Why cooperate?
An economic perspective is not enough

Richard Schuster*, Amir Perelberg

Department of Psychology, University of Haifa, Haifa 31905, Israel

Abstract

Cooperation is usually explained from an *economic perspective* focused mainly on the tangible outcomes received by individuals that are also dependent on the behavior of others, with little reference to the actual behaviors used when cooperating. The potential consequences of social dimensions associated with cooperative behaviors are minimized in Skinnerian and game-theory models by means of anonymous subjects that behave individually while physically isolated in separate chambers. When cooperation and non-cooperation occur in the real world, however, they are often associated not only with different outcomes but also with different behaviors. Unlike non-cooperation, cooperative behaviors are usually intrinsically *social*, influenced by the presence and behaviors of familiar partners. Research is described that addresses whether the social dimensions of cooperative actions go beyond mere description of behaviors to also explain *why* cooperation occurs. One way to resolve the relative importance of economic and social factors for explanations of cooperation is to measure *choice* between the options of cooperation and non-cooperation. The economic perspective, linked to models derived from game theory, frames the question as a choice determined by differences in tangible outcomes such as food or money that, in evolutionary terms, are surrogates for gains in fitness. From a behavioral perspective, the choice between cooperation and non-cooperation is also determined by social dimensions associated only with cooperation. The influence of social cooperation on preference was examined by means of two rectangular chambers interconnected by a T-maze. In one chamber, pairs of laboratory rats were reinforced with saccharine solution for coordinating back-and-forth shuttling; in the second chamber, a single animal was reinforced for back-and-forth shuttling performed in isolation. With outcomes equalized between the two options, cooperation was preferred by the majority of subjects. Moreover, variation in the relative rate of reinforcement during cooperation was not a strong predictor of choice whereas the level of intra-pair coordination was positively related to preference. Implications of this result are discussed for both method and theory, including the hypothesis that the preference is influenced by intrinsic reinforcements evoked by cooperating. The consequences for evolutionary fitness would then arise not only from tangible outcomes but from the relationships that develop when cooperating *even when immediate and tangible pay-offs are absent, insufficient or sub-optimal*. The impact of cooperative relationships on fitness may therefore not occur immediately but in the future, and perhaps in another context, when they influence outcomes that have a significant impact on survival and reproduction.
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1. Introduction

Current explanations of cooperation usually focus on an economic perspective. For both experimental psychologists (Hake and Vukelich, 1972;

* Tel.: +972-4-8240924/8253069; fax: +972-4-8240966.
  E-mail address: Schuster@psy.haifa.ac.il (R. Schuster).

Skinner, 1953; Weingarten and Mechner, 1966) and evolutionary biologists (Clements and Stephens, 1995; Dugatkin, 1997; Krebs and Davies, 1993; Mesterton-Gibbons and Dugatkin, 1992; Stephens and Anderson, 1997; Trivers, 1985), cooperation occurs when outcomes for an individual are dependent not only on its own behavior but also on the behavior of others. Outcomes are usually tangible and beneficial events such as gaining access to food, mates, mating sites or money. From the standpoint of evolution, such outcomes are surrogates for gains in fitness. Moreover, the evolution of cooperation is also predicted when access to beneficial outcomes results in a gain in fitness for *all participants* (Dugatkin, 1997; Krebs and Davies, 1993; Mesterton-Gibbons and Dugatkin, 1992; Trivers, 1985).

1.1. Cooperation as social behavior

In an economic analysis, there is nothing special about *how* cooperation is expressed in behavior (Dugatkin, 1997; Stephens and Anderson, 1997). Whether performed alone or with others, behaviors are mainly a way for individuals to gain outcomes. When cooperative and non-cooperative behaviors are performed in the real world, however, they are liable to differ not only in the outcomes obtained by individuals but also in how the behavior is performed. Cooperation is usually an intrinsically *social* phenomenon associated with many interactive components that are not present when animals do not cooperate (Hinde, 1979; Roberts, 1997; Schuster, 2001, 2002a; Schuster et al., 1988, 1993). Social dimensions can be particularly pronounced when pairs or larger groups coordinate actions for shared outcomes. Real-world examples include group hunting (e.g., in lions *Panthera leo*, Scheel and Packer, 1991; Stander, 1992; in chimpanzees *Pan troglodytes*, Boesch and Boesch, 1989; in bottlenose dolphins *Tursiops truncatus*, Connor, 2000) and intergroup aggression (e.g., in lions: Heinsohn and Packer, 1995; in chimpanzees: Boehm, 1992). In humans, Hutchins (1995) analyzed team navigation as typical of groups working together.

When compared with individual behavior, the social dimensions of such coordinated behaviors can render them, a priori, very different from behaviors performed alone for the same outcomes. For a start, cooperation can be more complex than acting alone when the coordination is based on individuals that *learn to act cohesively by attending to, and anticipating, each other's behaviors and locations*. Evidence of sensitivity to the fact of cooperating was obtained with capuchin monkeys *Cebus apella* in which food sharing was more likely after coordinating actions than after behaving individually (de Waal and Berger, 2000). Moreover, coordinating actions can sometimes be based on a clear division-of-labor based on different and complementary roles (Boehm, 1992; Boesch and Boesch, 1989; Connor, 2000; Heinsohn and Packer, 1995; Stander, 1992). As a result, individuals may engage in behavior when cooperating that would be ineffectual if performed alone. In the group hunting of both lions and chimpanzees, for example, some participants may have the role of hiding and catching the prey that is chased in their direction by other group members. It is obvious that the same individuals, when hunting alone, would need to use other tactics. Hutchins (1995) used the term "distributed cognition" to characterize this phenomenon in human group performance. Because such behavior emerges from a dynamic that develops within each cooperating group, marked differences become likely *across* cooperating groups of the same species with respect to levels of coordination, roles, ranks, and social cues.

Perhaps less complex are examples of pairs that coordinate by *matching* each other's behavior. In the context of aggression, rival males compete in this way from adjacent territories. This is expressed in birds as song duets (Beecher et al., 2000; Dugatkin, 1997, pp. 71–73; Serpell, 1981; Todt, 1981) and in antelope as highly ritualized "challenge rituals" (e.g., Schuster, 1976; Leuthold, 1977). The cooperative essence of such aggression has been linked to reducing the cost of serious injury while demarcating shared boundaries, the so-called "dear enemy" phenomenon (Krebs, 1982). In the context of courtship and reproduction, females appear to select a male based on levels of coordination when jointly performing songs, movements and/or aerobatic displays (Maynard Smith, 1978). In humans, pair-wise coordination occurs in "behavior matching" of postures and gestures, often without awareness (e.g., Chartrand and Bargh, 1999). Matching also occurs in large groups characterized by highly ritualized and orchestrated displays in contexts that include praying, marching, applauding, singing, and dancing (McNeill, 1995).

In addition to the actual cooperative behavior, individuals may also engage in *adjunct social interactions* before, during, or after acts of cooperation that can be affiliative and/or agonistic. For example, anecdotal evidence from documentary films has shown that, at the conclusion of a successful hunt, lions engage in mutual body rubbing and grooming, whereas chimpanzees exhibit loud vocalizations, physical contact and general excitement. Though never analyzed, such interactions have the flavor of a "victory" ceremony. Lions have also been observed to engage in similar behavior following episodes of conflict over access to prey. In non-human primates, such behavior would be elevated to the status of "reconciliation" to support a hypothesis of sophisticated social skills (de Waal, 1986).

