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Original Article

Comparative Approaches to Studying Strategy: Towards an Evolutionary Account of Primate Decision Making

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Abstract: How do primates, humans included, deal with novel problems that arise in interactions with other group members? Despite much research regarding how animals and humans solve social problems, few studies have utilized comparable procedures, outcomes, or measures across different species. Thus, it is difficult to piece together the evolution of decision making, including the roots from which human economic decision making emerged. Recently, a comparative body of decision making research has emerged, relying largely on the methodology of experimental economics in order to address these questions in a cross-species fashion. Experimental economics is an ideal method of inquiry for this approach. It is a well-developed method for distilling complex decision making involving multiple conspecifics whose decisions are contingent upon one another into a series of simple decision choices. This allows these decisions to be compared across species and contexts. In particular, our group has used this approach to investigate coordination in New World monkeys, Old World monkeys, and great apes (including humans), using identical methods. We find that in some cases there are remarkable continuities of outcome, as when some pairs in all species solved a coordination game, the Assurance game. On the other hand, we also find that these similarities in outcomes are likely driven by differences in underlying cognitive mechanisms. New World monkeys required exogenous information about their partners' choices in order to solve the task, indicating that they were using a matching strategy. Old World monkeys, on the other hand, solved the task without exogenous cues, leading to investigations into what mechanisms may be underpinning their

responses (e.g., reward maximization, strategy formation, etc.). Great apes showed a strong experience effect, with cognitively enriched apes following what appears to be a strategy. Finally, humans were able to solve the task with or without exogenous cues. However, when given the chance to do so, they incorporated an additional mechanism unavailable to the other primates - language - to coordinate outcomes with their partner. We discuss how these results inform not only comparative psychology, but also evolutionary psychology, as they provide an understanding of the evolution of human economic behavior, and the evolution of decision making more broadly.

Keywords: behavioral economics, co-operation, decision-making, non-human primates

Introduction

Social animals are constantly faced with decisions about how to interact with other members of their groups. Psychology and economics have revealed much information about what decisions people make in different circumstances, while neuroscience has provided evidence about the brain activity linked with these decisions. In species other than humans, much is known about decision making in non-social situations such as foraging, but a similar understanding of decision making in the social realm is relatively minimal in comparison. This difference in knowledge about social decision making in comparison to individualistic decision making hinders a full understanding of the evolution of decision making. This gap must be filled, but it is not an easy task.

In this paper, we describe a comparative research program to better understand the evolution of some forms of decision making. We come from a variety of backgrounds (evolutionary biology, psychology, and economics) but have found a common language in a structured game theoretical and experimental approach. This program has already allowed us to describe both similarities and differences among four primate species in a coordination game, generating data that are informative in our understanding of how decision making has evolved in this taxon, at least with regard to a coordination game. In this review, we begin with some historical background of the study of decision making in our disciplines, and then we discuss current research in comparative experimental economics, focusing on our own research as an example of this approach. We end with a consideration of how this work informs the evolution of decision making more broadly, and some specific suggestions for new directions for the nascent field of comparative experimental economics. We hope that similar and complementary methodologies will be undertaken by others to expand this approach beyond the types of decisions and taxon described herein (e.g., to taxa with different social organizations) for a fuller understanding of the evolution of decision making.

Challenges to a “species-fair” approach

One challenge to comparative research is designing studies that are both comparable and “species-fair.” It is easy to err on the side of designing tasks that are comparable so that spurious factors in the procedure do not affect outcomes, but this is

inappropriate if the task is so challenging that the species in question is unable to learn it, precluding the research from saying anything meaningful about comparative decision making. This balance is challenging. For instance, researchers who are adapting paradigms used with humans for non-verbal species often design apparatuses that (hopefully) lead the animals to a similar understanding as is achieved through verbal instruction in humans. In this way, the same questions can be addressed, albeit in different ways. However, this is not without its perils. Too often it turns out that the apparent differences between humans and other species disappear when humans are given the other species' task without instruction, indicating that even small differences in procedure may be critical for comprehension (e.g., Jensen, Call, and Tomasello, 2007; Smith and Silberberg, 2010). One way to address this issue is to test new methodologies in both the species in question and a species for whom typical responses are already known, to verify that the novel procedures generate the same results. For instance, when testing humans and other species, non-verbal procedures should be validated in the humans as well as the other species to see how humans perform. If humans' behavior varies from "typical" responses, then these differences should be considered in drawing conclusions about the comparison.

Previous researchers have attempted to address this gap (e.g., Jensen, Call, and Tomasello, 2007), but the methodologies and procedures typically differed in tests given to different species to the degree that a comparison was difficult or impossible. Human studies typically involve a high degree of verbal interaction and/or written instruction. Although it is obvious that non-human species cannot be expected to follow verbal instruction, and obviously not written instructions, at a more basic level non-human subjects may not identify with the (human) experimenter in the same way that human participants do. Also, non-human primates are potentially influenced to perform as they perceive the experimenter desires them to due to the inevitable relationships that are fostered between humans and captive animals, with potential implications for the results (David and Balfour, 1992). Additionally, there are constraints based on disciplinary traditions, physical constraints, and practical constraints. Regarding the first, humans often are not working for actual rewards (at least in the psychology tradition, which often involve hypothetical outcomes, as opposed to the experimental economics tradition, in which participants are always paid in cash), which may influence the responses made by humans compared to other species, which are virtually always working for immediate food rewards. Physical constraints on the researchers' ability to set up an experiment are also a problem, particularly with large-bodied species, such as the apes, who cannot be moved to a separate testing area designed for a particular experiment's specifications. Inevitably, species are tested in different configurations that may affect results (e.g., next to one another vs. facing one another; discussed in Brosnan, Talbot, Ahlgren, Lambeth, and Schapiro, 2010, sharing an enclosure vs. separated from one another; Freeman, Sullivan, Schultz-Darken, Williams, and Brosnan, in review; or in differently sized enclosures; Burkart, Fehr, Efferson, and van Schaik, 2007; Cronin, Schroeder, Rothwell, Silk, and Snowdon, 2009; Cronin, Schroeder, and Snowdon, 2010). While this is unavoidable, researchers should take such variations into account when drawing conclusions, particularly in comparative studies. Regarding the final point, concessions must also be made when comparing species that differ in other factors, such as body plan (e.g., whether they can grasp an object or use a computer), preferred

sensory modality (e.g., visual vs. olfactory vs. auditory), or ecology (which may have led to similar behaviors being expressed in very different ways or contexts). Finally, not all research is explicitly comparative, and many studies are designed to address a specific question for a specific species, leading to procedures that are not ideally designed to be comparative and applicable across species.

