagram of a version of the Rescorla–Wagner model for the game phase in Experiment 1. A and B represent the 2 partners. The intention to peck in S in a given trial was given a value of either 1 or 0, with a probability equal to the associative value between S and X^+ for that bird at the moment. Actual pecking in each trial was decided with the outcome matrix. Updating of the associative values followed the diagram in the bottom part of the figure.

sequence S → Y^- → ITI or S → ITI, as in those cases when neither partner pecked. In fact, the observed probability of pecking in S was higher after reinforced trials than after trials with a sequence S → ITI, but responding was maximal following trials with a sequence S → Y^- → ITI.

To express these ideas formally, we developed a model of our game (Experiments 1 and 2) inspired by the Rescorla–Wagner model with an ad hoc rule for translating associative values into pecking probability. The model is based on a linear operator in which the changes between successive trials in the associative strength between a meaningful and a conditional stimulus are given by the expression

$$\Delta V = \alpha\beta(\lambda - V),$$

where α is the salience of the meaningful stimulus, β is the salience of the conditional stimulus, λ is the maximum associative strength that can be reached between them, and V is the current associative strength ($0 \leq \alpha, \beta, \lambda, V \leq 1$).

We considered S as the conditional stimulus and X^+ as the unconditional stimulus, assuming that the associative strength between X^+ and the biologically relevant event (food) was asymptotic and equal to 1. In order to generate responding, we postulated that the probability of attempting a response during S was proportional to the associative strength between S and X^+. Not all pecking attempts result in pecks, because the behavior of one bird "censors" the behavior of the other. The model is based on the premise that the associative strength between S and X^+ increased each time the bird experienced the sequence $S \rightarrow X^+ \rightarrow$ food and decreased with the sequences $S \rightarrow Y^- \rightarrow$ ITI and $S \rightarrow$ ITI (Figure 7).

The salience of these three sequences was assumed to be different and was reflected in the value of the parameter β. The 2 birds were given identical parameters. Thus, from trial to trial, the variation in associative value between S and X^+ for Birds A and B when Bird A pecked was

$$\Delta V_A = \alpha\beta_{Y^-}(0 - V_A)$$

$$\Delta V_B = \alpha\beta_{X^+}(1 - V_B).$$

When Bird B pecked it was

$$\Delta V_A = \alpha\beta_{X^+}(1 - V_A)$$

$$\Delta V_B = \alpha\beta_{Y^-}(0 - V_B),$$

and when neither bird pecked it was

$$\Delta V_A = \alpha\beta_{ITI}(0 - V_A)$$
$$\Delta V_B = \alpha\beta_{ITI}(0 - V_B).$$

β_{X^+}, β_{Y^-}, and β_{ITI} represent the salience of the stimuli predicting food and no food, and the ITI, respectively, and V_A and V_B represent the current associative value of $S \rightarrow X^+$ for each bird.

The "behavioral" output was as follows: In each trial each subject made a decision as to whether to attempt to peck or not. This decision was probabilistic and was based on the current associative value between S and X^+. A decision to attempt a peck was taken with a probability exactly equal to V. Under this rule, four combinations could take place in each trial: None of the birds attempts to peck (in this case neither pecked), either of the subjects attempts to peck while the other does not (in that case the bird which attempts the peck actually pecks), or both attempt a peck (in which case a coin-tossing procedure is used, namely one of them, chosen at random with equal probability, pecks, censoring the other's decision). The model ignores interindividual interactions other than those expressed through the reward contingencies of each subject.

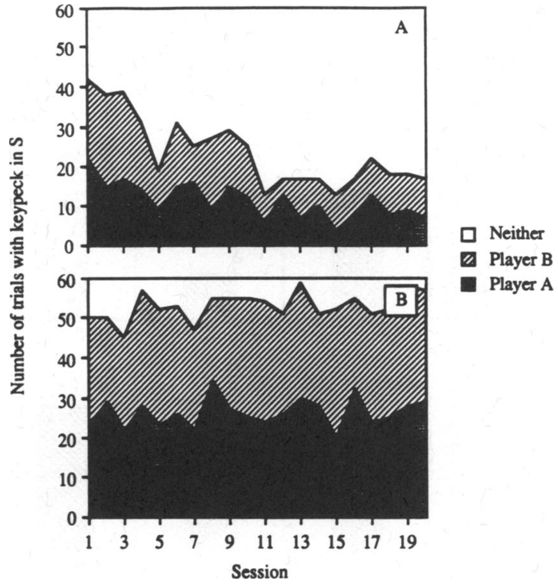

Fig. 8. Distribution of responses for two sets of parameters of the model presented in Figure 7. The format is the same as in Figure 1. The results are the means of 10 runs (60 trials per session, 20 sessions) for each condition. (A) $\beta_{X^+} = 0.2$, $\beta_{Y^-} = 0.1$, $\beta_{ITI} = 0.2$. (B) $\beta_{X^+} = 0.4$, $\beta_{Y^-} = 0.15$, $\beta_{ITI} = 0.1$. In both cases $\alpha = 0.1$, and initial conditions were $V_A = 0.5$ and $V_B = 0.5$.