Another social dimension associated with cooperation is *familiarity*. Cooperators are usually known to each other from shared membership in a group, kinship and/or a history of repeated encounters that may include many previous episodes of cooperation. Familiarity is also thought to be crucial to another form of cooperation expressed as *reciprocal altruism* or delayed-return benefit whereby individuals exchange favors that can be widely separated in time (Trivers, 1971, 1985). Although based on a sequence of individual acts, mutual benefits from reciprocity have been linked to social exchanges between familiar individuals that share a social context within which they repeatedly interact and assess past encounters (de Waal, 1996; Dugatkin, 1997, pp. 19–30.)

Finally, social interactions can also be crucial during the *outcome stage* of a cooperative act by determining how cooperators share access to outcomes. If the outcome is tangible, such as a single prey item (Packer and Ruttan, 1988) or estrus female (Noë, 1990), this may not be shared equally as a result of competition and/or dominance over access. In chimpanzee group hunting, usually performed by males, dominants have priority of access to prey items which can mean that other participants gain little or nothing, particularly when prey are small (Boesch and Boesch, 1989). In humans as well, social strategies of manipulation and bargaining can impact upon outcomes (Forsythe et al., 1994; Frank, 1988; Palameta and Brown, 1999). Moreover, some species seem sensitive to what others are receiving. In capuchin monkeys, food exchange with humans is disrupted by outcome inequities (Brosnan and deWaal, 2003).

The main issue to be addressed here is whether the social dimensions of cooperative actions go beyond mere description of behaviors to explain both why and how cooperation occurs. One reason to examine the potential role of social processes in determining cooperation is the accumulating evidence that tangible outcomes alone are unable to explain the likelihood of both cooperating and choosing whether or not to cooperate. During the acquisition of cooperation, for example, tangible reinforcement may be minimal, perhaps because learning to coordinate, based on the behaviors and locations of others, is difficult. In young lions cooperative hunting only becomes proficient at about 2 years of age (Scheel and Packer, 1991). A recent documentary film on the development of this behavior (A Spy in the Den, British Broadcasting Company) showed anecdotally that coordination for months remained haphazard and poorly executed, the targets poorly chosen, and the probability of food reinforcement minimal. Perhaps this should be classified more as play, and not serious hunting for food (Bekoff and Byers, 1998). But either way, if cooperation learning in lions is based on reinforcement, nutritional gain does not seem to be the exclusive or even the primary motive. Moreover, when outcomes were compared between cooperative and individual hunting in experienced hunters, both lions (Packer et al., 1990) and cheetahs *Acinonyx jubatus* (Caro, 1994) seemed to cooperate more than expected based on analyses of nutritional gains per individual. In a detailed analysis of chimpanzee hunting, male participation was unrelated to either food needs or exchange of food for sex with females (Mitani and Watts, 2001). The best predictor of cooperation was the relationship between cooperators. A recent study of synchronized breathing of dolphins came to the same conclusion (Perelberg and Schuster, submitted).

The examples cited above are consistent with the possibility that acts of cooperation in animals are associated with outcomes that go beyond tangible events such as food and mates to include *intrinsic reinforcement* from engaging in the behavior (Schuster, 2001, 2002a,b). A process of intrinsic reinforcement is in part inferred from examples of behaviors whose probability cannot be explained entirely from tangible outcomes. Intrinsic reinforcement can also explain the persistence of coordination in situations where immediate and tangible reinforcements are not obvious, as

in the examples of courtship and territorial aggression cited above. More explicit support for intrinsic reinforcement can be obtained from experiments on choice between cooperation and non-cooperation revealing a level of preference for cooperation that can not be predicted from rates of reinforcement alone. These will be described below.

The idea that cooperation in humans may be associated with intrinsic reinforcement and emotions has already been proposed (Frank, 1988; Rachlin, 2002; Sober and Wilson, 1998). In humans, such processes have been linked to the complex socio-cultural milieu of human behavior. But humans, like other animals, seem to be reinforced by little more than coordinating behaviors. Humans have described feelings of rapport, excitement, pleasure and power when participating in ceremonial behaviors performed by large groups (McNeill, 1995). The "behavior matching" of postures and gestures has also been linked to rapport and positive evaluations of others (Lakin and Chartrand, 2003). A recent experiment showed that waitresses received higher tips after they verbally mimicked the orders of their customers (van Baaren et al., 2003).

Evolutionary biologists sometimes claim that the social aspects of cooperation should be limited to the less interesting question of *how* the behavior is actually performed, whereas the economic perspective alone addresses the more fundamental issue of *why* (e.g., Dugatkin, 1997; Krebs and Davies, 1993; Stephens and Anderson, 1997). The dichotomy between the *how* and the *why*, between proximate (psychological) and ultimate (evolutionary) explanations, is compromised if reinforcement includes both tangible outcomes linked directly to fitness and affective responses from cooperating with others. This is not meant to refute the likelihood that cooperation is an adaptive behavior. But if cooperation is influenced by a process of intrinsic reinforcement linked to working with others, the problem is *how* such reinforcements might contribute to individual fitness. Some suggestions for resolving this issue will be offered in the last section.

2. Choosing between cooperation and non-cooperation

A powerful way to address the problem of causation is to ask what happens *when an individual can choose between the options of behaving cooperatively or non-cooperatively*. Preference, for example, ought to reveal whether there is any merit to the hypothesis of intrinsic reinforcement from cooperating. In the real world, there may be no choice between whether or not to cooperate, i.e., there is no go-it-alone alternative that is beneficial or adaptive. In the context of reproduction, for example, monogamous cooperation between a male and a female can be *obligate* when the presence of both males and females is necessary for the survival of offspring, i.e., when males cannot benefit from pursuing additional females (Emlen and Oring, 1977). Another possibility is for both males and females to have the option of choosing between reproducing by means of monogamy or polygyny, depending on factors that influence the ability of females to raise young on their own (Emlen and Oring, 1977; Orians, 1969). In the context of predation as well, there can also be the option of hunting alone or in a group, as in lions (Packer et al., 1990).

2.1. Choice from the economic perspective

When a choice exists between whether or not to cooperate, the economic perspective frames the question as a choice made by an individual between two behavioral responses, cooperation and non-cooperation, determined by the difference in outcomes. In laboratory experiments, outcomes are represented by amounts, rates or delays of events such as food presentations, money or points. The focus on individual outcomes can become confusing because, as noted above, cooperation for evolutionary biologists is also "... an outcome that ... is 'good' in some appropriate sense for (all) the members of a group and whose achievement requires collective action" (Mesterton-Gibbons and Dugatkin, 1992). But since social factors are rendered irrelevant, the possibility that others might also benefit from a preference for cooperation is usually dismissed a priori as an unintended "by-product" that has nothing to do with the reason why any individual might choose to cooperate (Brown, 1983). For this reason, the terms *mutualism*, or *by-product mutualism*, are sometimes preferred by behavioral ecologists when describing cooperative coordination (e.g., Dugatkin, 1997).

An additional assumption underlying the economic perspective is that both cooperation and

non-cooperation are behavioral acts *performed by individuals*. In one sense this is trivial. As Skinner (1953) noted, "... a 'social law' must be generated by the behavior of individuals. It is always an individual who behaves ...." But Skinner went further, adding "... and he behaves with the same body and according to the same processes as in a non-social situation.... The individual behavior explains the group phenomenon." In practice, this was translated into experiments in which two or more subjects behave *alone* when cooperating. These include the popular game-theoretical models of "social dilemmas" such as the well-known Prisoner's Dilemma or PD (Clements and Stephens, 1995; Colman, 2003; Dugatkin, 1997; Rapoport and Chammah, 1965). A game is reduced to a choice between options identified as "cooperation" and "non-cooperation" (or "defection") that are represented entirely by different outcomes. With respect to behavior, the options do not differ. They are both individual acts, such as pressing two different keys, with outcomes determined by the choices of all participants. Moreover, using what Colman (2003) characterized as "the bedrock of methodological individualism," *anonymous individuals* are asked to express their preference while *physically isolated in separate compartments that minimize or totally eliminate social interaction both when behaving and when receiving reinforcements*. This approach has been used with both animals (e.g., Baker and Rachlin, 2002b; Clements and Stephens, 1995; Flood et al., 1983; Green et al., 1995) and humans (e.g., Baker and Rachlin, 2002a; Colman, 2003; Fehr and Gachter, 2002; Fehr and Rockenbach, 2003; Rapoport and Chammah, 1965). In some models, the opponent is not even a live subject but a computer (e.g., Baker and Rachlin, 2002a).

