

COOPERATIVE COORDINATION AS A SOCIAL BEHAVIOR

Experiments with an Animal Model

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Coordinating behavior is widespread in contexts that include courtship, aggression, and cooperation for shared outcomes. The social significance of cooperative coordination (CC) is usually downplayed by learning theorists, evolutionary biologists, and game theorists in favor of an individual behavior → outcome perspective predicated on maximizing payoffs for all participants. To more closely model CC as it occurs under free-ranging conditions, pairs of rats were rewarded for coordinated shuttling within a shared chamber with unrestricted social interaction. Results show that animals learned to work together with sensitivity to the task and type of partner. Moreover, social interaction and coordination influenced both consumption of the reward solution immediately following a session and preference for cooperation, suggesting that affective states and incentives related to cooperation extend beyond the outcomes obtained. These results support field studies by showing not only *how* cooperation is performed but also the importance of considering how the behavior of cooperating affects outcomes and preference for cooperating.

KEY WORDS: Cooperative coordination; Incentive to cooperate; Individual behavior / outcome perspective; Laboratory models; Laboratory rats; Mutualism; Preference for cooperating; Social behavior perspective.

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This article concerns what is learned when animals cooperate by coordinating actions, and how they are affected by coordinating, based in part on a model of cooperative coordination with laboratory rats, *Rattus norvegicus* (Schuster, Berger, and Swanson 1993). A sample of results obtained with this model will be used to address theoretical issues raised by a recent debate regarding cooperation and its evolution in the journal *Animal Behaviour* (Roberts 1997; Stephens and Anderson 1997). Roberts wants our understanding of cooperation to include evidence that it is a *social behavior* whereby the presence and behaviors of participants influence cooperative strategies (e.g., Boesch and Boesch 1989; Roberts 1997; Schuster et al. 1993). A social behavior perspective would also be supported by evidence that individuals are affected by working together in ways that, for example, might bias the preference between whether to cooperate or act alone. In contrast, Stephens and his colleagues (see also Clements and Stephens 1995) downplay the social elements of cooperating in favor of an individual behavior → outcome perspective. Based on principles derived from game theory and selfish-gene theory, cooperation is explained by the economic consequences for each participant from cooperating with others (e.g., Dugatkin 1997; Mesterton-Gibbons and Dugatkin 1992; Packer, Scheel, and Pusey 1990; Stephens and Anderson 1997). This article will also address how these very different perspectives influenced the design of experimental models used in the study of cooperation for addressing the basic question: *why cooperate?*

The behavioral phenomenon of individuals engaging in highly coordinated actions is widespread in pairs or larger groups of both humans and animals. In humans, highly orchestrated ceremonies are associated with diverse contexts, including armies, political movements, religions, sporting events, and music (McNeill 1995). Even without deliberate orchestration, individuals tend to “behaviorally match” the actions or postures of others (Bernieri and Rosenthal 1991; Chartrand and Bargh 1999). In human and animal courtship, the degree of synchronization in dance or acrobatic display seems to influence the choice of partners for copulation or long-term pair bonds (Maynard Smith 1978). Aggression can also be expressed in highly coordinated actions, such as the song “duets” that are used by mated pairs to advertise and defend their territory cooperatively and perhaps also to strengthen their pair bond (e.g., Hall 2000; Serpell 1981a, 1981b; Todt 1975). Dueting, however, does not depend on male-female pair bonds. Coordinated behavioral matching is also known between rival males competing from adjacent territories, as in both the singing of birds (e.g., Beecher, Campbell and Nordby 2000; Todt 1981) and the “challenge rituals” of antelope (e.g., Schuster 1976). Coordinated dueting and displays of ritualized aggression between rivals have also been interpreted as cooperative (Krebs 1982; Serpell 1981b; Todt 1981). But cooperation is per-

haps most obvious when individuals develop highly coordinated joint actions for achieving a tangible, immediate outcome (for reviews, see Dugatkin 1997; Mesterton-Gibbons and Dugatkin 1992). In nature, cooperative coordination (hereafter CC) has been documented in varied contexts that include *intergroup aggression and defense* (e.g., in lions [*Panthera leo*], Heinsohn and Packer 1995; Grinnell, Packer, and Pusey 1995; in chimpanzees [*Pan troglodytes*], Boehm 1992), *within-group aggressive alliances* (e.g., in several nonhuman primates, de Waal 1986; Noë and Sluijter 1995), and *group hunting* (e.g., in hyenas [*Crocuta crocuta*], Kruuk 1972; in lions, Packer et al. 1990; and in chimpanzees, Boesch and Boesch 1989).

EXPLAINING CC: THE INDIVIDUAL BEHAVIOR → OUTCOME PERSPECTIVE

From the standpoints of both behavior and theory, the emphasis on the economic consequences for each individual has led to a characterization of cooperative coordination as a simple and even uninteresting phenomenon. Explanation requires little more than what is needed to account for any individual that is rewarded for its own behavior (Dugatkin 1997: 31–32). As a social phenomenon, each participant in CC need only learn to time its own individual actions by using cues from the presence and/or behaviors of others. Implicit is the expectation that animals would also behave in much the same way, and for the same reasons, whether operating alone or with others (Brown 1983). CC thus stands in marked contrast to cooperation by means of *reciprocity* whereby individuals exchange favors that can be widely separated in time (Dugatkin 1997:19–30; Trivers 1971). Unlike CC, reciprocity is assumed to depend upon a level of cognitive complexity that accounts for its rarity among animals. But is CC, in contrast, nothing more than a collection of individual behaviors and their outcomes?

Learning Theory

This is the conclusion reached by learning theorists such as B. F. Skinner (1953:297–306). Operant conditioning techniques can readily generate CC by having rewards contingent on two subjects emitting their behaviors within a short span of time, for example, 0.5 sec (Hake and Vukelich 1972; Lindsley 1966; Skinner 1953). Under these conditions, coordination is readily acquired, sometimes with a tendency for “leadership” whereby one partner’s behavior reliably precedes that of the other. In all other respects, CC has no special status as a social behavior. This becomes clear from the design of most experimental models that typically *isolate cooperating partners within separate chambers* in which each subject is individually

rewarded for actions such as bar pressing or key pecking (Hake and Vukelich 1972; Skinner 1953:306). What remains of CC as a social phenomenon is that outcomes follow from the combined behaviors of two or more individuals. As defined by Weingarten and Mechner (1966): *cooperation occurs when the reinforcements for each participant depend on the behavior of the individual and that of its partner(s).*

The above definition is independent of whether partners actually interact socially. Some models retain a degree of social interaction by placing partners on opposite sides of a transparent partition that allows the behavior of each partner to provide the timing cue for the other. But other isolation models generate comparable levels of CC *without any social interaction*. Known by the oxymoron "non-social cooperation" (Hake and Vukelich 1972), partners are now separated by an opaque partition that prevents visual contact. Coordination is instead achieved by having the behavior of one partner generate nonsocial stimuli such as lights or buzzers that are made available to the other. Based on such experiments, Skinner (1953:298) concluded that: "a 'social law' must be generated by the behavior of individuals. It is always an individual who behaves, 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." It is hardly surprising that terms like "social behavior" and "cooperation" rarely, if ever, appear in the index of contemporary textbooks on animal learning. In a field dedicated to the processes underlying learned behaviors, isolation models offer little more than the standard experiments with animals that live and behave alone.

Evolutionary Theory

The learning theory perspective is remarkably similar to both explanations and experimental models of cooperation derived from the selfish-gene school of evolutionary theory (Krebs and Davies 1993), including models based on game theoretical approaches to social conflict (Axelrod and Hamilton 1980; Clements and Stephens 1995; Dugatkin 1997; Mesterton-Gibbons and Dugatkin 1992; Stephens and Anderson 1997). Considerations of individual fitness lead inevitably to the expectation that the evolution and performance of cooperation, like that of any individual strategy, are linked to the net benefits for each participant. In this spirit, CC has also been labeled as *mutualism* (Alcock 1998; Krebs and Davies 1993), *mutual selfishness* (Wilson and Dugatkin 1992), *no-cost cooperation* (Dugatkin 1997:32), or *by-product mutualism* (Dugatkin 1997:31–34). All of these terms emphasize that no special evolutionary explanation is needed to account for whether an individual works alone or alongside others (CC). Both are equated with individual actions directed toward achieving the

maximum gain. If others also benefit from CC, this is dismissed as an unintended "by-product" (Dugatkin 1997:32).

Thus, the evolutionary/game-theory perspective, like learning theory, is indifferent to whether a behavior is social or individual, or how dimensions of CC such as level of behavioral synchrony might affect the participants (Stephens and Anderson 1997). This is clear from the popular use of experiments with payoff matrices such as the Prisoner's Dilemma to predict how two players will choose between cooperation and "defection" (noncooperation). In a typical game, social dimensions are impoverished or entirely absent. Players, typically strangers, are isolated from one another and asked to choose between two keys representing "cooperation" and "defection." The experience of each participant is reduced to performing individual behaviors leading to different outcomes that are also experienced alone (see Roberts 1997). Human subjects, isolated in separate cubicles, can at least be made aware that their outcomes depend on the behavior of another (e.g., Forsythe et al. 1994), but this awareness is highly unlikely with isolated animals. For example, pairs of blue jays (*Cyanocitta cristata*) were isolated in separate chambers, each with two keys. Each bird was rewarded according to game-theory payoff matrices depending upon how *both* chose between the two keys that arbitrarily represented the "cooperation" and "defection" options (Clements and Stephens 1995). The relevant prediction from learning theory has nothing to do with social behavior: for each bird, the distribution of behaviors on the two keys should match the relative rates of reward for each option (Herrnstein 1961).