How, then, does one create a species-fair approach that both taps into the species' abilities and avoids the pitfalls of a non-comparable task that may over- or under- estimate performance? We argue that the best approach is to design studies that are as identical as possible across species, and then to compare responses between species whose outcomes are already known and the novel species. Of course, similar outcomes in such tasks do not necessarily reflect similarity in the underlying mechanisms, which can only be uncovered with further investigation into the necessary requirements for solving a given task. However, by using this approach we can avoid many procedural issues that may cloud a true comparison. There may be situations in which deviations are essential, such as in the constraints discussed in the previous paragraph. Nonetheless, meaningful comparisons are still possible (Salwiczek et al., 2012).

Our interest is to better understand the evolution of social decision making, broadly construed across a variety of species. To do so, we developed a direct comparative approach that involves procedures and practices that can be used widely and that meet our criteria for being "species-fair." An approach that we found fruitful was to use laboratory tests of game theoretical abstractions of strategic interactions. Game theory distills complex decision making situations to their essence in an attempt to better tease apart the mechanics of a decision. From a comparative perspective, this is ideal as these situations may not require instruction, training, pre-testing, or other verbal input, but are nonetheless a meaningful exploration of decision making across species, including humans (the species that most game-theory is intended to model). In this way, many diverse species may participate in the same procedure, yet one that is not so complex, complicated, or removed from their natural ecology that they have no chance of solving the task (and hence we have no chance of figuring out what they can really do).

Decision making in comparative psychology

Comparative psychology has traditionally been focused on understanding the performance of organisms in isolation, as reflected in the various apparatuses that have been designed for use with animals (e.g., Thorndike's puzzle box, the Skinner box, Harlow's Wisconsin General Test Apparatus, and others; see Washburn, Beran, Evans, Hoffman, and Flemming, in press). Even more recent experimental test paradigms, such as computerized testing, involve assessing an animal's performance in isolation rather than as part of a pair of animals working on a task at the same time (Washburn et al., in press). Testing in isolation misses important factors that might influence the choices of animals when they are faced with multi-option decisions. However, the methods of comparative psychology are adaptable for studying decision making in pairs or groups of animals, and so these methods are an asset in shaping a better understanding of economic decision making in an evolutionary context.

Understanding more complicated decision making situations requires establishing

the payoffs of two or more individuals to be dependent on each other, and determining how these individuals recognize, or learn, not only the “rules of the game” but also the tendencies of their partners and the contingencies for multi-player response patterns. Recent experiments, such as those we describe below, have tried to move in this direction using methods from comparative psychology. These have provided new tests that have multiple players working at the same time, in some cases on the same computer screen or with the same manual testing paradigm.

To give just one example, we recently investigated whether capuchin monkeys (*Cebus apella*) would engage in a joint-computerized task that required turn-taking by two animals, in which food rewards earned by one individual were subsequently delivered to the second individual, and vice versa (Parrish, Brosnan, and Beran, in review). In the task, the monkeys sustained performance, which required alternately working to deliver food rewards to their partner. Interestingly, male and female capuchin monkeys were differentially affected by their partner’s presence in this task, suggesting social facilitation (or not) based on the animal’s sex. Specifically, male monkeys (who were also dominant) completed fewer trials in the absence of their female partners than when their partners were present, but female monkeys completed more trials in the absence of their male partners than when their partners were present. These results suggest that capuchin monkeys will engage in sustained partner feeding behavior if a task is designed to require alternation of such behavior, whether or not they have a full understanding of the task’s contingencies (e.g., their own or their partner’s role in the interaction, a question that requires additional research). The results also suggest that monkeys may be sensitive to the social context of the interaction. These results highlight the utility of applying traditional comparative psychology paradigms such as joystick computerized tasks to the exploration of social questions. The joint-computer paradigm employed allowed for the almost complete control of multiple factors in the experimental environment, including the ability to hold most aspects of the procedure consistent across conditions and the removal of the human experimenter from the primates’ interaction. Joint-computerized testing is particularly useful in social tasks investigating contingent decision making with multiple players, and introduces a level of control that is difficult to achieve with other paradigms.

Decision making in experimental economics

Economics was once considered to be more like astronomy and meteorology than like physics or chemistry, more “observational” than “experimental” (Smith, 1987). There was no reciprocal feedback between *a priori* theory and experimental observation (Smith, 1989). By randomly assigning conspecifics to treatments, a laboratory experiment submits economic propositions to the test of being observed or not. Importing the laboratory method of inquiry into economics has revamped how economists build market institutions (Smith, 2008) and refashioned how social scientists construct game theory (Camerer, 2003; Smith, 2008). Although research in experimental economics has overwhelmingly involved human participants, there has been some investigation of the economic behavior of other species. Kagel, Battalio, and Green (1995) summarize many different experiments on rats and pigeons designed to explore the basic tenets of individual choice theory in economics. For instance, they find that rat and pigeon behavior conforms to the “law of demand”; as

the price of food increases in terms of lever presses (rats) or time (pigeons), individuals demand less of the commodity. On the supply side, Kagel et al. (1995) report that mice, rats, and humans working for fortified milk, sucrose solution, and alcohol, respectively, all exhibit backward-bending labor-supply functions; as wages increase, individuals work more until at some point individuals substitute more leisure for work to the point where less labor is supplied than at initially low wages. However, as with traditional work in comparative psychology, the work by experimental economists on animals is limited to organisms in isolation; what these authors do not explore with non-human species are strategic interactions between conspecifics. As discussed in the preceding section, this is the goal of our current work.

Why focus on coordinated and cooperative decision making?