A precursor of such isolation models, in both method and theory, was offered by Skinner (1953) who argued from his individual-behavior perspective that the essence of cooperation was captured by reinforcing the synchronizing of simple responses such as a bar pressing or key pecking of two subjects isolated in separate chambers (for a review, Hake and Vukelich, 1972). By preserving the individual properties of both behavior and reinforcement, Skinner sought to extend the processes underlying individual learning to cooperation. In some Skinnerian experiments, a remnant of social interaction was introduced

by using transparent partitions between the two chambers. Subjects then had to respond to the operant behavior of their partner as the timing cue for executing their own responses. But in so-called "non-social cooperation" experiments (Hake and Vukelich, 1972), interaction was completely eliminated by opaque partitions. Synchronization became possible only if the behavior of one subject provided a non-social light or tone to the other subject that signaled the opportunity to gain reinforcement by responding.

The reliance on "isolation experiments" reflects the underlying assumption that a choice between cooperation and non-cooperation is really the same as a choice between two individual behavioral acts associated with different outcomes. In behavior analysis, this problem was analyzed using individual animals exposed to concurrent schedules of reinforcement (e.g., Herrnstein, 1961). Since the motivation governing choice is linked only to outcomes, individuals are expected to behave optimally in this situation by distributing behavior between the two options in a ratio that matches the proportion of reinforcement from each option, i.e., the *matching law*. Although the pay-off contingencies in a game such as a PD are more complex, the expectations are similar. Individuals are expected to behave optimally, distributing their choices between cooperation and non-cooperation so as to maximize their individual outcomes (Axelrod and Hamilton, 1981; Rapoport and Chammah, 1965). Non-cooperation is the selfish option in the short-term if the contest is limited to a single trial whereas, over repeated trials, cooperation can become the selfish option for each player if both players adopt the same strategy, e.g., tit-for-tat (Axelrod and Hamilton, 1981). The dilemma is therefore not about self-interest versus cooperative altruism but about whether self-interest emerges over the short or long term. Rachlin (2002) and Baker and Rachlin (2002a, b) characterized this not as a social dilemma but as a problem of individual self-control.

Game theory has been a valuable tool for gaining insights into processes underlying rational decision-making (Luce and Raiffa, 1957), economics (Nash, 1950; von Neumann and Morgenstern, 1953) and the evolution of evolutionary stable strategies or ESSs (Maynard Smith, 1984). Using both conceptual and mathematical analyses, game theorists have shown how these processes lead to selection of the most profitable options that, in the evolutionary context,

also predict the direction of gene selection (Dugatkin, 1997; Krebs and Davies, 1993; Mesterton-Gibbons and Dugatkin, 1992; Stephens and Anderson, 1997; Trivers, 1985). Moreover, the route taken to achieving optimal outcomes is explained without reference to the kinds of proximate psychological processes that underlie the *actual behavior* of an individual making a decision (for a review, Colman, 2003). Optimization, however, was also expected to emerge from the behavior of live subjects. This is tantamount to arguing that the proximate psychological processes generating "instrumental rationality" and "maximization of expected utility" are supposed to mimic the optimality resulting from the kinds of "mindless" processes thought to underlie economics and natural selection. The clear intention was to generate a direct link between rational behavior and evolutionary fitness (Dugatkin, 1997; Stephens and Anderson, 1997). The use of models with anonymous subjects and physical isolation can be seen, in retrospect, as a core component of this program. Without social interaction, outcome differences by default were expected to be the dominant influence over choice.

2.2. Choice from a behavioral perspective

In contrast to a purely economic perspective, the determinants of choice from a behavioral perspective are framed as a *choice between two kinds of behavior that differ qualitatively*, one a cooperative behavior associated with social dimensions and the other an individual behavior associated with the *absence* of those social dimensions (Roberts, 1997; Schuster, 2000, 2001, 2002a,b, 2003). This is not meant to deny that outcome differences can be an important factor governing choice. But if the social context of cooperation is also important, choices would be determined not only by parameters of tangible outcomes but also by dimensions of cooperative behaviors such as the fact of collaborating with others, the level of behavioral coordination when cooperating and the relationship among cooperators with respect to dominance, control, age, sex and past encounters. To the extent that the social context is linked to processes of motivation, emotion and reinforcement that are intrinsic to behaving cooperatively, the expected result is a preference that could deviate markedly from expectations based only on tangible outcomes (Perelberg and Schuster,

submitted). The direction of the bias would depend on whether the affect associated with these processes is positive or negative.

Game-theory experiments, by minimizing exposure to social dimensions, are not appropriate for analyzing the extent to which the *behavior* of cooperating is also a significant determinant of choice. There has to be some irony in the fact that evidence for a *cooperation bias* is nevertheless accumulating from game theory experiments with human subjects. Despite their isolation and anonymity, human subjects are cooperating more than they should if guided by instrumental rationality alone (Colman, 2003; Fehr and Gachter, 2002; Fehr and Rockenbach, 2003; Palameta and Brown, 1999). Moreover, if subjects are explicitly informed about the participation of others, their behavior can be modified (e.g., Baker and Rachlin, 2002a). It appears, therefore, that human subjects play the games as if they are social. Some game theorists had already noted that the choice of a cooperative option ought to be influenced by playing iterated games in which participants experience and recall repeated trials with the same players (Dugatkin and Wilson, 1992). Dugatkin (1995) and Noë and Sluijter (1995) have also pointed out that partner preference can be a factor when choosing between cooperation and defection.

In contrast to games played by humans, games with *animal* subjects present the opposite problem: in a variety of species, animals act as if they are *unaffected* by the participation of another subject in a separate chamber. Their behavior, in other words, remains truly individual. In experiments limited to synchronizing individual operants, there is little difference between the results obtained with transparent or opaque partitions (Hake and Vukelich, 1972). And in PD games, animals consistently chose non-cooperation, revealing a strong bias towards the larger, immediate outcome associated with a preference for "non-cooperation" (Clements and Stephens, 1995; Flood et al., 1983; Green et al., 1995). Again, the result is not affected by whether the partition isolating the animals is transparent or opaque (Clements and Stephens, 1995). Preference can be shifted to the "cooperative" option by manipulations that have no special relevance to social behavior. These include canceling out the deleterious consequences of "discounting" on the effectiveness of delayed reinforcers (Stephens et al., 2002) or associating

external cues to facilitate the discrimination between the consequences of prior choices (Baker and Rachlin, 2002b).

3. Modeling choice between social cooperation and non-cooperation in animals

The remainder of this paper addresses two questions: (1) What happens to the choice between cooperation and non-cooperation in an animal model if social dimensions are restored to the cooperative option? (2) What implications do the results have for method and theory in the study of cooperation?