Figure 8 shows examples of runs of the model with two sets of parameters, plotted as shown for real birds in Figure 1. The model generates a cooperative equilibrium at least as stable as that observed in the real subjects. The actual level of the equilibrium depended strongly on the parameters, as shown by the two examples in Figure 8, but some form of cooperative performance was observed for a wide range of parameter values.

To examine the model's performance at the molecular level, we did a first-order sequence analysis on series of 10 runs of the model under each set of parameters. The average results are shown in Figure 9. Naturally, the outcome of this analysis also depended on the choice of parameters, and this is illustrated in the two examples in Figure 9. Nevertheless, although for some parameter values there was greater probability of responding after a response by the other bird than after a trial when no bird responded, we found no set of parameters that would produce the highest probability of responding after having experienced a trial with

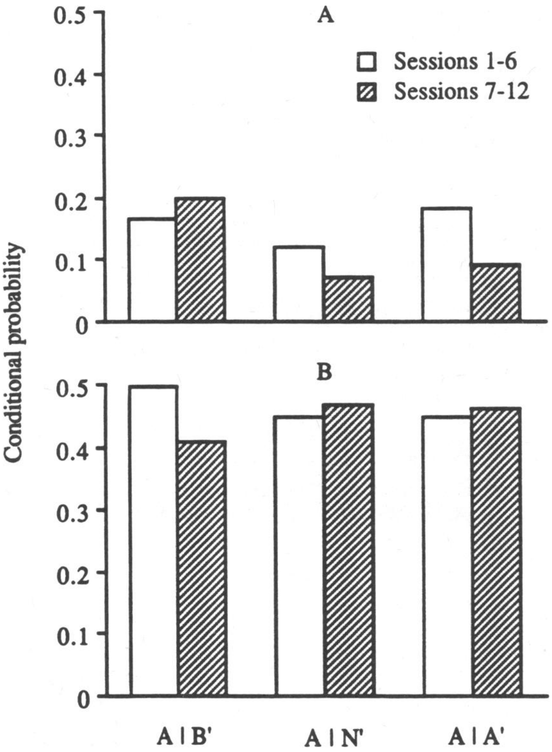

Fig. 9. Conditional probabilities according to the model presented in Figure 7. The parameters used in A and B are the same as in Figure 8. Notation as in Figure 2.

the negative contingency generated by a peck of the same subject.

The failure of this implementation of the Rescorla–Wagner model to reproduce our molecular data can be interpreted in different ways. It is possible that the basic structure of the process was correctly modeled but that an additional, longer term process was superimposed that generates bouts, or inertia, of behavior. Alternatively, the changes in associative value may not act trial by trial, as implied in our model, but with a "memory" of several trials, so that once a bird crosses some threshold that leads it to attempt a response, the consequences of the response take several trials to have an effect. Our results are consistent with those of Prokasy and Gormezano (1979), who examined the process of conditioning in rabbits using an aversively controlled nictitating membrane response and an appetitive jaw-movement response to water delivery. These authors found that although the Rescorla–Wagner model was effective in explaining molar differences between groups exposed to either intermittent or 100% reinforcement, the model could not account for the microstructure of the data in terms of conditional probabilities of responses after trials with or without reinforcement and with or without responses. Their results, as well as ours, seem to require multitrial integration of the consequences of each event, which is not implemented either in the Rescorla–Wagner or the game-theoretical models discussed in this paper (TFT, GTFT, and WSLS).

In summary, our results are compatible with the maintenance of cooperation in situations derived from the iterated prisoner's dilemma, but the processes by which this cooperation is maintained are not compatible with any available single-trial performance model. Our study does not solve the problem of evolution of cooperation, but points to the need for detailed analysis of the microstructure of the data beyond the usual practice in studies of cooperation by behavioral ecologists and conditioning processes by experimental psychologists. Although we are aware that psychological mechanisms of real cooperation may be very different from our contrived laboratory experiments, we hope that our study illustrates some of the limitations of available experimental tests of models for the evolution of cooperation, and point to the need for a deep fusion between psychological and functional thinking for the development of credible (testable) accounts for the mechanisms of cooperation.

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