An appropriate place to start any consideration of social decision making is in the realm of cooperation. Cooperation has been an evolutionary puzzle for decades; after all, how and why do individuals who are supposedly focused on their own survival and reproduction work together with others in situations that might lead to a benefit only for the other? Despite this puzzle, cooperation occurs in a wide variety of species (Brosnan and Bshary, 2010; Dugatkin, 1997), covering a wide range of behaviors from very simple ones with no cognitive component (e.g., in plants; Kiers, Rousseau, West, and Denison, 2003) to complex ones that appear to rely on cognitive processes (reviewed in Brosnan, Salwiczek, and Bshary, 2010). Although we know much about the cooperative situations that occur in different species, what is lacking is an approach that is easily comparable across species. Given that forms of cooperation are so broadly practiced across the animal kingdom, it seemed to be a logical starting point for a truly comparative investigation of decision making. Thus, the initial goal of our research was to see how four primate species, including humans, solved a simple coordination game derived from experimental economics, the Assurance Game.

Current Research in Comparative Experimental Economics

As discussed above, experimental economics is a relatively new method of inquiry in economics (introduced within the last 50 years) that grounds economics as a behavioral science. This focus on observation with random assignment of subjects to treatments, rather than formalized models of axiomatic logico-deduction, marks a methodological convergence with psychology¹. With the concurrent advent of game theory, experimental economists then applied their empirical methodology to the formal predictions of behavior in strategic interactions. Below, we discuss our program to expand the experimental economics approach to other species, comprehensively investigating a series of games

¹ Indeed, the 2002 Nobel Memorial prize in economics was shared by an experimental economist (Vernon Smith) and an experimental psychologist (Daniel Kahneman).

across four primate species, including humans, to determine wherein lie the similarities and the differences.

Coordination games

Coordination games require individuals to coordinate their decisions in order to achieve a payoff dominant outcome. The Assurance, or Stag Hunt, Game models a situation of mutual coordination in which two individuals each have a choice of playing *Stag* or *Hare*. If both individuals play *Stag*, they both receive a payoff of $4x$, where x is a single unit of a reward (one food pellet for animals or one quarter for humans). If an individual chooses to play *Hare*, regardless of what the other conspecific does, he receives a payoff of x . However, if an individual plays *Stag* and the other conspecific *Hare*, the *Stag* player receives no reward. Thus, the pair of actions (*Stag*, *Stag*) is a Nash equilibrium² because it benefits neither conspecific to switch to *Hare* if the other is playing *Stag*. By the same reasoning, the strategy pair (*Hare*, *Hare*) is also a Nash equilibrium. There is no incentive to deviate from (*Hare*, *Hare*) because switching to *Stag* would result in a zero payoff if the other individual is playing *Hare*. The former equilibrium is said to be “payoff dominant” because it results in mutual payoffs of $4x > x$, but the latter is “risk dominant” in avoiding a zero payoff when the individuals are not assured that the counterpart will play *Stag*. This game was initially described by Rousseau and has since been argued to be an excellent representation of many social dilemmas (Skyrms, 2003).

In our version of the task, individuals chose between a pair of tokens (Brosnan et al., 2011) or a pair of icons on a computer screen (Brosnan, Wilson, and Beran, 2012) to indicate a choice of *Stag* or *Hare*. Rewards were commensurate with the choice of both players. We used different versions of the task, as human subjects in experimental economic games are typically tested on computers, while non-human primates are often tested in a “hands-on” or manual format in which they interact with the experimenter. As we did not know *a priori* whether there was an inherent advantage to one protocol over the other, we chose to utilize both procedures with humans and non-humans.

We tested four primate species on this task: humans, chimpanzees, capuchin monkeys, and rhesus monkeys. These four species were chosen as they represent a range of primates known to cooperate, including great apes (humans and chimpanzees), Old World monkeys (rhesus monkeys), and New World monkeys (capuchin monkeys). Humans cooperate extensively (e.g., Fehr and Fischbacher, 2003), across cultures (Gächter, Herrmann, and Thöni, 2010), and do so to a degree unprecedented amongst the primates (Silk, 2005). For instance, economic systems may be considered the ultimate cooperative endeavor, in which each individual relies on others to produce the breadth of goods required for survival (Seabright, 2004; Smith, 2000 [1776]). Chimpanzees are also highly cooperative. In the field, chimpanzees cooperate socially through a series of coalitions and alliances (Goodall, 1986), as well as for material outcomes such as in cooperative hunting

² A pair of strategies (actions) is a Nash equilibrium if neither conspecific can increase its payoff by deviating unilaterally to another strategy.

(Boesch, 1994; Boesch and Boesch, 1989). In the latter case, individuals may coordinate different roles to maximize success in the hunts (Boesch, 2002). Chimpanzees also cooperate in laboratory tests, and are highly sensitive to the relevant features and qualities of their partner, preferring partners that are more tolerant over those that are less so (Melis, Hare, and Tomasello, 2006a, 2006b). Rhesus monkeys cooperate extensively, for instance working together in coalitions and alliances (Maestripieri, 2007). Finally, capuchin monkeys cooperate in the wild, engaging in group hunting, food sharing, and providing coalitionary support to conspecifics (Perry, Manson, Dower, and Wikbert, 2003; Perry and Rose, 1994; Perry, 1996, 1998; Rose, 1997). They have become one of the work horses of the experimental study of cooperation, at least based on the sheer number of studies completed. Capuchin monkeys appear to understand many of the contingencies of cooperation and are highly successful in many laboratory tests of cooperation (reviewed in Brosnan, 2010).