These questions were addressed by experiments with animals that were designed to rehabilitate cooperation as a social behavior in order to address the issues of explanation discussed above (Schuster, 2001, 2002a,b; Schuster et al., 1988, 1993). In contrast to experiments focused on outcome differences, outcomes were deliberately equalized between the two options. The choice instead was between *two qualitatively different behavioral responses*: cooperation based on social interaction, and non-cooperative behavior based on the same behavior performed alone.

3.1. The options: social cooperation versus non-cooperation

Social cooperation consists of two animals that use each other to coordinate movements in space. The model therefore incorporates the kinds of social dimensions characterizing behaviors such as cooperative hunting and aggression in the real world (Boesch and Boesch, 1989; Schuster, 2001, 2002a; Stander, 1992). The non-cooperation option involves performing the same behavior alone. This model also shares many features with a pioneering experiment on cooperation in which pairs of rats had to coordinate an exchange of locations within a shared chamber to obtain reinforcement while also avoiding electric shocks (Daniel, 1942).

In the choice experiments, Norway rats *Rattus norvegicus* of the Wistar strain could enter one of two identical rectangular chambers, length 94 cm, with three contiguous floors and reinforcement (0.9 mM saccharine solution) available from one or two cups

adjacent ("*near*") to floor N (see Fig. 1). The other floors were M for *middle*, and D for *distant* from the cups. Operationally, reinforcement was contingent on micro-switches *only under D* that remained closed for a minimum of 0.5 s followed by micro-switches *only under N* that remained closed for a minimum of 0.5 s. In terms of behavior, reinforcement was delivered for back-and-forth shuttling, first to floor D and then back to floor N. The difference between cooperation and non-cooperation resided in whether the D → N contingency was satisfied by an individual or a pair. In the chamber associated with *non-cooperation*, shuttling alone was reinforced in individual animals by presentation of a single cup. In the chamber associated with *cooperation*, coordinating back-and-forth shuttling (remaining *together* on D and then *together again* on N) by pairs of animals was reinforced by presentation of two cups. No limitations were placed on how pairs satisfied the cooperation contingency, whether by shuttling together or sequentially. There were also no restrictions on social interactions. The only cues available when behaving were from the locations and behavior of the subjects themselves without the aid of non-social feedback such as a light cue. Cooperating partners in each pair remained the same throughout. Taken together, the design features of the model loosen the tight experimental control over individual behavior that characterizes physical isolation models in favor of a context within which pairs develop their own idiosyncratic ways of satisfying the outcome contingency.

3.2. Criteria of social cooperation

The claim that coordinated shuttling is a form of *social* cooperation requires verification. A series of experiments showed that pairs learn to work together and develop behaviors that are social (summarized in Schuster, 2001, 2002a). Some of the criteria would be relevant to assessing the validity of *any model* of social behavior. Among the criteria tested were the following:

1. *Coordination is based on the use of social cues from locations and behaviors*: Without the assistance of non-social cues, pairs could only coordinate when run in the same chamber but not when isolated in separate chambers.
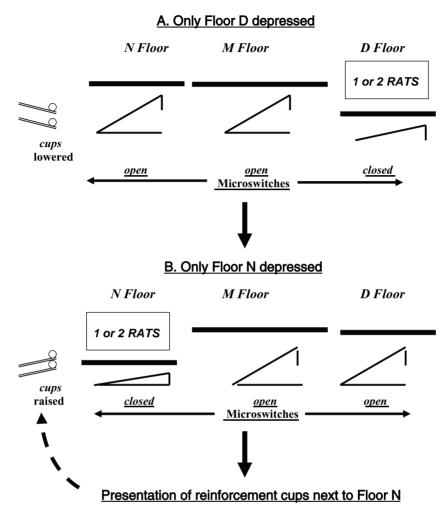
Fig. 1. Diagram of the contingency of reinforcement for individual rats or cooperating pairs. Reinforcement for both individual and cooperating rats was contingent on subjects that were first only on the D-floor (0.5 s) and then only on the N-floor (0.5 s). Reinforcement, 3 mM saccharine solution, was presented adjacent to Floor N in one cup to individual rats or in two cups to cooperating rats.

2. *Coordination is under the control of the cooperative contingency of reinforcement*: When pairs were run in the same chamber, both coordination and adjunct social interactions increased over sessions only when reinforcement depended on coordination, but not when reinforcement depended on individuals shuttling independently.

3. *Sensitivity to partners*: Coordinated shuttling was sensitive to factors known to affect other social behaviors including housing (social or individual), sex (male versus female pairs), rat strain (Wistar,

Sprague–Dawley, or S3—maze dull), and kinship (litter-mates versus non-litter-mates.)

4. *Pairs learn to work together*: Evidence for learning to work together was obtained from pairs comprising one experienced and one naïve partner. When the prior experience was in cooperating, cooperation learning was facilitated, whereas prior experience in non-cooperation interfered with acquisition. Since the prior experience included matched reinforcement (see Section 3.4, below), the difference in learning with new partners reflects

acquisition of elements associated with cooperation that were absent in animals that had learned to behave alone.

5. *Partners learn different "roles"*: In 4, above, evidence of complementary role differences was obtained from experienced cooperating pairs that sometimes differed in their ability to learn with new, naïve partners. The behavior was acquired more rapidly and performed at higher levels when the experienced pair members had been *initiators* of social interactions. Such behavior had been observed previously (Schuster et al., 1993) and was similar to descriptions of touching and tail-pulling which were embedded in the coordinations reported by Daniel (1942). It seemed possible that initiators were "controlling" the behavior and timing of more passive partners by means of social cues. This was tested by selecting experienced pairs with unambiguous asymmetry between initiators and receivers of social cues, and providing all animals with new partners (Schuster, 2001). Partners were either *switched* among cooperating pairs, initiators with initiators and receivers with receivers, or experienced partners were given naïve partners, thus replicating the procedure described in 4, above. The results from the two procedures were the same: initiators of social interactions learned faster, and to a higher level of coordination.

6. *Physiological substrates*: Qualitative differences between cooperation and non-cooperation were supported by evidence from high-pressure liquid chromatography (HPLC) that cooperative and individual shuttling differ in monoamine activation (Tsoory Youdim and Schuster, submitted). A complementary result was shown in humans using magnetic resonance imagining or fMRI (Rilling et al., 2002).

3.3. Rats as subjects

Since coordinated shuttling is offered as an ecologically valid alternative to isolation models, legitimate questions arise about the use of rats as subjects. Although Norway rats are not renowned for spontaneously cooperating under free-ranging condition, they are nevertheless a highly social and adaptable species that, in the wild, live in colonies characterized by dominance and a repertoire of social signals

(Barnett, 1975; Grant and Mackintosh, 1963). Rats also exhibit social learning whereby feeding habits can transfer between individuals in a variety of ways (Galef, 1990). It is also noteworthy that cooperative hunting by means of coordinated behaviors can develop under free-ranging conditions in species that typically hunt alone, such as Harris' hawks *Parabuteo unicinctus* (Bednarz, 1988) and cheetahs (Caro, 1994). Cooperative hunting has also been reported *across unrelated species*, as in the example of badgers *Taxidea taxus* and coyotes *Canis latrans* (Minta et al., 1992). It may be that many species can readily learn to coordinate behaviors if there is sufficient sensitivity to the presence and behaviors of others.

Numerous experiments have confirmed that both male and female rats readily learn to coordinate shuttling (Berger et al., 1980; Schuster, 2001, 2002a; Schuster et al., 1988, 1993, 1982; Swanson and Schuster, 1987). Prior to working together, individual partners' shuttling is first reinforced alone until reaching a criterion rate. They are then run together with reinforcement occurring only for correctly coordinated shuttles. Most pairs show improvement on Day 1 and typically reach asymptotic rates within 4 or 5 sessions. Failures to learn are almost always associated with violent fighting.