EXPLAINING CC: A SOCIAL INTERACTION PERSPECTIVE

Much less emphasis has been placed, both in method and theory, on the fact that coordinated behaviors and their consequences under free-ranging conditions are also highly social acts (Roberts 1997; Schuster 2000; Schuster et al. 1993). The capacity to coordinate, often with great precision, implies an interlocking of both mutual attention and action that have rarely been measured in field studies. Cooperators may also interact socially if they congregate in a group prior to beginning their joint action. Describing cooperative behaviors, and the relationships that emerge, is not, however, only about *how* cooperation is performed. The research to be described below complements accumulating examples from field studies in showing that the ways individuals cooperate can also influence both the tangible outcomes they obtain and the incentive to work together. In both respects, the purely economic analysis of cooperation may become seriously compromised when results are used to explain why individual

animals or humans actually cooperate without considering how they cooperate.

One social influence on cooperating is the emergence of stable role differences such as those exhibited by lions (Stander 1992a, 1992b) and chimpanzees (Boesch and Boesch 1989) in cooperative hunting. In these species, the roles described can sometimes be qualitatively different, a phenomenon characterized by Boesch and Boesch as "complementarity," in contrast to mere synchrony. Hutchins (1995) adopted a similar perspective in his analysis of team navigation in humans when he suggested the term "distributed cognition" to characterize how group performance is divided among team members. While cooperating, each performs a role so specialized that it would be ineffectual if the individual were forced to perform the entire task alone. This kind of organization "permits individuals to combine their efforts in ways that produce results that could not be produced by any individual . . . working alone" (Hutchins 1995:175). Even when coordinating *similar* behaviors, as in laboratory models of coordinated lever pulling by great apes (Chalmeau and Gallo 1996; Chalmeau, Lardeux, et al. 1997) or the coordinated shuttling of laboratory rats (Schuster et al. 1993), asymmetries can arise with respect to initiating coordinated acts or adjunct social interactions.

The phenomenon of roles, however, is not limited to qualitative difference in the behaviors used while cooperating. Roles can also impact on differences among participants in the costs and net benefits from cooperating. In lion predation, for example, the animal making the initial attack on a large prey item also runs a greater risk of injury. Lions show "leading" and "lagging" in intergroup fights as well, in which the lead attackers would be more vulnerable to injury (Grinnell et al. 1995; Heinsohn and Packer 1995). This has led game theorists to characterize some participants as "cheaters" or "scroungers" that adopt an individual selfish strategy to exploit the actions of more active and risk-taking participants (Caro 1994; Grinnell et al. 1995; Heinsohn and Packer 1995; Packer and Ruttan 1988; Scheel and Packer 1991). An alternative, from the social behavior perspective, is that the differences between the exploiters and the exploited may reflect consequences of long-term relationships that influence roles within a cooperative strategy. Unfortunately, research under free-ranging conditions has rarely addressed the determinants of roles and how they might reflect differences in factors such as age, rank, temperament, and relationships within the group.

Social interaction under free-ranging conditions also extends beyond the coordination stage to the *outcome* stage that follows, a point emphasized by Noë (1990). This, too, can impact costs and benefits. Films of lions and cheetahs, for example, have documented mutual facial grooming and rubbing at the conclusion of successful cooperation, even before reaping

the rewards. These acts are presumably affiliative, affectively positive, and rewarding. In the opposite direction, competitive and sometimes violent confrontations can be observed when cooperators compete over access to single items such as prey (e.g., in chimpanzees, Boesch and Boesch 1989; in lions, Packer and Pusey 1982) or mating partners (e.g., in savanna baboons, Noë 1990; Noë et al. 1991). One result of competition is that outcomes may not be allocated equally among cooperators, and some individuals may gain little or nothing from their participation. In group-hunting chimpanzees, for example, dominants typically gain larger shares of the prey (Boesch and Boesch 1989).

Finally, the impact of social interaction on cooperation can begin well before the cooperative episodes if, as is often the case, participants are also well known to each other as members of a group. As a result, cooperators may have preferred partners. Moreover, cooperating partners may also be competing members within a hierarchy, as in male chimpanzees (Boesch and Boesch 1989), or within a network of adjacent territories, as in antelope (e.g., Schuster 1976). As a result, competition and cooperation can become intertwined not only when competing over outcomes but whenever the same individuals that gain from cooperating in one context, for example in hunting, also gain from competing selfishly in another context, for example in mate choice (Chase 1980).

From a theoretical standpoint, the impact of cooperative behavior on outcomes among participants provides a good example of potential disadvantages that can arise from maintaining an unbridgeable divide between analyses of function and causation, the *why* and the *how*. Advocates of theories based on individual outcomes argue that the economic approach is more powerful because it alone explains the “why” of cooperation and its evolution, whereas the social behavior perspective is limited to the less interesting question of proximate mechanisms or “how” they actually do it (e.g., Dugatkin 1997:32; Stephens and Anderson 1997). But as Tinbergen (1963; also in Krebs and Davies 1993) reminded us with his famous “four questions,” the answer to the “why” question can incorporate both *function* and *causation*, the latter based on evolved behavioral and physiological mechanisms that underlie an adaptive function.

The example of cooperative coordination shows the extent to which the issues of function and causation are intertwined. If analysis of function can specify the *optimal* strategy based on payoff maximization, behavioral mechanisms alone offer insight into why cooperation “in the real world” might deviate significantly from the expectation of payoff maximization derived from the individual perspectives of learning theory and the selfish gene. This can only emerge from describing what actually happens when animal cooperators work together and develop a cooperative relationship influencing roles, ranks, and resource allocation. Humans, too,

use social strategies based on more than payoff maximization by engaging in manipulation, bargaining, and long-term planning that can impact outcomes (Forsythe et al. 1994; Frank 1988; Palameta and Brown 1999). Even in games with isolated partners, subjects tend to cooperate more than expected (for a recent review, see Palameta and Brown 1999). This probably occurs because human subjects may not "feel" isolated even within the sterile context of a laboratory experiment. Being aware that others are involved may evoke concerns about their anonymity and social reputations (Forsythe et al. 1994; Frank 1988).

The issues of both outcomes and incentives for cooperating become even more complex if species evolve to experience affective consequences from the very *act* of cooperating. The outcomes from cooperating would therefore go beyond the tangible, measurable outcomes to include affective states that are evoked by actually working together and by the cohesive relationships that emerge (see, e.g., Frank 1988; Sober and Wilson 1998; Todt 1981). If individuals "enjoy" the act of cooperating with others, then the *motive* underlying an act of cooperation would include not only the tangible individual gains but also the experience of working with others. In humans, for example, coordinated actions are often associated with subjective reports of pleasure, "rapport," and group cohesion (Bernieri and Rosenthal 1991; McNeill 1995). Even the simple act of "behavior matching," performed without awareness or conscious intent, can positively influence how other people are judged (Chartrand and Bargh 1999). If animals are experiencing analogous states, these could help explain why they might cooperate when capable of gaining more by individual action (e.g., in lion hunting; Packer et al. 1990). Such states could also explain how females are able to use the level of coordination during courtship dances as a criterion of mate choice (Maynard Smith 1978) or how violence in the coordinated rituals of territorial aggression is restrained to an extent that has earned the name "dear enemy" (Dugatkin 1997:71–73; Krebs 1982). Some game theorists have implied the existence of such states when predicting that the choice of a cooperative option ought to be influenced by playing iterated games within groups in which participants are likely to experience and recall repeated encounters (Dugatkin and Wilson 1991). Dugatkin (1995) and Noë and Sluiter (1995) have also pointed out that partner preference can be a factor when choosing between cooperation and defection.

Another route whereby coordination might also influence the incentive to cooperate is by *modifying the value of the outcomes* obtained via cooperating. What if obtaining a reward cooperatively makes the actual reward more desirable than if it was achieved alone? A change in value can be expressed as an increase in need (consumption), a change in hedonic affect, or both (Berridge 2000). In our own species, people sometimes report that the pleasurable experiences associated with drinking a fine wine, seeing a

movie, or viewing a spectacular natural vista are enhanced by sharing it with another. This is consistent with the idea that cooperating for an outcome can influence the incentive value of that outcome.

In addition to behavioral measures, the existence of affective states evoked by coordination would gain support from identification of adaptive changes in underlying physiological systems. One candidate is opioid function, which has been related in a general way to social interaction based on evidence that includes the release of endogenous opioids following social interaction and effects of opiate antagonists on a variety of social behaviors, including gregariousness, play fighting, social exploration, and grooming (Panksepp et al. 1980; Panksepp, Siviý, and Normansell 1985). A related hypothesis is that the secretion of opioids during social interaction is part of a mechanism generating *social rewards* that are behaviorally and physiologically distinct from other reward mechanisms (Panksepp, Nelson, and Bekkedal 1997). Changes in the values of outcomes from cooperating would implicate both opioid function (e.g., Gagin, Cohen, and Shavit 1996) and dopamine function (Wise and Rompre 1989).