Standardized procedures. We standardized our procedures as much as possible so that they were identical across the four species. As discussed above, this is an important part of creating tests that are fair to all species. Individuals were tested in pairs with either a group-mate (non-human primates) or another individual from their university (humans). Pairs were not anonymous and were seated immediately adjacent to each other throughout the experiment. Individuals were allowed to communicate to the fullest extent of their species' ability, including talking between the humans. No subject of any species, including humans, received instructions on the game, a copy of the payoff matrix, or pre-testing on the game. The only training took the form of training the non-human primates, who had never been tested sharing a computer screen, to jointly select a single icon to receive a reward prior to the computer version of the task. Humans were simply told that they were going to make decisions that could result in monetary rewards and that they would not be able to ask the experimenter any questions during the course of the experiment. All subjects, including humans, were paid trial-by-trial in rewards that were theirs to keep (food rewards for non-human primates, quarters or dollar bills for humans). In the computerized version of the task, primates were paid using pellet dispensers and humans with standard coin dispensers, and no experimenter was present. Finally, as all non-human primates had previous experience working in the laboratory making decisions that resulted in tangible food outcomes, we recruited only humans who had previously completed a study at the Economic Science Institute at the Chapman University to ensure similar expectations regarding payment. Subjects who previously had been tested on the Assurance Game or another normal form game were excluded.

Exchange version. In the exchange version of the task (Brosnan et al., 2011), subjects were each given two tokens, one of which represented the *Stag* decision and one of which represented the *Hare* decision (tokens were the same for both members of a pair). Subjects could choose which of the two tokens to return to a human experimenter, who, after both subjects had made a decision, first held up the tokens, followed by the appropriate rewards, and then gave the rewards to the subjects. In this way, subjects saw both their own and their partner's responses and earnings, and received those earnings

immediately. All subjects worked with a human experimenter who they could see, but from whom they were separated by a barrier. Subjects could see each other and, if they chose, their partners' decisions, except for one test with chimpanzees in which we completely obscured their view of their partner's choice (described below).

At least one pair of every species was able to find the payoff dominant outcome, with both partners predominantly choosing *Stag* (at least 75% of the time; chance was 25%). However, the frequency of achieving this outcome varied across species; amongst six capuchin monkey pairs (involving eight unique monkeys), only one pair did so. Amongst 26 unique human pairs, five pairs found the payoff dominant outcome, although two others showed a tendency in that direction. Perhaps more interesting were the 10 human pairs who settled on the *Hare-Hare* strategy. We note that of these pairs, none ever played the *Stag-Stag* strategy on any trial, indicating that this outcome was largely due to these pairs assuming that they had found the payoff dominant outcome, and so they failed to explore the strategy space further. There were also three pairs who matched their partner's choice, and the rest showed no discernible strategy.

The chimpanzees' performance patterns were apparently based heavily on previous experience. Ten pairs of chimpanzees (20 total chimpanzees) were socially housed in large, multi-male, multi-female groups at MD Anderson Cancer Center. They interacted extensively with humans in a highly enriched environment, but had little previous experience with cognitive and behavioral testing. Among these 10 pairs, six matched their partner's choice, but never settled on any particular strategy (two additional pairs played *opposite* their partners, which resulted in the lowest overall possible payoff). We were curious whether these outcomes might have resulted from one partner understanding the task and making the best of a partner who did not. We assessed whether the order of play was consistent, but found that pairs in which this was the case were equally distributed between those who showed the matching strategy and those who showed no strategy at all (see below for more on this; Bullinger, Melis, and Tomasello, 2011).

Four additional chimpanzees were housed at the Language Research Center of Georgia State University, where they had had extensive cognitive training and enrichment since a few weeks after birth. Three of these chimpanzees had been trained to use a symbolic language system to communicate with humans (Rumbaugh and Washburn, 2003) and all were tested almost daily on cognitive and behavioral studies. Of these chimpanzees, two pairs (made up of three unique chimpanzees) found the payoff dominant outcome. To assess whether they could maintain this outcome when they could not see their partners' choices, we erected a barrier that completely occluded their view of their partner's interaction with the experimenter and the tokens. One pair maintained their preference for the payoff dominant outcome. However, this could have been due to a learned preference for the token that acquired more food items rather than an understanding of the strategies involved in the task itself. To test this, we tested both of these pairs using novel tokens, but with the same payoff structure. Both pairs easily re-acquired a preference for the now-different *Stag* token, indicating that they understood the task demands and were following a strategy to maximize their rewards.

The differences seen between the two populations of chimpanzees are intriguing as they indicate an experience effect similar to what might be expected in humans. The

reactions of the chimpanzees at MD Anderson probably more closely reflect the initial response of naïve chimpanzees to this sort of structured economic experiment. These chimpanzees are highly attuned to their social environment and their partners' behavior, as all lived in large, age-stratified, multi-male, multi-female social groups. These social interactions are closer to those in natural settings than was possible in the smaller group at the Language Research Center at Georgia State. However, the chimpanzees at Georgia State (who were also socially housed with multiple adult males and females, albeit with fewer individuals in the group) had far more experience with experimental paradigms, which may have allowed them to more easily understand the task and intuit the solution that would provide the best outcomes (i.e., the most rewards). We are excited to see how future research will tease apart the role of experience and rearing history, including which experiences are most critical in shaping various decision making behaviors and how much experience is required to solve these sorts of tasks.

For our next series of experiments, we repeated the same protocol with a computerized version of the task. This allowed us to explore whether a different methodology might improve performance. We were particularly interested in whether additional experience would affect behavior, and this procedure allowed us to complete more trials per session with the non-human primates and to hold more features of the experimental environment constant. Specifically, the computerized version of the task allowed for additional control by removing experimenters from the test area and hiding the other's choice. Based on the exchange results, we were interested in how being able to observe one's partner's choice would affect outcomes. Thus, the computerized task allowed us to control whether or not subjects had any cues to their partners' behaviors without changing other aspects of the task (e.g., the erection of the barrier, which may also have limited vital social communication).

Computerized version. In the computerized version (Brosnan et al., 2012), all species used the same computer program on a shared computer screen. All species controlled their cursor with joysticks, which were covered to obscure their partner's view of their choices. To further obscure the partners' choices, the cursor did not move on the screen (it disappeared when the joystick was deflected). In order to evaluate the role of seeing the partner's choice, we utilized two procedures. In the synchronous procedure, when an individual made a decision, his or her side of the screen went blank until their partner made a choice, at which point both subjects' choices were displayed and rewards were given. In this way, subjects had no clues as to their partner's choices until after both had played. In the asynchronous procedure, when an individual made a decision, it was displayed on their side of the screen so that the partner had that information available as he or she made a choice. However, subjects' choices were never constrained, so we did not dictate who went first or include any time-out period between one individual's response and their partner's.