3.4. Matched reinforcement

Special procedures are required to isolate the social dimensions distinguishing cooperation and non-cooperation from differences in reinforcement conditions associated with the two options. Without special procedures, subjects behaving individually would receive reinforcement for a higher proportion of their shuttles, with the potential for a higher rate of reinforcement. This happens because cooperating subjects do not receive reinforcement whenever there is a *coordination error*. An error is scored for a coordinated shuttle if the first animal to reach the D floor fails to await the arrival of its partner. In contrast, subjects shuttling individually rarely make errors, once the behavior is acquired. One way to rectify the outcome disparity is to reinforce shuttling alone according to the *proportions of reinforced shuttles obtained by individuals when cooperating*. These proportions, based on previous data, vary from about 0.30 on Day 1 and rise to about 0.80 by Day 10. Using these
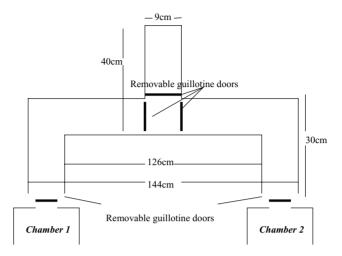
Fig. 2. Diagram of T-maze used in choice experiments. Chambers 1 and 2 refer to experimental chambers associated with cooperation and non-cooperation, counterbalanced across subjects. The behaviors and reinforcement contingencies are described in the text.

proportions to reinforce non-cooperation is referred to as the technique of *matched reinforcement*.

3.5. Measuring choice

To measure choice, two identical chambers, one associated with cooperative shuttling and the second with individual shuttling, were interconnected by a T-maze (Fig. 2). To aid in learning the locations, the floor of one arm of the maze was black, the other white, with the locations of the two options counterbalanced. A three-stage procedure was used:

- *Stage 1*: Subjects were placed directly into the two chambers in order to learn the tasks associated with each. This stage continued for 10 sessions, with exposure to both options in counterbalanced order. Each option was terminated after 20 reinforcers or 20 min, whichever came first.
- *Stage 2*: Subjects were run from the T-maze and learned the *locations* of the chambers associated with the two tasks by means of *forced choice*. Using barriers at the choice point, each subject received a total of six sessions, each with two entries from the maze into both options. After entering a chamber, subjects remained for 5 min or after receiving 10 reinforcers, whichever came first.
- *Stage 3*: Subjects received four sessions, each with two forced choices followed by two free choices, for a total of eight free-choice trials per subject. As

in Stage 2, subjects remained in the chamber after entry for 5 min or after receiving 10 reinforcements, whichever came first.

Free-choice trials were always based on *equalizing prior experience* with the cooperation and non-cooperation options. The problem of equal exposure arose during both Stages 2 and 3 when permanent pair members were alternated as "subject" or "drop-in" during successive sessions. In each session, the "subject" was the partner in each pair that entered the respective chambers from the T-maze during Stages 2 and 3, and also had the option during Stage 3 of choosing between the alternatives. The "drop-in" was the partner placed directly into the cooperation chamber as soon as the subject had entered from the T-maze. Drop-ins during forced-choice trials therefore received additional exposure to the cooperation option whenever their partners entered the relevant chamber from the T-maze. In addition, imbalance also arose for both subjects and drop-ins from free choice during Stage 3. To equalize prior exposure, animals were given extra runs by placing them directly into the chamber that had been experienced less.

3.5.1. Experiments

There were two experiments. Experiment 1 was based on the procedure of *matched reinforcement* (Section 3.4) described above. In Experiment 2, both individual and cooperative shuttles were reinforced
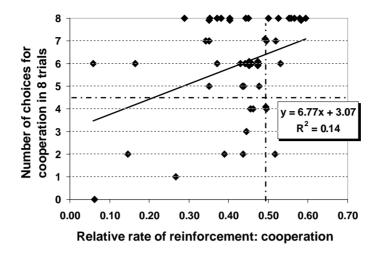
Fig. 3. Relationship between the number of choices for cooperation (maximum: 8) during Stage 3 and the relative rate of reinforcement when cooperating during the last five sessions of Stage 1. Data are from Experiments 1 and 2 combined (see text for description of experiments, stages, and the measure of relative rate).

for 100% of correctly-performed D $\rightarrow$ N shuttles, thereby elevating the proportion of shuttles associated with reinforcement from engaging in the almost error-free behavior of non-cooperation. Rates of reinforcement for both options were calculated from the ratios of reinforcements to total time *inside* the respective chambers. The *relative rate of reinforcement during cooperation* was calculated as the ratio of the

rate when cooperating to the sum of the rates when cooperating and not cooperating.

3.5.2. Results

Figs. 3 and 4 show that coordinated shuttling was preferred by the majority of subjects in both experiments, with preference defined as choosing the cooperation option in a minimum of five out of eight trials.
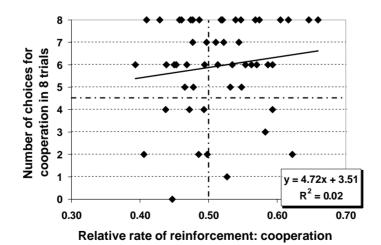

Fig. 4. Relationship between the number of choices for cooperation (maximum: 8) and the relative rate of reinforcement when cooperating during the forced-choice trials of Stage 3. Data are from Experiments 1 and 2 combined (see text for description of experiments, stages, and the measure of relative rate).
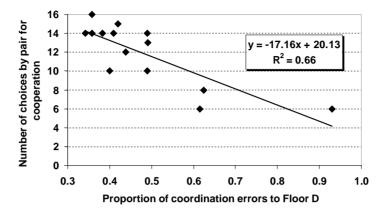
Fig. 5. Relationship between the total number of choices for cooperation by both pair members (maximum: 16) during Stage 3 and the proportion of coordinated shuttles with errors during the last five sessions of Stage 1 of Experiment 1 (see text for explanation of errors and conditions of Experiment 1).

The total number of subjects showing preference in both experiments was 78%, with separate chi-square tests showing significance in each experiment. This *bias towards cooperation* was obtained despite a mean relative rate of reinforcement associated with cooperation that was below 0.5 during the last five sessions of Stage 1, reaching about 0.5 by Stage 3. In other words, when averaged across subjects, there was little or no incentive for choosing either option at the time that the choice was offered. The economic perspective therefore predicts, at most, indifference between cooperation and non-cooperation or even preference for non-cooperation associated with higher relative rates of reinforcement during earlier stages.

Figs. 3 and 4 also show that despite wide variation in relative rate of reinforcement during cooperation, this was not a strong predictor of choice. Fig. 3 shows the relationship between reinforcement during the last five sessions of Stage 1 and preference during Stage 3; Fig. 4 shows the relationship between reinforcement during the forced-choice trials of Stage 3 that immediately preceded free choice. Both figures reveal that a large number of subjects preferred to cooperate even when their relative rates of reinforcement during cooperation were less than 0.5. Fig. 5 shows that one factor predicting preference was the *intra-pair level of coordination* as measured by the proportion of coordinated shuttles with errors (see description of this measure in Section 3.4, Matched Reinforcement, above). Preference was higher in pairs with fewer coordination er-

rors. This relationship provides support for the claim that preference was not due merely to the difference between social proximity in the cooperation chamber and isolation in the non-cooperation chamber. Instead, the preference by pair members was also linked to how well they were coordinating their behaviors.