MODELING COORDINATED BEHAVIOR IN THE LABORATORY

The kinds of questions that arise from treating cooperative coordination as a social behavior have obvious implications for designing experimental models. A valid model should generate cooperative coordination based on partners using each other's behaviors and locations with unrestricted social interaction. The model should also exhibit sensitivity to factors that under free-ranging conditions influence social behaviors such as sex, kinship, prior relationship, and the outcomes of social interactions. Socially mediated cooperation, for example, was shown in great apes rewarded for coordinating the pulling of two handles located too far apart to be pulled by a single animal (Chalmeau and Gallo 1996; Chalmeau, Lardeux, et al. 1997), but an analogous procedure failed to generate coordinated pulling in capuchin monkeys (*Cebus apella*, Chalmeau, Visalberghi, and Gallo 1997; Visalberghi 1997; Visalberghi, Quarantotti, and Tranchida 2000). Socially mediated coordination in capuchins was shown, however, with a task that required the combined efforts of two animals to pull in a baited tray (de Waal and Berger 2000; Mendres and de Waal 2000). In Daniel's pioneering work with laboratory rats (*Rattus norvegicus*), pairs had to coordinate an exchange of locations to obtain rewards while also avoiding electric shocks. Daniel (1942) described behaviors directed "more and more towards each other," including touching, crawling on the other's back, and tail biting and pulling, which were apparently inserted by partners into their coordination strategies.

THE MODEL: COOPERATIVE SHUTTTLING IN LABORATORY RATS

In our laboratory, a model of socially mediated coordination was designed in collaboration with Barry D. Berger to address issues raised by the social behavior perspective. Pairs of rats are positively rewarded with saccharine-sweetened water for coordinating back-and-forth shuttling within a shared chamber that allows for unrestricted social interaction (Berger, Mesch, and Schuster 1980; Schuster, Berger, and Swanson 1993). The chamber, sketched in Figure 1, is $94 \times 24 \times 30$ cm, with three separate, contiguous grid floors. An opaque partition with two rectangular passages divides the chamber into two compartments, the smaller (25×24 cm) enclosing only the D floor (distant with respect to reward cups) and the larger (42×24 cm) enclosing both the M (middle) and N (near) floors. Four micro-switches under each floor relay information about the locations of the animals to a computer programmed to run the experiment and collect certain data on-line (e.g., running time, completed coordinations, reinforcements, and cumulative locational data by floor).

Reinforcement Contingency

Whether animals are run singly or in pairs, the reward (3 mM saccharine solution) is contingent upon satisfying the same requirement: shuttling between floor D and floor N, with a minimum 0.5 sec located *only* on floor D and then a minimum 0.5 sec located *only* on floor N. For *pairs* of cooperat-

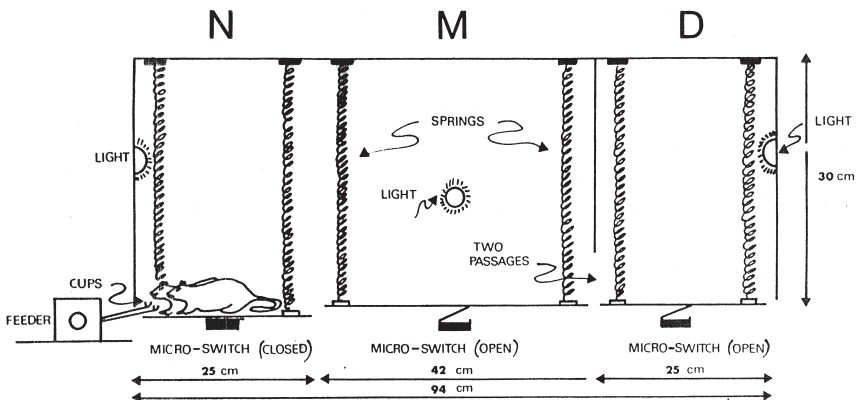


Figure 1. Sketch of the learning chamber. The designations N, M, and D refer to distance of the designated floor section from the reward cups: Near, Middle, Distant. Rewards for both individuals and pairs depend upon shuttling to D and then back to N. See text for details.

ing rats, this requires *coordinating* shuttling between the floors so that *both* animals are simultaneously located *only* on floor D and then *only* on floor N—in other words, Floor D together → Floor N together. As soon as this D→N contingency has been satisfied, the reward is delivered from two 0.06 cc cups that can be presented independently.

Cues

There are no nonsocial stimuli—lights or sounds—to facilitate coordination; sensory feedback while shuttling is limited to cues provided by the animals themselves from their locations, movements, and social interactions. The only nonsocial stimuli available are a light above the cups that accompanies the delivery of reward and another light over the M floor that signals the end of a session.

Measures

To assess how pairs work together, three dimensions of the behavior are measured: acquisition, social interaction, and coordination performance. *Acquisition* refers to the improvement (if any) over sessions in measures such as the *number of completed coordinations* or the *total time* expended to complete that number. *Social interactions* are species-typical behaviors and their outcomes that are scored by trained observers. *Coordination performance* refers to how pairs work together, based on separate measures of coordination, proximity, and precedence:

- *Coordination* is measured by the proportion of completed *coordinations with errors* that are scored when the first animal to reach a floor fails to wait for its partner.
- *Proximity* is measured indirectly by “separation” events, defined as partners simultaneously located at opposite ends of the chamber, on the D and N floors.
- *Precedence* provides information about roles and stability within pairs by measuring the proportion of coordinations in which one partner leads or lags.

Learning Procedure

Details of the general cooperation procedure can be found in Schuster et al. (1993). Unless otherwise noted, subjects in the experiments reported here were adult males c. 90 days of age and housed socially, either with their partners or a cage-mate. The animals used in the first four experiments were Sprague-Dawley derived; in the last two experiments, Wistar.

The learning procedure always includes the following three stages:

- *Pre-learning.* Prior to cooperating, subjects first undergo daily handling, weighing, and water deprivation of initially one hour (for the first two days) and then 30-min access per day with food available *ad libitum*.
- *Learning individual shuttling.* Subjects are then pre-trained in individual D→N shuttling until reaching a predetermined criterion. This guarantees comparable levels of individual shuttling across all subjects so that variation in the acquisition of CC can be attributed to social phenomena. Pre-training begins with free exploration, including repeated access to filled reward cups, followed immediately by self-shaping in which all completed D→N shuttles are rewarded.
- *Cooperation.* Upon reaching criterion, animals are assigned to cooperating pairs and now rewarded only for coordinating shuttling that satisfies the requirement of "Floor D together → Floor N together." This stage continues for a fixed number of sessions regardless of whether or not cooperation is developing. Every session is now automatically terminated after either a predetermined number of completed coordinations or elapsed time.

Summary: Features of the Model for Studying Cooperative Behavior

Several features of the model reflect the goal of sacrificing the high degree of control over individual behaviors that is characteristic of isolation models in favor of a laboratory context within which the partners themselves, and their relationships, become more influential. There is considerable latitude in how pairs can satisfy the requirements to coordinate D→N shuttling. The space is large, almost 1 m in length. Rewards are provided whether partners arrive together or sequentially onto a floor. In the latter case, a correct performance requires the first animal reaching a floor to remain until the arrival of its partner, and then both have to remain together for at least 0.5 sec. Pairs are also left free to engage in the full range of species-typical social behaviors, from affiliative to violent, while coordinating. In some pairs, stereotyped social behaviors seem to emerge that facilitate cooperation when repeated actions initiated by one animal reliably evoke shuttling in its partner (Schuster et al. 1993). Analogous behavior was reported by Daniel (1942). Finally, animals are free to compete directly over outcomes. Reward cups are presented within narrow openings that restrict drinking from each cup to one animal at a time. If a single cup is presented, a contesting partner can only gain access by displacing the other.

IS COORDINATED SHUTTTLING BASED ON SOCIAL INTERACTION?

The experiments described in this section have been selected from a larger series revolving around different aspects of a single question: Is coordinated shuttling based on social interaction? Some of these experiments arose from a collaboration with Barry D. Berger. Most have not yet been published in detail. All differences reported below were statistically significant at the level of at least 0.05.

1. Social Cues: Does the Presence of a Partner Influence CC?

Perhaps the most basic question concerning social interaction is whether animals are using each other while coordinating. This was tested by comparing levels of D→N coordination when partners were either *together* within a single chamber and able to interact socially (hereafter “paired”) or *isolated* in separate chambers located within different rooms and denied any possibility of interaction (hereafter “yoked”). The same two conditions were also compared with the addition of a nonsocial light cue over the D floor that provided additional feedback whenever the animals were together on the D floor.

Figure 2 shows that, *without the nonsocial light cue*, paired animals in the same chamber were superior to yoked individuals in improving their total time to coordinate. Yoked subjects also showed some improvement in rate across sessions, but measures of proximity and coordination (not shown) indicate that the increase in rate was achieved by increasing individual rates of uncoordinated individual shuttling. This was sufficient to increase the likelihood of satisfying the D→N reinforcement contingency by chance. It is possible to conclude that two animals in the same chamber were able to benefit by their proximity to use each other’s behaviors and/or locations.