We also found an interesting result with the humans that led to an additional procedure which differed slightly from the established protocol. In the synchronous "standard" version of the task, humans always spoke to one another, probably because the absence of an experimenter removed any inhibition and led to normal social interactions.

However, not every pair spoke about the game. Those that discussed the task invariably settled on the payoff dominant (*Stag, Stag*) outcome, while those who did not discuss the task never did so. As a result, we had to choose how to test the synchronous versus simultaneous versions of the task in humans. We chose not to forbid people from speaking to one another, as we were concerned that the social awkwardness of this procedure would bias results. Instead, we tested both the synchronous and the asynchronous versions of the task using a traditional normal form game format in which multiple individuals were tested in the room at the same time but separated by visually-isolated carrels. Thus, in this case, individuals were not sitting next to one another, they could not communicate, and their partners were anonymous. Additionally, we could not pay trial-by-trial as the noise from the coin dispensers was a cue as to individuals' partnerships, so we accumulated earnings in the corner of the screen and paid them at the end of the session, as is typical in normal form game set-ups. This also allowed us to compare humans' reactions in the "primate version" of the task to the more typically utilized normal form game format.

In the computerized version, we found more similarity in performance across species than was seen with the exchange task, however intriguing differences remained. Given the capuchins' previous experience and relatively less strong performance as compared to the humans and chimpanzees, we began the capuchins on the asynchronous procedure, in which they could see their partners' choices. We initially tested capuchins on 40-trial sessions, as is our habit for computer testing sessions. Only one pair of the subjects was able to solve the task. Thus, to see if the number of trials was a factor, we tried 60-trial blocks (which are more typically used for our rhesus monkeys). All pairs of capuchins were able to solve the task quickly when switched to 60-trial sessions. While of course the number of trials in a block and experience is confounded, we find this result compelling, and hope that others will consider trial number as an important variable when constructing comparative tests.

In 60-trial blocks, all pairs of capuchin monkeys found the payoff dominant outcome in the asynchronous task, where they could see each other's choices. We then moved capuchins to the synchronous task, where no pair found any structured outcome, despite the fact that there were no other modifications to the task. We then re-tested the subjects on the asynchronous task in as many pairings as possible given our social group constraints (subjects were only tested with partners from within their social group) and, again, found that subjects solved the task. However, when pairs were re-tested on the synchronous procedure, they again failed. Thus, it seems that capuchin monkeys can solve the task when they can match their partner's play, but cannot generalize a response strategy about specific token types when this is not possible, indicating that a fairly simple behavioral strategy, such as matching, is responsible for their performance.

We also tested eight male rhesus monkeys who were naïve to the task, thus half were started on the synchronous task and half on the asynchronous task. All pairs in the asynchronous task were able to find the payoff dominant outcome quite rapidly, and unlike the capuchins, all were able to maintain their performance when they moved to the synchronous task. More surprisingly, all pairs who started on the synchronous task also found the payoff dominant outcome quite rapidly (they were not re-tested on the asynchronous version). Thus, the rhesus monkeys are apparently able to solve the task

using something more than matching. Below we consider further the possible strategies they may have utilized.

Of the 27 human pairs tested in the synchronous version, all spoke, unlike in the exchange task. This was likely because there was no experimenter in the room to inhibit conversation (the pair was alone in a room and the video camera recording their behavior was mounted behind them, out of their view). However, only 22 pairs spoke about the task at hand. Of these, all 22 pairs found the payoff dominant outcome and stayed with it, including one pair who did not talk about the task until the last quarter of the game. On the other hand, of the five pairs who failed to discuss the game, all settled on the (*Hare, Hare*) outcome. We propose that the successful humans used language to essentially turn a synchronous game into an asynchronous one, while the unsuccessful pairs may have thought that they had solved the task (both were receiving a quarter) and so did not discuss it. Of course, this meant that they failed to explore the action space and missed the opportunity to gain additional benefits. When language is removed as a possibility, humans may also use other cues. Of the humans tested in the normal form game design, those playing the asynchronous task did indeed find the payoff dominant outcome more than those playing the synchronous task, although this difference was not large, and the pairs playing the asynchronous task earned more than did those playing the synchronous task.

Considering only the rhesus monkeys and the humans, both species were equally capable at solving the task even when they did not know their partner's choice prior to making a decision. Whether this similar outcome is due to a similar underlying mechanism is unknown; however, we hypothesize that they may differ. Specifically, we think it is possible that the humans viewed the interaction as a social strategy, and saw their decision as part of the pair's strategy. Rhesus monkeys, we think, may have used a more associative mechanism, such as the matching law (Herrnstein, 1961), in which they sampled choices until they learned which had the highest probability of paying the most food, then settled on this response. Given our payoff structure (4:1), as long as one's partner plays *Stag* more than one quarter of the time, then the reward maximizing strategy is to always play *Stag* despite the fact that close to 75% of these trials will result in a zero payoff. Even if both partners start by choosing randomly, *Stag-Stag* will happen on one out of every four trials, and the large payoff should reinforce the *Stag* choice for both partners. However, if humans conceive the decision as playing *with* a partner, they are unlikely to tolerate such frequent "defections." On the other hand, of course, it is possible that humans and rhesus are using the same cognitive mechanism. In particular, there is a danger in assuming a purely cognitive explanation for any species – including humans – without evidence. It is possible that humans, too, are relying on associative mechanisms in this task. In order to evaluate these hypotheses, we are currently testing humans and rhesus on simulations which alter the frequency of *Stag* choices by the (simulated) partner to see when both species cease coordinating on the *Stag* option.