4. Implications of the preference for cooperation in animals and humans

There are three implications of the above result that will be addressed here. The first is for *explanation*, focusing on problems that arose historically from predicting that instrumental rationality would result from psychological processes underlying cooperation. The second implication, a reflection of the first, concerns the *methodology* of designing experiments to generate rationality by means of anonymous subjects, social isolation and individual behaviors. The third implication is *comparative*, and concerns whether the cooperation bias in humans and animals reflects underlying psychological processes that might be shared.

4.1. Explanation

Schuster (2003) has suggested that the goal of using isolation experiments to generate "instrumental rationality" from live subjects is a reflection of underlying explanatory confusion between ultimate (evo-

lutionary) and proximate (psychological) processes. This is not an argument against the likelihood that cooperative behavior is adaptive, but *against the hypothesis that the same economic principles, based on tangible and beneficial outcomes, underlie both natural selection and proximate psychological processes in determining the likelihood of cooperation*. Instead, as suggested earlier, the evidence for a cooperation bias, including the results of the choice experiments with rats, are compatible with proximate processes of reinforcement underlying learning and performance that include both tangible outcomes and *immediate and intrinsic pay-offs associated with the performance of social cooperation*.

The practical consequence of intrinsic reinforcement is that cooperative behavior can be learned and maintained *even when immediate and tangible pay-offs are absent, insufficient or sub-optimal* (Schuster, 2001, 2002a). At first glance, this would seem to violate not only expectations of instrumental rationality, but also evolutionary fitness. But one way for "irrational" reinforcement from cooperating to increase fitness is via strengthening social relationships among habitual cooperators. Relationships would also be influenced by adjunct social interactions before, during and after cooperating, including the use of affiliative interactions that follow conflicts over outcomes. The adaptive significance of intrinsic reinforcement from cooperating would become more obvious when the impact of cooperative relationships on fitness does not occur immediately but in the future, and perhaps in another context. Returning to the example of lion cooperative hunting, it may not always pay in terms of food gained per individual (Packer et al., 1990; Scheel and Packer, 1991). But if social relationships develop from cooperative hunting, the most significant evolutionary pay-off can arise from adult females that have to jointly defend their cubs against dangers that include infanticidal males (Packer et al., 1990), hyenas and members of other lion prides. Similarly, food and sex did not seem to be the primary motives when male chimpanzees hunted cooperatively (Mitani and Watts, 2001). Instead, cooperation was linked to the strength of social bonds with the potential to influence outcomes of intergroup encounters that have direct consequences for mating success and fitness (Watts and Mitani, 2001). And in bottlenose dolphins as well, male pairs have been seen

to form alliances long before they begin to cooperatively consort for females (Connor, 2000). In general, these examples are consistent with evolutionary advantages from cooperation that emerge indirectly and only over the life span.

In one important sense, an economic perspective based on instrumental rationality and individual selfishness can be reconciled with intrinsic reinforcement if individuals are *maximizing affective responses* related to outcomes. Cabanac (1992), for example, has linked reinforcement from various sources to common mechanisms that evoke "pleasure." Individuals could then be said to behave selfishly and rationally by opting for cooperation over individual behavior when they maximize "pleasure" from all sources of reinforcement, both explicit and intrinsic. The total reward from cooperating in the short-term would then provide a proximate mechanism for maximizing the eventual long-term pay-off in reproductive success. One difficulty with an economic perspective based on "pleasure" is that it renders the relationship between "selfishness" and "rationality" virtually meaningless. Any reinforced behavior, by definition, would then become a rational act if it led *only* to maximization of pleasure, including drug addicts who do anything to gain the next dose, or religious fanatics who rejoice in their prayers and ceremonies while endangering themselves, their kin and their countries. Such behaviors surely qualify psychologically as selfish, but their negative impact on fitness hardly qualifies them as rational.

In order to maintain the distinction between proximate and ultimate explanations, it seems useful to maintain a distinction between the long-term consequences of behaviors on maximizing fitness and the short-term consequences of behaviors on access to explicit outcomes that may eventually be linked to fitness, such as immediate economic gains in food or mates. Returning to the example of choosing between cooperation and non-cooperation, if individuals in the short-term fail to maximize explicit outcomes because of affective feedback from cooperating, this could still lead to maximization of fitness despite a significant deviation from instrumental rationality. The difference between ultimate and proximate explanations of cooperation is reminiscent of the historical distinction between *need* and *drive*. Even though the term "drive" has fallen on hard times, it is still worthwhile to recall

why psychologists, concerned about the issue of motivation, saw merit in talking about psychological processes underlying drives that are ultimately related to biological processes underlying needs but not isomorphic with them (Bolles, 1967). The use of isolation models in the study of cooperation, by blurring the differences between social and individual behaviors, also obscured the psychological reasons why individuals might choose to cooperate even when immediate pay-offs are not optimal.

This perspective regarding cooperation can be extended to *any behavior* characterized by a pronounced lag-time between its first appearance and its impact on fitness. Lion cooperative hunting is typical of "play behaviors" that first appear early in development, long before they lead to tangible outcomes with adaptive significance (Bekoff and Byers, 1998). Another example is the conspicuous, stiff-legged jumping of several species of antelope known as "stotting" or "pronking" (Leuthold, 1977). This behavior first appears spontaneously in young fawns, with the adaptive significance only becoming apparent when performed vigorously in the presence of a predator. If the performance of such behavior is determined in part by processes of intrinsic reinforcement, this would provide a mechanism that compensates for an inability to comprehend long-range consequences of actions. More generally, processes of intrinsic reinforcements would bypass the problem of self-control that plagues both animals and humans when choosing between behavior leading to smaller, immediate reinforcements, and other behaviors leading to larger but delayed reinforcement (Logue, 1988; Rachlin, 1995). As noted above, this is analogous to the choice facing subjects in a PD game (Baker and Rachlin, 2002a,b) and in any situation when cooperation is associated with less tangible reinforcement than non-cooperation.

4.2. Methodology in the study of cooperation

With respect to *methodology*, the rat data suggest an alternative to isolation models for explaining the cooperation bias that seems to be shared by humans and animals. If the design of Skinnerian and game-theory models was appropriate for studying optimization and rationality, the evidence for a cooperation bias raises questions about the advantages from continuing to study cooperation under conditions that preclude any

experimental control over the social context experienced by subjects (Schuster, 2003). In the absence of social interaction, and with few social variables to manipulate, it is necessary to assume that the bias in humans emerges from some level of *awareness* that the games are in fact social. Colman (2003) tried to solve this problem by amending classical game theory with a variety of post hoc intervening variables lumped together as "psychological game theory." These include "group-identity," "social value orientation," "collective preferences" and "team reasoning." Others have suggested less lofty motives such as avoiding the potential embarrassment from meeting another player that has just been victimized by selfish defection (e.g., Forsythe et al., 1994; Palameta and Brown, 1999). Given the social isolation and the unreliability of the bias, it is far from obvious how any of the above explanations could remain much more than sheer speculation. And, we would still be left with the problem of animals that prefer not to cooperate when run in isolation models (Clements and Stephens, 1995; Flood et al., 1983; Green et al., 1995).

In contrast to isolation models bereft of any social context, the kind of model described above with rats was able to generate a reliable bias towards cooperation under conditions that made the social context of cooperation *explicit and distinct* from the non-social context associated with non-cooperation. If the cooperation bias is a genuine and widespread phenomenon, the advantage of the cooperation model described here is that it incorporates social dimensions with external validity vis a vis cooperation in the real world. This kind of model also offers the potential for isolating and manipulating the social elements associated with a cooperation task that renders it potentially more attractive than working alone. And by offering a choice between social cooperation and non-cooperation, it becomes possible to separate the effects of explicit from intrinsic outcomes. The dimensions of social behavior that contribute to intrinsic reinforcement are not yet known. But experiments are planned in which social cooperation will be dissected into components that can be separately analyzed for their effect on preference. Candidates include the reinforcement for pairs contingent on cooperating versus behaving independently, the levels of coordination and proximity when cooperating, role and rank differences between cooperators, and variation in cooperative relationships associated

with factors such as sex, age, species, early stress, and prior encounters. Overall, this approach offers the advantages of an experimental analysis of social variables over experiments in which a social behavior is studied without social interaction.