The same conclusion, however, is not possible for the paired group run *with the nonsocial light cue*. The learning curve of the paired/light group was indistinguishable from that of the yoked/light group and, moreover, both were superior to the paired group without the light cue. Since the yoked group could only have been coordinating so well by relying on the nonsocial light cue, this means that the light cue, and not the presence of the partner, was also the dominant stimulus controlling the coordination of the paired group. In other words, even though partners in the paired/light group were physically together within the same chamber, their highly coordinated behavior was the expression of a *nonsocial strategy* based on using the light cue. More generally, this outcome warns about the necessity of going beyond the physical proximity of subjects to test for

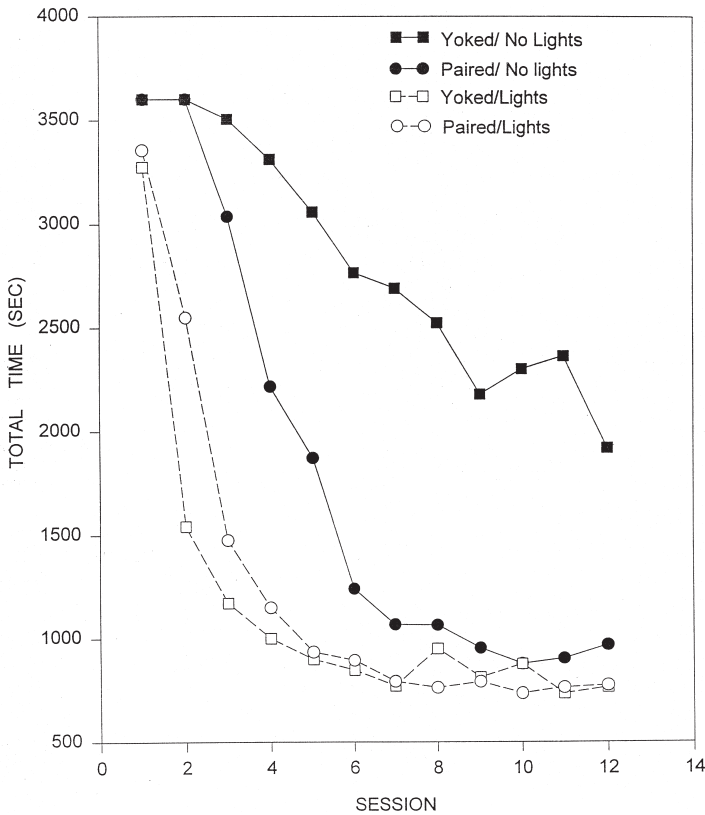


Figure 2. Learning curves of paired and yoked partners with or without nonsocial light cues ($n = 19$ pairs across all groups). The measure is total time (seconds) to complete a maximum of 50 coordinations during a session. Maximum session time was 1 hr (3,600 sec).

stimulus control when making claims for the social validity of an experimental model of social interaction.

The experiment did not investigate why, in the paired/light group, the light cue gained control over coordinating even though subjects were together in the same chamber. It seems likely that learning to use the reliable and unvarying nonsocial light cue was easier than using the variety of possible cues from a partner's presence and behavior on the D-floor. The latter requires that each animal learn to position itself on the D-floor by generalizing from a multitude of cues provided by its partner—locations, movements, postures, and/or social behaviors—that will typically vary from moment to moment. As a result, coordination is nonstereotyped,

with variation in leading, following, postures, and floor location, and with frequent interruptions for social interactions and self-grooming. Learning to coordinate based on social cues is tantamount to forming a *concept* about the necessary condition leading to reward: joining the partner on the D floor and again on the N floor.

2. Does the Partner Make a Difference?

A model sensitive to social interaction ought also to be sensitive to the partners that have to work together. Under free-ranging conditions, we expect cooperation, like any social behavior, to vary with factors such as species, sex, age, kinship, or prior social relationship. The examples below show that the rat model is sensitive to such factors.

Housing. Isolated housing is known for its potent negative influence on social behavior in rodents, heightening aggression and reactivity to physical contact (Cairns 1972). When adult male rats were housed in isolation, CC was severely impaired (Schuster et al. 1982). When pairs were housed socially, either together or separately with other males, coordination was readily acquired. The deleterious influence of isolated housing on behavior was specific to cooperation: individual shuttling was unaffected by whether animals were housed alone or together.

Sex and strain. Another experiment on sex differences across three strains of laboratory rats showed that the deleterious influence of isolated housing on CC was selective to males, and, moreover, in only two strains (Schuster et al. 1988, 1993). In contrast, females of all three strains were able to learn, whether they were housed in pairs or in isolation. These results were related to marked sex and strain difference not only in levels of violence but also in the consequences of violent fighting. Male “losers” usually froze and tended thereafter to respond by freezing to the mere presence of their tormentor. Males, in other words, strongly differentiated into dominants and subordinates. Females, in contrast, did not freeze after being attacked, even in the very aggressive S3 strain (better known as “maze-dull”). This selective influence of isolated housing on male cooperation was supported by a link to testosterone. Castrated males were unimpaired by isolation, whereas impairment was shown in both intact males and castrated males given testosterone replacement (Swanson and Schuster 1987).

Kinship. Kinship is believed to influence cooperation both by making it more likely between close kin and by increasing their tolerance of payoff asymmetries (Krebs and Davies 1993; McFarland 1985). In a preliminary experiment, cooperation was compared in pairs comprising either former litter-mates or non-kin in a situation that also included competition over

periodic single rewards (Hareli, Katzir, and Schuster 1996). In the non-kin pairs, one member was bred in the laboratory whereas the partner of the same strain was purchased from a local supplier. Pairs, formed at c. 60 days of age, were housed together for at least four weeks prior to the start of experimentation. The requisite cross-fostering for such comparisons, however, was not carried out and so the results remain tentative.

Pairs first learned by being rewarded with two cups following every completed coordination. Figure 3 shows that, during this stage, kin pairs

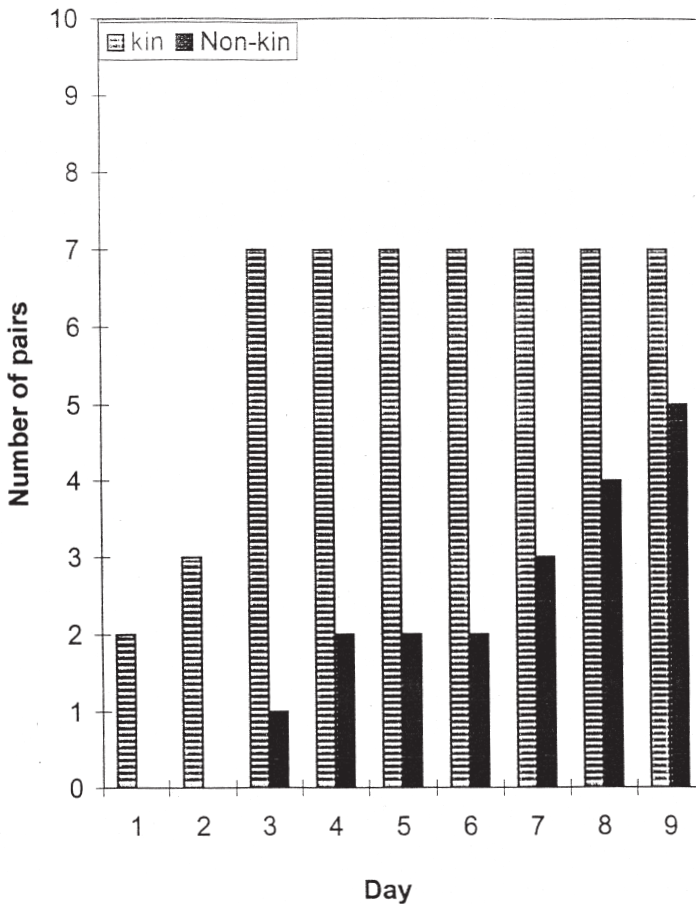


Figure 3. Comparison of litter-mates and non-litter-mates on learning to coordinate with 100% reward following correct coordinations ($n = 7$ pairs in each group). The measure is the number of pairs per session that reached the maximum of 50 completed coordinations within 1 hour.

learned to coordinate more rapidly. Competition was then evoked by intermittent and quasi-random presentations of two cups, left cup alone, right cup alone, or no cups, each with a 0.25 probability. An individual could now increase its share of total rewards by drinking from a disproportionately larger share of individually presented cups, in other words, by always drinking from its own cup and also “invading” its partner’s cup when it was presented alone. (“Ownership” over cups was assigned based on the tendency for each partner to drink almost always from the same cup whenever two cups were presented.) Figure 4 shows that the dominants in kin-based pairs invaded less than the dominants in non-kin pairs. In kin pairs, the most common behavior in dominant partners was to drink