What does this mean? These results show that there are both concurrences and differences amongst primate species in how they play these games. Given the right circumstances, New World monkeys, Old World monkeys, apes, and humans all find the payoff dominant outcome in this coordination game. What is intriguing is the difference in

performance across species. Capuchin monkeys, despite both their extensive ability to achieve cooperation in experimental tasks (Brosnan, 2010) and their much larger brain-to-body ratio than any other non-ape (Rilling and Insel, 1999), a feature that has been linked to increased cognition (Clutton-Brock and Harvey, 1980; Marino, 1996), do the least well on the task. Without an ability to match the play of the partner, capuchins are unable to solve this task. Rhesus monkeys, who have brains of absolute larger size than capuchin monkeys (also linked to cognitive ability; Deaner, Isler, Burkart, and van Schaik, 2007), do as well as humans. Nonetheless, as discussed above, we are curious to see whether the mechanism is the same, despite the similar outcomes. Also, given our results with the two different populations of chimpanzees, we are eager to see if rhesus monkeys with relatively less experience with cognitive testing would perform differently than our highly experienced monkeys (note that our capuchin monkeys were also very experienced on cognitive and behavioral tasks).

Of course, social decisions extend beyond symmetric coordination. What happens in coordination games in which outcomes vary (e.g., one individual earns more for cooperation than the other)? What about other types of games? We are particularly interested in games of conflict, and are currently extending this research to investigate the Chicken Game. The Chicken Game is an anti-coordination game in which two conspecifics can either take a strong action or a weak action. Also called the “Hawk-Dove Game” (Maynard Smith, 1982), the Chicken Game is based on the biological model first introduced by Maynard Smith and Price (1973) to describe animal conflict over a shared resource. The two strategies are to either yield (*Dove*) or not to yield (*Hawk*) to the other conspecific. In a symmetric game, there are three different types of outcomes: 1) two hawks do not yield and a fight ensues, leading to potential injury; 2) two doves both yield with the resource randomly acquired by one conspecific; and 3) a dove yields to a hawk, allowing the hawk to monopolize the resource. The two symmetric Nash equilibria are if one individual yields (*Dove*) and the other does not (*Hawk*). Our early results indicate that there are, again, both commonalities and discontinuities across the primates (Price, Beran, Wilson, and Brosnan, 2012) and we are eager to see whether these follow similar patterns as those seen in the Assurance Game.

Comparison to the existing literature. Surprisingly little research exists on coordination in non-human species. One exception is group hunting, an activity during which chimpanzees and lions take complementary roles and fill the same role consistently across hunts (e.g., Boesch, 2002; Stander, 2002). In laboratory studies mimicking such coordination, however, it seems that while chimpanzees are *capable* of coordinating (Fletcher, Warneken, and Tomasello, 2012), they do not always choose to do so (e.g., if other viable options for independent action are available; Rekers, Haun, and Tomasello, 2011). Research with chimpanzees indicates that coordination is preferred only when the rewards for coordination are greater than those that can be achieved through individual effort (Bullinger, Melis, and Tomasello, 2011). This may partially explain, for instance, why chimpanzees coordinate on hunts at only some field sites. It has been argued that forest-dwelling chimpanzees are more likely to coordinate than are savannah-dwelling chimpanzees due to the continuous canopy cover, which gives the monkeys an easier

escape route, thus increasing the difficulty for the chimpanzees (Boesch and Boesch, 1989). As a result, forest chimpanzees may be able to acquire monkey meat only through coordinated effort.

One other study that has explored chimpanzees' behavior in an Assurance Game, using a methodology that differs from our own, indicates that the tendency to coordinate on (*Stag, Stag*) is widespread in chimpanzees, or at least among those with experience in such tasks. Bullinger, Wyman, Melis, and Tomasello (2012) gave chimpanzees the opportunity to cease foraging alone on a lower-value food item (*Hare*) in order to achieve a higher-value one (*Stag*) by jointly foraging. Although there were differences between the studies (e.g., subjects in the Bullinger study were trained to pay attention to their partner, could consume some of the *Hare* option before pursuing the *Stag* one, and had fewer trials), results were largely similar. Both our Georgia State chimpanzee subjects and Bullinger et al.'s (2012) subjects were successful both when they could and could not see one another (e.g., a barrier condition). Moreover, subjects overwhelmingly chose the *Stag* option in both studies. One similarity between these populations is both groups' extensive experience in cognitive and social tests, which differs from the experience level of the Bastrop chimpanzees, who have relatively low levels of cognitive testing and did not coordinate on the (*Stag, Stag*) outcome. Although such a correlation does not prove causation, it is even more clear that the subjects' experience level is a factor that should be further explored. One difference between the studies is that in the Bullinger et al.'s (2012) study, there was evidence of a "leader-follower" dynamic in which chimpanzees consistently made the first or second move. We found that there was no correlation between order of play and outcome in the Bastrop chimpanzees, although this may also be confounded with their relatively lower level of previous experience. Thus chimpanzees are capable of finding the (*Stag, Stag*) outcome across a variety of methodologies, but may require previous experience to do so (see also Martin, Bhui, Bossaerts, Matsuzawa, and Camerer, in review).

Inequity games

Another class of games that has received attention is those that investigate subjects' responses to inequity. This response has been well studied in humans, both in psychology and economics (for a recent review, see *Social Justice Research*, 2012, volume 25, issues 2 and 3). Although there are decades of studies and entire journals dedicated to human concepts of fairness and justice, their application to economic behavior in the laboratory is far from understood (Wilson, 2012), and investigations of the common foundations of these concepts in other species are quite recent. To date, non-human studies have primarily focused on determining whether or not individuals even noticed when their outcomes differed from those of their partners. We briefly consider these games to highlight another area in which comparative experimental economics is shedding light on the evolution of decision making.

These responses are commonly studied using experimental approaches, in particular the Ultimatum Game (UG), in which one individual is given a sum of money that they divide between themselves and a partner. Following this, the partner can either accept or decline their allocation. If the responder chooses to decline the allocation, then neither partner receives anything. Humans in modern, Western societies tend to donate

approximately half of the initial allocation (reviewed in Camerer, 2003), and although allocation behavior in this game varies across cultures, in no culture do people routinely offer the lowest possible amount (Henrich et al., 2001). A related game, the Impunity Game (IG), is similar, except that if the responder declines only they receive nothing; their partner still gets their allocation as they had proposed. This game is far less well-studied as declining increases both relative and absolute inequity, which is worse for the partner and thus assumed to be an outcome that humans would avoid (Bolton and Zwick, 1995). Nonetheless, partners routinely chose to do so (at approximately half the rate seen in an equivalent Ultimatum Game distribution; Yamagishi et al., 2009), even when the allocator does not know their decision, implicating emotions such as anger in their responses.