4.3. Cooperation in comparative focus

The third point is *comparative* and concerns the kinds of proximate processes that might underlie the cooperation bias in other species, and especially humans. The rat data point to intrinsic reinforcement and positive emotions associated with social cooperation that are almost certainly more elementary, and also phylogenetically more ancient, than hypothetical states such as "team reasoning" and "social value orientation" that are products of the unique socio-cultural life of humans. It is tempting, if premature, to suggest that such elementary processes may be evolutionarily homologous or analogous with processes in a human species that, in all cultures, is characterized by working in groups (Hutchins, 1995) and experiencing positive emotions linked to both coordinated ceremonial behaviors (McNeill, 1995) and simpler acts of "behavior matching" (Lakin and Chartrand, 2003; van Baaren et al., 2003). Ideas like these arise from a behavioral perspective that is rarely incorporated into experimental models deliberately designed to minimize the influence of social interaction. It is hardly surprising that cooperation, and social behavior in general, are absent from contemporary textbooks on animal learning. Perhaps the time has come for the experimental analysis of behavior to recognize that "social" is not just a feature of reinforcement contingencies but also of behavior.

Acknowledgements

References

Axelrod, R., Hamilton, W.D., 1981. The evolution of cooperation. Science 211, 1390–1396.

Baker, F., Rachlin, H., 2002a. Teaching and learning in a probabilistic Prisoner's Dilemma. Behav. Proc. 57, 211–226.

Baker, F., Rachlin, H., 2002b. Self-control by pigeons in the Prisoner's Dilemma. Psychon. Bull. Rev. 9, 482–488.

Barnett, S.A., 1975. The Rat: A Study in Behavior, second ed. University of Chicago Press, Chicago.

Bednarz, J.C., 1988. Cooperative hunting in Harris' hawks (*Parabuteo unicinctus*). Science 239, 1525–1527.

Beecher, M.D., Campbell, S.E., Nordby, J.C., 2000. Territory tenure in song sparrows is related to song sharing with neighbors, but not to repertoire size. Anim. Behav. 59, 29–37.

Bekoff, M., Byers, J.A., 1998. Animal Play: Evolutionary, Comparative, and Ecological Perspectives. Cambridge University Press, New York.

Berger, B.D., Mesch, D., Schuster, R., 1980. An animal model of "cooperation" learning. In: Thompson, R.F., Hicks, L.H., Shvyrkov, V.B. (Eds.), Neural Mechanisms of Goal-directed Behavior. Academic Press, New York, pp. 481–492.

Boehm, C., 1992. Segmentary warfare and management of conflict: a comparison of East African chimpanzees and patrilineal-patrilocal humans. In: Harcourt, A., de Waal, F.B.M. (Eds.), Coalitions and Alliances in Humans and Other Animals. Oxford University Press, Oxford, pp. 137–173.

Boesch, C., Boesch, H., 1989. Hunting behavior of wild chimpanzees in the Tai National Park. Am. J. Phys. Anthropol. 78, 547–573.

Bolles, R.C., 1967. Theory of Motivation. Harper & Row, New York.

Brosnan, S.F., deWaal, F.B.M., 2003. Monkeys reject unequal pay. Nature 425, 297–299.

Brown, J.L., 1983. Cooperation—a biologist's dilemma. In: Rosenblatt, J.S. (Ed.), Advances in the Study of Behavior. Academic Press, New York, pp. 1–37.

Cabanac, M., 1992. Pleasure: the common currency. J. Theor. Biol. 155, 173–200.

Caro, T.M., 1994. Cheetahs of the Serengeti Plains: Group Living in an Asocial Species. University of Chicago Press, Chicago.

Chartrand, T.L., Bargh, J.A., 1999. The chameleon effect: the perception–behavior link and social interaction. J. Pers. Soc. Psychol. 76, 893–910.

Clements, K.C., Stephens, D.W., 1995. Testing models of non-kin cooperation: mutualism and the Prisoner's Dilemma. Anim. Behav. 50, 527–535.

Colman, A.M., 2003. Cooperation, psychological game theory, and limitations of rationality in social interaction. Behav. Brain Sci. 26, 139–198.

Connor, R.C., 2000. Group living in whales and dolphins. In: Mann, J., Connor, R.C., Tyack, P.L., Whitehead, H. (Eds.), Cetacean Societies. University of Chicago press, Chicago, pp. 199–218.

Daniel, W.J., 1942. Cooperative problem solving in rats. J. Comp. Psychol. 34, 361–368.

de Waal, F.B.M., 1986. The integration of dominance and social bonding in primates. Q. Rev. Biol. 61, 459–479.

de Waal, F.B.M., 1996. Good Natured: The Origins of Right and Wrong in Humans and Other Animals. Harvard University Press, Cambridge, MA.

de Waal, F.B.M., Berger, M.L., 2000. Payment for labour in monkeys. Nature 404, 563.

Dugatkin, L.A., 1995. Partner choice, game theory and social behavior. J. Quant. Anthropol. 5, 3–14.

Dugatkin, L.A., 1997. Cooperation Among Animals: An Evolutionary Perspective. Oxford University Press, Oxford.

Dugatkin, L.A., Wilson, D.S., 1992. Rover: a strategy for exploiting cooperators in a patchy environment. Am. Nat. 138, 687–701.

Emlen, S.T., Oring, L.W., 1977. Ecology, sexual selection and the evolution of mating systems. Science 197, 215–223.

Fehr, E., Gachter, S., 2002. Altruistic punishment in humans. Nature 415, 137–140.

Fehr, E., Rockenbach, B., 2003. Detrimental effects of sanctions on human altruism. Nature 422, 137–140.

Flood, M., Lendenmann, K., Rapoport, A., 1983. A 2×2 game played by rats: different delays of reinforcement as payoffs. Behav. Sci. 28, 65–78.

Forsythe, R., Horowitz, J., Savin, N., Sefton, M., 1994. Replicability, fairness and play in experiments with simple bargaining games. Games Econ. Behav. 6, 347–369.

Frank, R.H., 1988. Passions Within Reason: The Strategic Role of the Emotions. W.W. Norton, New York.

Galef Jr., B.G., 1990. An adaptationist perspective on social learning, social feeding, and social foraging in Norway rats. In: Dewsbury, D.A. (Ed.), Contemporary Issues in Comparative Psychology. Sinauer, Sunderland, MA, pp. 55–79.

Grant, E.C., Mackintosh, J.H., 1963. A comparison of the social postures of some common laboratory rodents. Behaviour 21, 246–259.

Green, L., Price, P.C., Hamburger, M.E., 1995. Prisoners Dilemma and the pigeon: control by immediate consequences. J. Exp. Anal. Behav. 64, 1–17.

Hake, D.F., Vukelich, R., 1972. A classification and review of cooperation procedures. J. Exp. Anal. Behav. 18, 333–343.

Heinsohn, R., Packer, C., 1995. Complex cooperative strategies in group-territorial African lions. Science 269, 1260–1262.

Herrnstein, R.J., 1961. Relative and absolute strength of response as a function of frequency of reinforcement. J. Exp. Anal. Behav. 4, 267–272.