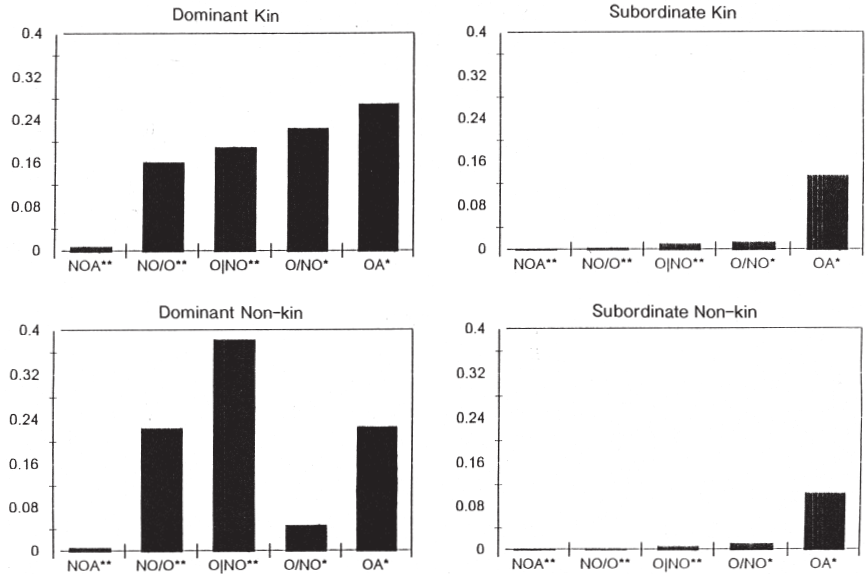


Figure 4. Comparison between pairs of litter-mates and non-litter-mates on competition over single rewards following successful coordination. Within-pair dominants and subordinates were identified from the overall outcomes of the competition over all sessions. The key on the abscissa refers to the categories used in classifying the outcomes of potential competition: NOA = non-owner takes owner’s cup unchallenged; NO/O = non-owner displaces owner from owner’s cup; O|NO = owner and non-owner compete over owner’s cup without displacement by either one; O/NO = owner displaces non-owner from owner’s cup; and OA = owner drinks from its own cup unchallenged. See text for explanation of “ownership.” Y-axis: overall proportion of observations of each type.

from their own cups, a tactic that, in essence, represents a degree of “sharing.” The dominants in non-kin pairs, in contrast, were more likely to access their partner’s cup. This result, while not supporting the hypothesis that kinship should tolerate more inequality in outcomes, may mean that kinship reduces either overall aggression or the specific incentive to contest outcomes clearly “owned” by others.

3. Do Cooperating Pairs Learn to Work Together?

If pairs are using social cues when cooperating, this implies that partners have actually learned a strategy of working together. This was directly tested by comparing how rapidly animals learned to cooperate with new, naive partners after first gaining experience either in *coordinated shuttling* or *individual shuttling*. Two groups of 10 subjects each, five pairs and 10 singles, first learned their respective tasks during 10 sessions. There was, however, another dimension that could have differed between the two tasks, namely a higher proportion of *unrewarded* shuttles for individual animals in the cooperation group due to coordination errors. Individual shuttling, by contrast, is nearly error-free, except for occasional short shuttles that don’t reach the D floor. To cancel out potential differences in the individual experience of reward probabilities, the proportions of rewarded shuttles by individuals were precisely matched to those obtained by cooperators during every session. The result, shown in Figure 5, was that pairs and singles had virtually identical learning curves based on the rate measure, time / reinforcement.

With subjects differing mainly in their experience of shuttling together or alone, all were then rewarded for learning to coordinate with new, naive rats. These had been given only the usual pre-learning and initial learning to shuttling alone. Figure 6 shows that prior cooperation experience markedly facilitated learning to coordinate with new partners. This can be interpreted as showing that experience in coordinating leads to a learned ability to work with another animal that can be transferred to a new, naive partner.

4. Are Pairs Coordinating Because They Are Rewarded for Coordinating?

All the prior experiments show that pairs are indeed using each other when coordinating within a shared chamber. But the results by themselves do not guarantee that coordinated shuttling develops because rewards are dependent on cooperating—in other words, satisfying the cooperative D→N contingency. Rats also have a spontaneous tendency to approach each other (e.g., Latané, Cappel, and Joy 1970; Taylor 1976, 1977). This might suffice for generating coordinated shuttling even if pairs are not re-

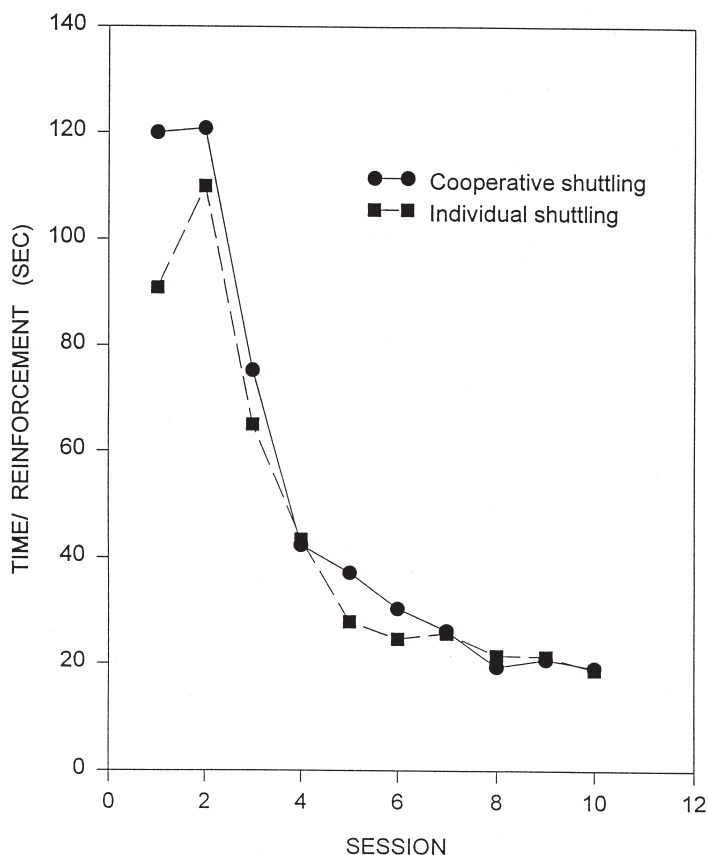


Figure 5. Learning curves of individual shuttling ($n = 10$) or cooperative shuttling ($n = 5$ pairs) when the proportions of rewarded shuttles by each subject were matched. The measure is mean time/ reinforcement.

warded specifically for coordinating, but rewarded only for individual shuttles in each other's presence.

An experiment therefore tested whether coordination of shuttling is selectively linked to the cooperative contingency by comparing two groups of pairs rewarded for shuttling while together in a single chamber. In one group, pairs were rewarded as usual for *coordinating* D→N shuttling. In the second group, pairs were run together in the same chamber but with *rewards only for independently performed individual shuttles*, in other words, without the requirement to coordinate. Instead, each subject was rewarded for its own D→N shuttling without regard to the shuttling and rewards obtained by the other. In both groups, the proportions of rewarded

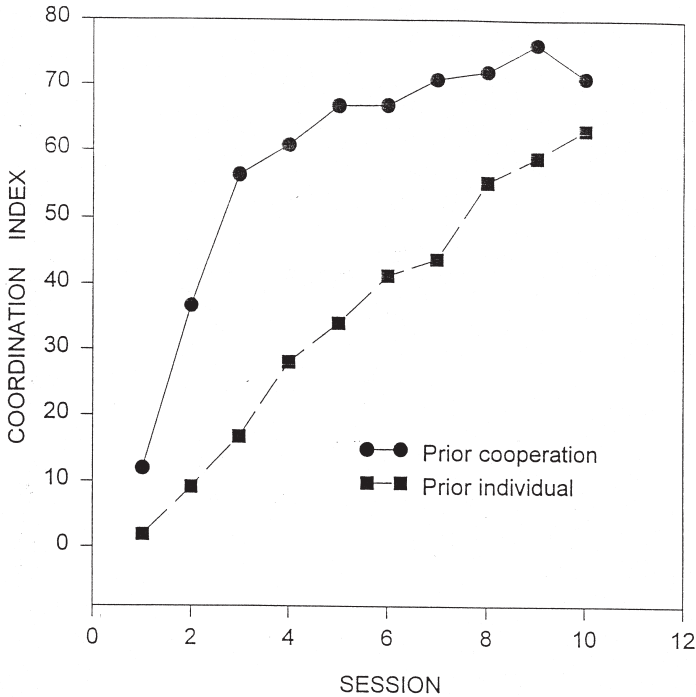


Figure 6. Learning curves of new pairs in which one partner was naive and the other was experienced in either coordinated shuttling ($n = 10$ pairs) or individual shuttling ($n = 10$ pairs). The measure is an index of coordination, mean percent of errorless coordinations per session.

shuttles were matched as described in (3), above. The upper part of Figure 7 shows that both groups learned to shuttle with increases in running speeds that were equivalent. The lower part of Figure 7 shows, however, that an increase in coordination was only obtained in the cooperation group.

DOES COORDINATED SHUTTLING AFFECT PARTNERS?