Initial studies examined whether non-human primates who had to work to receive a food reward responded differently to their outcome when their partner worked for a better reward relative to when their partner got the same reward (Brosnan and de Waal, 2003). These studies used a protocol reminiscent of the latter half of the Impunity Game; individuals could refuse, but it affected only their outcome, not their partner's outcome. Among non-human primates, responses vary both across species and individuals, the latter of which makes species comparisons all the more challenging (for recent reviews of this growing body of literature, see Bräuer and Hanus, 2012; Brosnan, 2011; Price and Brosnan, 2012). In particular, capuchin monkeys, macaque species and chimpanzees frequently respond negatively to inequitable outcomes, although this varies across social groups (Brosnan, Schiff, and de Waal, 2005) and procedures (Brosnan et al., 2010; Bräuer, Call, and Tomasello, 2006, 2009), including details such as the physical proximity and orientation of the subjects to one another (Brosnan et al., 2010; Freeman et al., in review). Despite this variation, however, what seems to be consistent is the tendency for these three species to respond more commonly than do other ape and New World monkey species. Thus far, the phylogenetic distribution most closely matches the hypothesis that species that routinely cooperate in social situations are the most likely to respond negatively to unequal outcomes between themselves and their partners, supporting earlier suggestions that inequity is a mechanism by which individuals can judge the value of their current partner (Brosnan, 2011; Fehr and Schmidt, 1999).

Far less work has been done on the Ultimatum Game in non-human species, and thus far all of it has involved chimpanzees. An initial analogue test of the UG found that unlike humans, chimpanzee allocators tended to donate the lowest possible offer, and that their partners accepted any offer (Jensen et al., 2007). However, in a replication with humans, using the same procedure, humans behaved as the chimpanzees had (Smith and Silberberg, 2010). A more recent test of the UG in chimpanzees and children compared responding in the UG to that of a Dictator Game analog, in which the partner has no recourse to respond to the allocation. Both chimpanzees and human children were far more likely to offer an equal split in the UG than in the Dictator Game, indicating that the partner's ability to respond influences decision making in chimpanzees as well as humans (Proctor, Williamson, de Waal, and Brosnan, 2013).

Again, one weakness of this literature is the over-reliance on non-human primates. However, more recent work on other species is beginning to fill this void. In particular, there is growing evidence that dogs, another socially cooperative species, respond

negatively to less favorable outcomes as compared to a partner (Horowitz, 2012; Range, Horn, Viranyi, and Huber, 2008; Range, Leitner, and Viranyi, 2012). On the other hand, a highly cooperative fish species, cleaner fish (*Labroides dimidiatus*), do not respond negatively to inequity in experimental tasks (Raihani, McAuliffe, Brosnan, and Bshary, 2012), possibly because they rely on punishment to alter partners' behavior (Raihani, Grutter, and Bshary, 2010) rather than finding a new partner (Raihani and McAuliffe, 2012). Such broadly comparative work is needed not only to understand the ways in which species other than primates successfully cooperate, but also as tests of the evolutionary hypotheses regarding the function of specific cognitive abilities, and in what situations different solutions may be used to address the same problem.

How Do Comparative Experiments Inform Us About the Evolution of Human Decision Making in Multi-player Decision Making Games?

Clearly, the work described above enhances our understanding of other species' cognition and behavior, but what can it tell us about human decision making? Of course, the main benefit is the increase in understanding of the evolutionary trajectory of these behaviors. It is impossible to elucidate the evolutionary function of a behavior by studying a single species, as there is no way to rule out competing hypotheses. By studying a wide variety of species, including those within the same taxon and those from other taxa who share features in common that are related to the hypothesis in question, we can investigate these hypotheses as well as generate new ones that might not have been obvious from the point of view of a single species. Additionally, comparing species' reactions across different situations may highlight previously missed commonalities and differences. With respect to experimental economics, for instance, additional studies on coordination and anti-coordination games will help us to tease apart whether success in one class of games is related to success in the other, and highlight some selective pressures that may have worked across species.

Aside from function, comparative work is also essential for understanding the mechanisms that drive behavior. Even in situations in which the same outcomes are reached by different species, the cognitive (or other) mechanisms that are used to do so may be very different. Evolution works with the material at hand, and thus if a behavior is beneficial it will evolve in whatever way is possible, given the cognitive and behavioral architecture already in place. This is extremely important to tease apart. First, it is useful to understand the relative strength of the selection pressure. For instance, was a trait so critical that multiple species evolved it independently (e.g., sight)? Second, it helps us to understand how selective pressures may have differed, particularly if species that are otherwise quite similar in cognitive architecture do *not* evolve similar behaviors. Third, differences in cognitive mechanisms may highlight situations in which behaviors do differ from one another, despite what appeared to be similarity on an initial investigation. Fourth, understanding what mechanisms underlie decision making may highlight the way in which a trait unique to a single species may affect its choice behavior.

Considering the last point, language is clearly one of the major factors separating humans and other species. Other species may have extensive communicative repertoires

that allow for complex communication (Bradbury and Vehrencamp, 2011), including complicated situations such as tactical deception (Brown, Garwood, and Williamson, 2012; Wheeler, 2009), and some species have even been trained to learn and use basic language, including both vocabulary and grammar (Hillix and Rumbaugh, 2004). However, human language exceeds the communication seen in other species. How might this help humans in the context of decision making? While humans can solve coordination games both with and without language (Brosnan et al., 2012), we are curious to see whether language increases efficiency in other, more challenging, contexts, perhaps by allowing language-using participants to transform games in which information is constrained (i.e., players are not told what the other player has done until both have acted) to more flexible and open formats (i.e., by telling each other what they plan to do on a given trial).