Hinde, R.A., 1979. Towards Understanding Relationships. Academic Press, New York, 367 pp.

Hutchins, E., 1995. Cognition in the Wild. The MIT Press, Cambridge, MA.

Krebs, J.R., 1982. Territorial defense in the great tit (_Parus major_): do residents always win? Behav. Ecol. Sociobiol. 11, 185–194.

Krebs, J.R., Davies, N.B., 1993. An Introduction to Behavioural Ecology, third ed. Blackwell, London.

Lakin, J.L., Chartrand, T.L., 2003. Using unconscious behavioral mimicry to create affiliation and rapport. Psychol. Sci. 14, 334–339.

Leuthold, W., 1977. African Ungulates: A Comparative Review of Their Ethology and Behavioral Ecology. Springer-Verlag, Berlin.

Logue, A.W., 1988. Research on self-control: an integrating framework. Behav. Brain Sci. 11, 665–709.

Luce, R.D., Raiffa, H., 1957. Games and Decisions: Introduction and Critical Survey. Wiley, New York.

Maynard Smith, J., 1978. The Evolution of Sex. Cambridge University Press, Cambridge, UK.

Maynard Smith, J., 1984. Game theory and the evolution of behavior. Behav. Brain Sci. 7, 95–101.

McNeill, W.H., 1995. Keeping Together in Time: Dance and Drill in Human History. Harvard University Press, Cambridge, MA.

Mesterton-Gibbons, M., Dugatkin, L.A., 1992. Cooperation among unrelated individuals: evolutionary factors. Q. Rev. Biol. 67, 267–281.

Minta, S.C., Minta, K.A., Lott, D.F., 1992. Hunting associations between badgers (_Taxidea taxus_) and coyotes (_Canis latrans_). J. Mammal. 73, 814–820.

Mitani, J., Watts, D., 2001. Why do chimpanzees hunt and share meat? Anim. Behav. 61, 915–924.

Nash, J.F., 1950. Equilibrium points in _n_-person games. Proc. Natl. Acad. Sci. U.S.A. 36, 48–49.

Noë, R., 1990. A veto game played by baboons: a challenge to the use of the Prisoner's Dilemma as a paradigm for reciprocity and cooperation. Anim. Behav. 39, 78–90.

Noë, R., Sluijter, A.A., 1995. Which adult male savannah baboons form coalitions? Int. J. Primatol. 16, 77–105.

Orians, G.H., 1969. On the evolution of mating systems in birds and mammals. Am. Nat. 103, 589–603.

Packer, C., Ruttan, L., 1988. The evolution of cooperative hunting. Am. Nat. 132, 159–198.

Packer, C., Scheel, D., Pusey, A.E., 1990. Why lions form groups: food is not enough. Am. Nat. 136, 1–19.

Palameta, B., Brown, W.M., 1999. Human cooperation is more than by-product mutualism. Anim. Behav. 57, F1–F3.

Perelberg, A., Schuster, R., submitted. Association patterns and synchrony levels in bottlenose dolphins (_Tursiops truncatus_).

Rachlin, H., 1995. Self-control: beyond commitment. Behav. Brain Sci. 18, 109–159.

Rachlin, H., 2002. Altruism and selfishness. Behav. Brain Sci. 25, 239–296.

Rapoport, A., Chammah, A.M., 1965. Prisoner's Dilemma: A Study in Conflict and Cooperation. University of Michigan Press, Ann Arbor, MI.

Rilling, J.K., Gutman, D.A., Zeh, T.R., Pagnoni, G., Berns, G.S., Kilts, C.D., 2002. A neural basis for social cooperation. Neuron 35, 395–405.

Roberts, G., 1997. Testing mutualism: a commentary on Clements and Stephens. Anim. Behav. 53, 1361–1362.

Scheel, D., Packer, C., 1991. Group hunting behaviour of lions: a search for cooperation. Anim. Behav. 41, 697–709.

Schuster, R., 1976. Lekking behavior in Kafue lechwe. Science 192, 1240–1242.

Schuster, R., 2000. How useful is an individual perspective for explaining the control of social behavior? Behav. Brain Sci. 23, 263–264.

Schuster, R., 2001. An animal model of cooperating dyads: methodological and theoretical issues. Mexican J. Behav. Anal. 27, 165–200.

Schuster, R., 2002a. Cooperative coordination as a social behavior: experiments with an animal model. Hum. Nat. 13, 47–83.

Schuster, R., 2002b. Altruism is a social behavior. Behav. Brain Sci. 25, 272–274.

Schuster, R., 2003. Why not go all the way.... Behav. Brain Sci. 26, 173–174.

Schuster, R., Berger, B.D., Swanson, H.H., 1988. Cooperative social coordination and aggression: sex and strain differences in the effects of housing on gonadectomized rats with hormone replacement. Aggressive Behav. 14, 275–290.

Schuster, R., Berger, B.D., Swanson, H.H., 1993. Cooperative social coordination and aggression. II. Effects of sex and housing among three strains of intact laboratory rats differing in aggressiveness. Q. J. Exp. Psychol. 46B, 367–390.

Schuster, R., Rachlin, H., Rom, M., Berger, B.D., 1982. An animal model of dyadic social interaction: Influence of isolation, competition and shock-induced aggression. Aggressive Behav. 8, 116–121.

Serpell, J.A., 1981. Duets, greetings and triumph ceremonies: analogous displays in the parrot genus *Trichoglossus*. Zeitschrift für Tierpsychologie 55, 268–283.

Skinner, B.F., 1953. Science and Human Behavior. Macmillan, New York.

Sober, E., Wilson, D.S., 1998. Unto Others: The Evolution and Psychology of Unselfish Behavior. Harvard University Press, Cambridge, MA.

Stander, P.E., 1992. Cooperative hunting in lions: the role of the individual. Behav. Ecol. Sociobiol. 29, 445–454.

Stephens, D.W., Anderson, J.P., 1997. Reply to Roberts: cooperation is an outcome, not a mechanism. Anim. Behav. 53, 1363–1364.

Stephens, D.W., McLinn, C.M., Stevens, J.R., 2002. Discounting and reciprocity in an iterated Prisoner's Dilemma. Science 298, 2216–2218.

Swanson, H.H., Schuster, R., 1987. Cooperative social coordination and aggression in male laboratory rats: effects of housing and testosterone. Horm. Behav. 21, 310–330.

Todt, D., 1981. On functions of vocal matching: effect of counter-replies on song post choice and singing. Zeitschrift für Tierpsychologie 57, 73–93.

Trivers, R., 1971. The evolution of reciprocal altruism. Q. Rev. Biol. 46, 35–57.

Trivers, R., 1985. Social Evolution. Benjamin/Cummings, MenloPark, CA.

Tsoory, M., Youdim, M.B.H., Schuster, R., submitted. The involvement of monoaminergic systems in a laboratory model of social cooperation in rats. Behav. Neurosci.

van Baaren, R.B., Holland, R.W., Steenaert, B., van Knippenberg, A., 2003. Mimicry for money: behavioral consequences of imitation. J. Exp. Soc. Psychol. 39, 393–398.

von Neumann, J., Morgenstern, O., 1953. Theory of Games and Economic Behavior, third ed. Princeton University Press, Princeton, NJ.

Watts, D.P., Mitani, J.C., 2001. Boundary patrols and intergroup encounters in wild chimpanzees. Behaviour 138, 299–327.

Weingarten, K., Mechner, F., 1966. The contingency as an independent variable of social interaction. In: Verhave, T. (Ed.), The Experimental Analysis of Behavior. Appleton-Century-Crofts, New York, pp. 447–459.