Taken together, the experiments described above confirm that pairs learn to coordinate shuttling by using each other's presence and behaviors. In short, the coordinated shuttling of rats satisfies criteria of a valid laboratory model of cooperation based on social interaction and influenced by factors known to influence social behavior under free-ranging conditions. This model can therefore be used to investigate whether and how cooper-

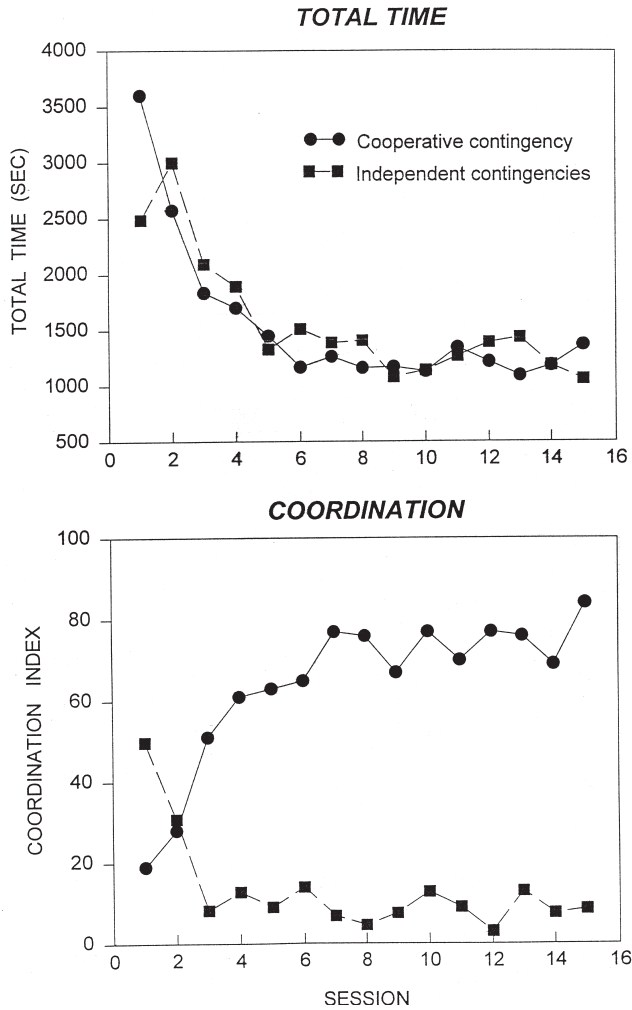


Figure 7. Learning curves of pairs within a single chamber rewarded either for cooperative coordination of D→N shuttling ($n = 3$ pairs) or independent individual D→N shuttling ($n = 3$ pairs). Upper: measure of total time; lower: measure of coordination index, percent of errorless coordinations per session.

ators are affected by coordinating. Two experiments are reported here. The first describes how the behavior used to obtain a reward—e.g., cooperative or individual shuttling—influences the *amount of the reward solution consumed after the session*. The second experiment examines *preference* between obtaining rewards by cooperation or by individual action. Both experiments therefore address the issue of incentives related to cooperation, and

specifically whether the motivation might extend beyond the rewards obtained by each individual for its own behavior while cooperating. The experiments in this section were planned in collaboration with Peter R. Killeen of Arizona State University.

5. Effects of Coordinated Shuttling on Post-Session Reward Consumption

One way to demonstrate an influence of coordinating on the state of the animals is to measure the effect of cooperating on each partner's consumption of the reward solution immediately following a session. The method was to compare post-session consumption within subjects across the following conditions:

Stage 1: pre-learning. Animals were housed with castrated cage-mates, handled daily, and water deprived.

Stage 2: learning individual shuttling. Animals were first trained as usual on individual D→N shuttling to a criterion of 30 completed shuttles within 20 min.

Stage 3: cooperation I with mesh partition. Pairs first learned to cooperate while *separated* by a partition of vertical bars. Basically an isolation model, this allowed coordination by means of social cues but with minimal physical contact. Rewards for all animals were 100% double cups following correctly coordinated shuttles.

Stage 4: cooperation II without partition. Pairs that learned to cooperate during Stage 3 were run for 12 sessions with no partition, allowing unrestricted social interaction. During this stage, pairs were also divided among nine subgroups differing in reward conditions: (a) 100% reinforcement from two cups (12 pairs); (b) competition over single cups evoked by intermittent presentations of one or two cups (47 pairs in four subgroups differing in the proportions of single and double rewards); (c) non-competition with intermittent presentation of two cups (47 pairs in four subgroups differing in the proportions of double rewards or no rewards; the total reinforcement obtainable by each non-competition subgroup matched one of the competition groups).

Stage 5: individual shuttling, post cooperation. A return to individual behavior, similar to Stage 2.

During Stage 1, consumption was measured following handling and weighing; during Stages 2–5, consumption was measured *immediately* following experimental runs when subjects were transferred from the learning chambers directly to *individual* drinking cages. During a 5-min test, subjects were offered a choice between drinking from two calibrated burettes, one with the rewarding saccharine solution and the other with water.

Differences in coordination behavior and reward allocation across the reinforcement subgroups of Stage 4 will be reported elsewhere. The result of interest here is the comparison across experimental stages in post-session consumption of the rewarding solution. Figure 8 shows that individual consumption of the saccharine solution was significantly and reliably elevated in all groups during Stage 4, cooperation without partition. Two comparisons are especially noteworthy. The first is between Stages 3 and 4, respectively cooperation *with* and *without* a dividing partition. Although both were generating coordination based on partners working together, only Stage 4 included unlimited social interaction. The Stage 4 condition was associated with markedly elevated drinking. Moreover, the level of drinking during Stage 3, coordination with partition, was not significantly different from that obtained during Stage 5, a return to individual shuttling.

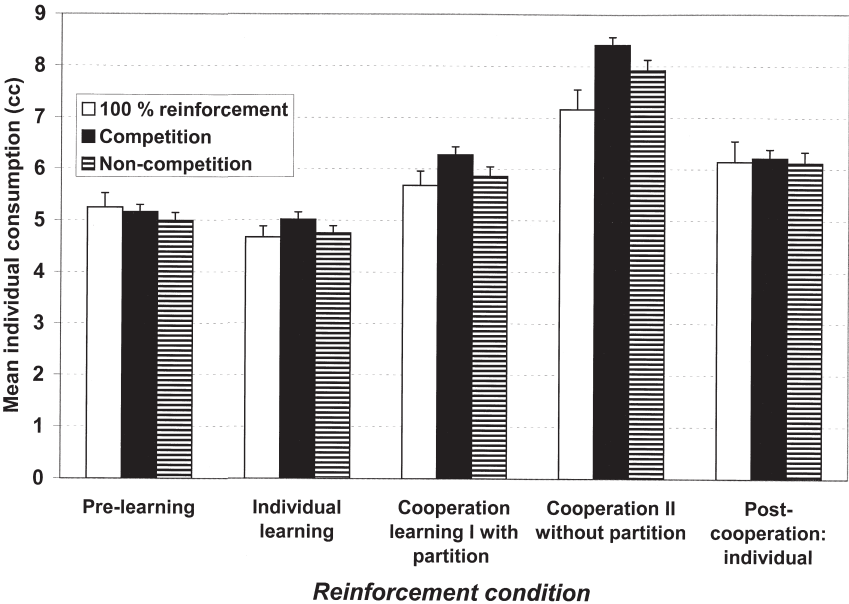


Figure 8. The mean total post-session consumption by individual subjects of the saccharine reward solution across the five experimental stages of the experiment on the effects of reward competition on coordination learning. Groups refer to the reward conditions: 100% double cups ($n = 24$ from 12 pairs); competition evoked by intermittent single and double cups ($n = 94$ from 47 pairs in four subgroups); and intermittent double or no cups ($n = 94$ from 47 pairs in four subgroups).

We suggest that the above result is consistent with a selective change in the state of the animals during Stage 4, leading them to consume more of the rewarding solution after coordinating with full social interaction. The increase is not a consequence of social facilitation since the animals were separated during the drinking test. We are less certain about what state is implied since increased consumption of the reinforcement solution may be an indicator of increased hedonic affect, increased need, or both (Berridge 2000). Either possibility suggests the interesting hypothesis that, for animals coordinating with unlimited social interaction, the *value of the reward* has itself been increased in some way. An experiment is currently under way to test whether there is a hedonic shift by measuring "facial reactivity" when drinking the rewarding solution and other solutions that are both palatable and unpalatable, based on research by Berridge (2000). Other studies underway are measuring if there are adaptive changes in physiological systems selectively linked to coordinated shuttling.

6. Choosing between Cooperation and Individual Behavior

The last experiment to be reported here concerns *preference* between gaining the same number of rewards by individual or coordinated shuttling. This choice is analogous to the game-theoretical options of "cooperation" or "defection" (non-cooperation), but in this experiment, the choice is between gaining the same rewards via two qualitatively different shuttling behaviors, one cooperative and social, the second individual. The individual behavior \rightarrow outcome perspective predicts no difference between the two options since both lead to the same rewards for back-and-forth shuttling. The social interaction perspective, on the other hand, predicts that choice ought to be influenced not only by outcomes but also by working together.

If working together affects the animals, they should also be influenced by *how well* they coordinate. This can be appreciated from a small sample of the results from the competition experiment described in (5), above. During Stage 4 with full social interaction, cooperation levels differed widely within all nine subgroups. Overall, 81 of 106 pairs (76%) were classified as "cooperators," having reached the daily maximum of 30 completed coordinations within $\frac{1}{2}$ hour during at least one of 12 sessions. The remaining "noncooperators," those that failed to reach the maximum during any session, were found in all groups and were always characterized by significant levels of aggression, including violent fights and freezing (see Schuster et al. 1993). Among the cooperators, pairs also varied widely in their learning rates and coordination levels. One indicator of cohesion is how much a given pair *improved* in their rate of completed coordinations as shown by the *slope* of the trend line linking coordination rates across ses-

sions. Higher slopes identify pairs whose rates improved significantly. Using the mean slope of 2.01 among all cooperators, we can roughly divide the pairs into “good cooperators,” with slopes above 2.01, and “poor cooperators,” with slopes below 2.01. Moreover, Figure 9 confirms that pairs with higher slopes were also more coordinated: an increase in slope is associated with a decrease in the proportion of completed coordinations with errors during the last six sessions.

The relevance of measuring how well pairs coordinate is becoming clear from the results of the preference experiment. The apparatus consists of two identical chambers, like those shown in Figure 1, interconnected by a T-maze with different floor surfaces (black or white) to aid in distinguishing between the two pathways. The actual methodology is somewhat complicated but the logic of the design is straightforward. Following the usual period of handling and water deprivation, subjects were run in a three-stage procedure:

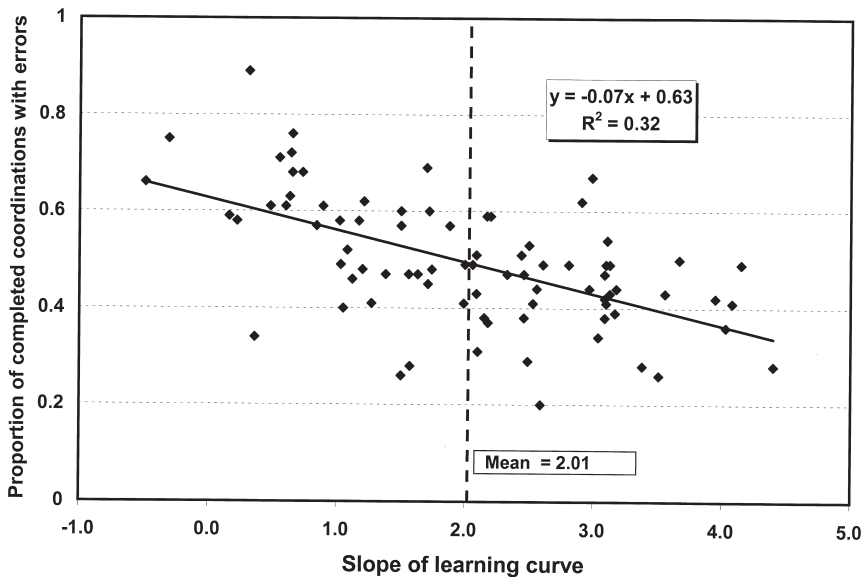


Figure 9. Relationship between the linear slope of the learning curve and level of coordination during Stage 4, cooperation with unrestricted social interaction. The slope for each pair is based on the measure of rate of completed coordinations over all 12 sessions; the level of coordination is measured by the mean percent of completed coordinations with errors for each pair during sessions 7–12. Data are from the 81 pairs (of a total of 106 pairs) classified as “cooperators” in the experiment on the effects of reward competition on coordination learning. The mean slope was 2.01.

- Stage 1, learning the two tasks;
- Stage 2, learning the task locations;
- Stage 3, choosing between the two options.

During Stage 1, each subject on each day was rewarded both for shuttling alone in one chamber and for coordinating with its partner in the other chamber. During Stage 2, using a forced-choice procedure, subjects learned where the two chambers were located within the T-maze. Turning left always led to one task (cooperation or individual), turning right to the other task. During Stage 3, subjects were first given a reminder of locations with two forced-choice trials, one to each option. This was followed immediately by two free choices. Stage 3 continued for eight sessions, four for each partner on alternating days, during which each partner was allowed a total of eight free choices. During both forced choice and free choice, the cooperating partner was only placed inside the cooperation chamber *after* the partner had fully entered from the T-maze and the guillotine entry door closed. This eliminated the possibility that entering the cooperation chamber would be affected by the mere presence of a known animal. Another feature of the procedure is that experience with the cooperation and individual options was always carefully balanced. For example, if one partner was forced to cooperate (a "drop-in") whenever its partner entered the cooperation chamber, an extra run was provided for the drop-in on the individual task. Choosing was therefore always based on equal prior exposure to the two options. Finally, reward probabilities were *matched* between the cooperative and individual options throughout the experiment, as described above for Experiments 3 and 4. This was intended to eliminate any incentive to either cooperate or work alone based only on differences in the likelihood of rewards following either behavior.

In the experiment reported here, 14 of 15 pairs (28 subjects) were "cooperators" as defined above. Figure 10 shows that, among the cooperating pairs, the relative rate of reward for the more difficult cooperation option gradually increased over the three stages, beginning well below 0.5 during the first two stages and reaching approximate equality (0.53) only during the forced-choice trials of Stage 3. In contrast, Figure 11 shows that the *preference* was overwhelmingly for the cooperative option. Of 224 total choices by all 28 cooperating subjects, 74% were to cooperate. Moreover, this preference was not equally apportioned across subjects. Figure 12 shows instead that preference for cooperation (5 or more choices out of 8) was expressed in 23 of 28 individuals; the remaining five individuals strongly preferred *not* to cooperate. Moreover, Figure 12 also shows that the increased preference for cooperating was associated with a higher slope during Stage 1; in other words, increased preference varied with how well coordination was developing *when the subject was learning to cooperate*. Of

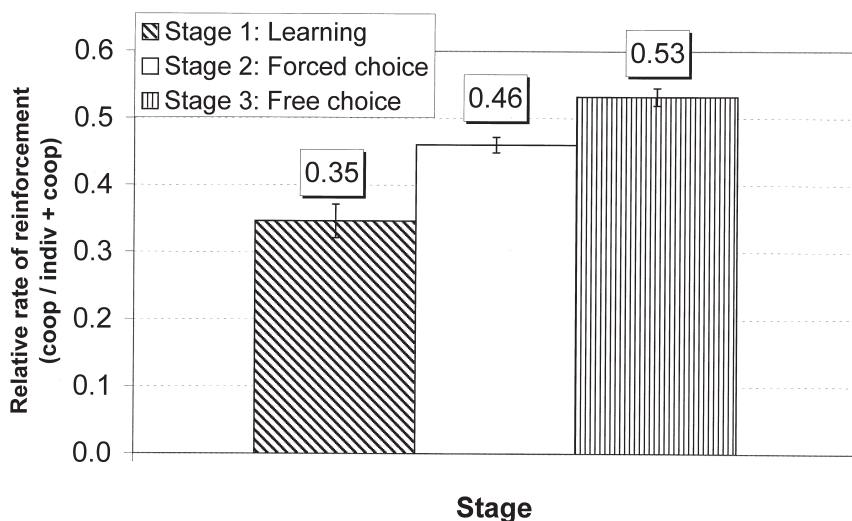


Figure 10. Relative rate of reward [rate during cooperation / (rate during cooperation + rate during individual)] during the three stages of the experiment on choice between cooperative and individual shuttling. The relative rate during Stage 1 (learning) was calculated from only the last half of the sessions; during Stage 2 (forced choice), from all six sessions (a total of 12 cooperation and 12 individual trials per subject); during Stage 3, from only the two forced-choice trials that preceded free choice during all four sessions (a total of 4 cooperation and 4 individual trials per subject).

the 12 individuals whose learning slopes were above the mean of 2.01 reported for Experiment 5, *all* preferred to cooperate. It is noteworthy, however, that attraction for cooperation was also shown by 11 of 16 subjects whose learning slopes were below 2.01. Incidentally, the efficacy of the choice procedure was shown by the one pair of aggressive noncooperators, both of whose members were almost never rewarded for cooperating. Both animals chose eight out of eight choice trials to work individually.

DISCUSSION AND SUMMARY

To summarize, a laboratory model based on rewarding coordinated shuttling in laboratory rats is able to generate socially mediated cooperation. This is sensitive to factors influencing social behaviors under free-ranging conditions, including the presence and type of the partner(s), unrestricted social interaction, and the contingency linking coordination to outcomes. In addition, social coordination seems to evoke changes in the states of the

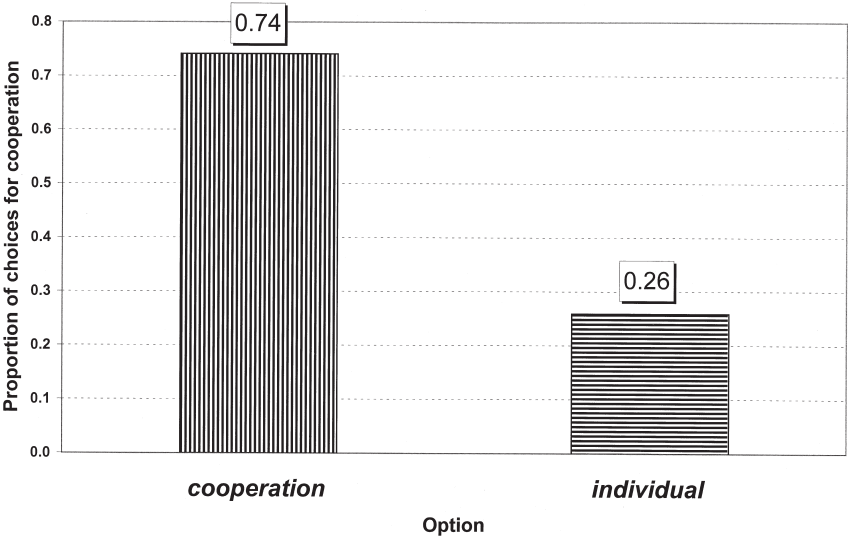


Figure 11. Proportions of all 224 choices for cooperation or individual shuttling from 28 subjects (in 14 pairs), each experiencing eight choice trials.

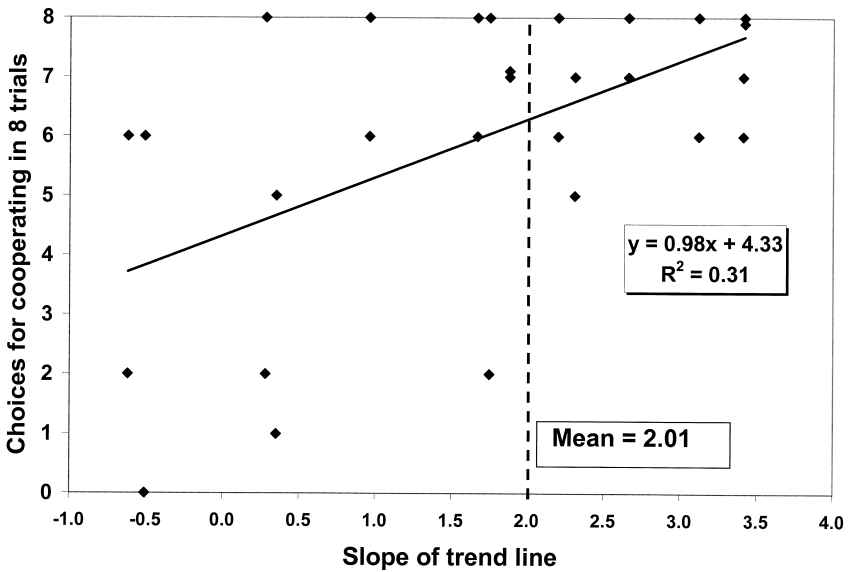


Figure 12. Relationship between the linear slope of the learning curve during Stage 1 (learning) and the number of choices for the cooperation option in pairs classified as “cooperators” ($n = 28$ subjects in 14 pairs). The mean of 2.01 refers to the data shown in Figure 9.

participants that influence post-session consumption of the rewarding solution and preference for cooperating.

These experiments have implications for method and theory. Methodologically, the model is offered as an experimental approach to studying CC in the laboratory with face validity as a model of CC as it occurs in the wild. While many of its properties were designed specifically for rats, the essence of the method allows pairs to develop their own strategies of CC within a shared space that leaves the animals free to engage in social acts and compete over outcomes. At first glance, experimental models based on game theory seem to offer an alternative way to look at how strategies adopted by one individual are modified by the behaviors of others. But the goal is achieved by isolating the subjects both when performing their tasks and when receiving their outcomes. The "social" in a game-theory model, like in Skinnerian models, is limited mainly to the contingency that links the outcomes for each participant, in part, to the behavior of others. There is little or no social behavior.

In terms of theory, this article has emphasized some of the limitations inherent in exclusive reliance on a functional perspective based upon individual behaviors and their outcomes, without considering the social phenomena that are intrinsic to cooperation under free-ranging conditions. The current popularity of the individual behavior \rightarrow outcome perspective is understandable given its diverse origins in selfish-gene theories of evolution (Krebs and Davies 1993), game theory (Dugatkin 1997; Stephens and Anderson 1997), and psychological learning theory (Skinner 1953). But the emphasis is on a catalog of what animals *ought* to do when cooperating, in other words, the optimal strategies for maximizing payoffs. Textbooks on behavioral ecology give the impression that there is supposed to be a close fit between adaptive behaviors and maximized payoffs. If not, then the payoffs have probably not been correctly identified or measured. Game-theory models modify this slightly by showing that, in a social context, payoffs can be influenced by what others are doing, but strategies ultimately remain individual and maximizing. The individual perspective is therefore neater by making fewer assumptions and offering better predictions about what to expect in both theoretical and behavioral models. But their success derives from cleansing the models of the kinds of social phenomena that are intrinsically unpredictable, a tactic fully compatible with the modern sciences of animal psychology and biology that strive, as in physics and chemistry, for maximum prediction and control of their phenomena. One obvious drawback is that isolation models offer the temptation of a self-fulfilling prophecy. Strategies governed by self-interest are almost guaranteed by isolating the consequences of individual action and its outcomes from the social elements that might lead to other results.

As noted in the introduction, perhaps the most serious problem faced by the individual behavior \rightarrow outcome perspective is that cooperation in the

real world is often characterized by payoffs that deviate markedly from the predicted maximization of outcomes. There are more and more examples of situations in which animals might even do better by not cooperating, usually owing to social factors that influence roles, competition, and/or dominance. In humans, the social factors are probably even more complex, with issues of reputation, manipulation, bargaining, and long-term strategizing that can impact on outcomes (Forsythe et al. 1994; Frank 1988; Palameta and Brown 1999). The outcome problem is further complicated by the evidence from Experiments 5 and 6 for affective states evoked by cooperation that influenced both the consumption of the reward and the preference for cooperating. In short, the outcome problem invites the question, "Why cooperate?"

There are ways to accommodate the outcome problem to the individual behavior \rightarrow outcome perspective without reference to actual behavior. Cooperation can be combined with kin-selected altruism if participants are also close relatives, as in lion and chimpanzee hunting (McFarland 1985). But this does not seem to be the situation for all cases of intra-pair asymmetries in outcomes, and kinship was definitely not a factor in Experiments 5 and 6. The individual perspective can also assume the existence of additional benefits for each cooperator that are not being immediately realized, as suggested for lion hunting in groups (Packer, Scheel, and Pusey 1990) and baboon coalitions (Noë 1990; Noë et al. 1991; Noë and Sluijter 1995). In either case, the idea seems to be that CC as a social strategy may still be better for all individuals in the long run because it is based on preserving relationships that are beneficial in other contexts. Cooperative hunting in lions, for example, can be explained by greater benefits from working together in territorial conflicts, a sort of "conditioning" to work jointly with others. But if the game-theory solution is to hypothesize selfish benefits from participating in joint actions at other times and for other goals, this invites the question of why and how individuals choose to cooperate at those times when it is not immediately profitable. Lurking behind the economic explanation of long-term profitability is the possibility that animals possess the ability to engage in coordinated action with known partners because it is also intrinsically rewarding, even when it is not immediately profitable. Most animal species, after all, are probably unaware of the long-range advantages of choosing one strategy over another. Whether humans are necessarily better at this is open to debate.

The more parsimonious way to answer the question "Why cooperate?" may be to combine both perspectives, the individual behavior \rightarrow outcome perspective for specifying optimal expected outcomes, and the social behavior perspective for explaining why cooperators often tolerate outcomes that deviate, sometimes markedly, from the optimum. To orthodox adherents of selfish-gene theory, this idea probably evokes horror by offering an ugly fit between individual behavior on the one hand and out-

comes, optimality, and fitness on the other. Moreover, if we allow that motivations evolve for directing adaptive behaviors to the satisfaction of critical needs (e.g., Cabanac 1992), there is too often a mismatch between the motivation to cooperate and the tangible outcomes obtained. In order to make up for the shortfall in payoffs, measures of calories, grams, or copulations must be padded with the addition of less tangible elements, such as level of cohesion, hedonic shift, "rapport," and social reward. But if the data show that cooperative coordination is reliably associated with evidence for such intangibles, how then should we formulate our theories of selfishness? Is it selfish to experience a reward from nothing more than working with others?

One solution is to relax the requirement that cooperation only exists to satisfy the demands of an exclusively selfish strategy for all participants. Sober and Wilson (1998), for example, argue for the evolution of proximate mechanisms of altruistic motivation above the level of individuals that could explain why individuals might be motivated to gain less by working with others. In a similar vein, Frank (1988) proposed that positive emotions are evoked in humans who adopt social strategies not rooted in self-interest. One difficulty is that these proposals are primarily linked to the sophisticated cognitive and social skills of humans and perhaps a handful of animal species, including higher primates (e.g., de Waal 1996). In order to account for results such as the increased saccharine consumption and preference in Experiments 5 and 6, we would have to propose behavioral processes that are far simpler for generating positive social emotions, motivations, and rewards from nothing more than working together. Moreover, the emotional and motivational states linked to cooperative coordination would not be dependent on an animal's awareness of its contribution to the welfare of others. The existence of such processes could also account for the role that coordination plays in the mate choice, dueting, and "dear enemy" phenomena of animals. In humans as well, remnants of these processes may explain the thrill and cohesion from watching or participating in human ceremonies that orchestrate the simultaneous behavior of anonymous multitudes (McNeill 1995) or the attraction to a dance partner based on nothing more than synchrony of movements, a kind of primitive "chemistry."

Many social behaviors, cooperation among them, may therefore be designed not only for achieving individual maximization of payoffs but also for maintaining cooperation by compensating participants that adopt less profitable strategies marked by riskier roles, reduced outcomes, or subordination. The above is not meant to deny the importance of specifying the optimal strategies, but more a plea to also pay attention, with the help of the appropriate models, to the ways in which optimality can be compromised by social interactions and their consequences. In this respect, cooperation will probably turn out to be not that different from many other

social strategies underlying ranks, roles, and outcome disparities within long-term social relationships and groups.

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