So what is needed next? As we have reiterated throughout this paper, a major need is for similar studies to be done in other species. This includes both primate species that have different ecologies (e.g., cooperative versus non-cooperative, solitary versus group living) and cognitive abilities, as well as non-primate species that vary on similar characteristics. Additionally, all of the tests that we know of have involved highly social species; it will be important to test non-social or less social species, which will highlight the ways in which sociality may have influenced selective pressure on decision making in multi-player settings, as well as situations in which “social” decision making may not rely on social interactions. It will, however, be critical to use methods that are as similar as possible across these taxa, otherwise it will be impossible to tell whether any differences found are due to the species’ ecology or cognition, or whether they are due to differences in procedure. As discussed in the introduction, this can be particularly challenging for animals that differ in body plan, but has been successfully accomplished (Salwiczek et al., 2013).

Secondly, of course, we need to understand a wider variety of situations than have currently been studied. Aside from needing to explore a wider variety of decision making situations, all of the games explored to date have involved pairs of individuals. However, most social interactions in the wild involve more than two individuals. Thus, we need to expand this line of inquiry to situations with three or more individuals.

Finally, we should remember that comparative psychology offers insight into the nature of an animal’s psychology, in terms of what drives behavior and what might underlie the mental life of that animal. Thus, comparative psychology opens a window into the minds of animals, but we must remain cautious about over- or under-interpreting what it is that animals are thinking by relying solely on what they are doing. A cautious but optimistic approach to anticipating strategic decision making in animals when faced with economic games or other tasks that require some degree of social coordination will shed the best light on the emergence of strategic decision making in our species, and the best possible evidence for analogous processes as they might occur in non-human animals.

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References

- Boesch, C. (1994). Cooperative hunting in wild chimpanzees. *Animal Behavior*, 48, 653-667.
- Boesch, C. (2002). Cooperative hunting roles among Tai chimpanzees. *Human Nature*, 13, 27-46.
- Boesch, C., and Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Tai national park. *American Journal of Physical Anthropology*, 75, 547-573.
- Bolton, G. E., and Zwick, R. (1995). Anonymity versus punishment in ultimatum game bargaining. *Games and Economic Behavior*, 10, 95-121.
- Bradbury, J. W., and Vehrencamp, S. L. (2011). *Principles of animal communication* (2nd ed.) Sunderland, MA: Sinauer Associates.
- Bräuer, J., Call, J., and Tomasello, M. (2006). Are apes really inequity averse? *Proceedings of the Royal Society B*, 273, 3123-3128.
- Bräuer, J., Call, J., and Tomasello, M. (2009). Are apes inequity averse? New data on the token-exchange paradigm. *American Journal of Primatology*, 7, 175-181.
- Bräuer, J., and Hanus, D. (2012). Fairness in non-human primates? *Social Justice Research*, 25, 1-21.
- Brosnan, S. F. (2010). What do capuchin monkeys tell us about cooperation? In D. R. Forsyth and C. L. Hoyt (Eds.), *For the greater good of all: Perspectives on individualism, society, and leadership* (Vol. Jepson Studies in Leadership Series, pp. 11-28). New York: Palgrave Macmillan Publishers.
- Brosnan, S. F. (2011). A hypothesis of the co-evolution of inequity and cooperation. *Frontiers in Decision Neuroscience*, 5, 43.
- Brosnan, S. F., and Bshary, R. (Eds.) (2010). *Cooperation and deception: From evolution to mechanisms* (Vol. 362): *Philosophical Transactions of the Royal Society, Series B*.
- Brosnan, S. F., and de Waal, F. B. M. (2003). Monkeys reject unequal pay. *Nature*, 425, 297-299.
- Brosnan, S. F., Parrish, A. R., Beran, M. J., Flemming, T. E., Heimbauer, L., Talbot, C. F., . . . Wilson, B. J. (2011). Responses to the Assurance game in monkeys, apes, and humans using equivalent procedures. *PNAS*, 108, 3442-3447.
- Brosnan, S. F., Salwiczek, L., and Bshary, R. (2010). The interplay of cognition and cooperation. *Philosophical Transactions of the Royal Society B*, 365, 2699-2710.
- Brosnan, S. F., Schiff, H. C., and de Waal, F. B. M. (2005). Tolerance for inequity may increase with social closeness in chimpanzees. *Proceedings of the Royal Society B*, 1560, 253-258.
- Brosnan, S. F., Talbot, C., Ahlgren, M., Lambeth, S. P., and Schapiro, S. J. (2010).

- Mechanisms underlying the response to inequity in chimpanzees, *Pan troglodytes*. *Animal Behavior*, 79, 1229-1237.
- Brosnan, S. F., Wilson, B. J., and Beran, M. J. (2012). Old World monkeys are more similar to humans than New World monkeys when playing a coordination game. *Proceedings of the Royal Society B*, 279, 1522-1530.
- Brown, C., Garwood, M. P., and Williamson, J. E. (2012). It pays to cheat: Tactical deception in a cephalopod social signalling system. *Biology Letters*, 8, 729-732.
- Bullinger, A. F., Melis, A. P. and Tomasello, M. (2011). Chimpanzees, *Pan troglodytes*, prefer individual over collaborative strategies towards goals. *Animal Behaviour*, 82, 1135-1141.
- Bullinger, A. F., Wyman, E., Melis, A. P. and Tomasello, M. (2012). Coordination of chimpanzees (*Pan troglodytes*) in a Stag Hunt game. *International Journal of Primatology*, 32, 1296-1310.
- Burkart, J., Fehr, E., Efferson, C., and van Schaik, C. P. (2007). Other-regarding preferences in a non-human primate: Common marmosets provision food altruistically. *Proceedings of the National Academy of Sciences*, 104, 19762-19766.
- Camerer, C. (2003). *Behavioral game theory: Experiments in strategic interaction*. Princeton, NJ: Princeton University Press.
- Clutton-Brock, T., and Harvey, P. H. (1980). Primates, brains, and ecology. *The Journal of Zoology*, 190, 390-423.
- Cronin, K. A., Schroeder, K. K. E., Rothwell, E. S., Silk, J. B., and Snowdon, C. (2009). Cooperatively breeding cottontop tamarins (*Saguinus oedipus*) do not donate rewards to their long-term mates. *Journal of Comparative Psychology*, 123, 231-241.
- Cronin, K. A., Schroeder, K. K. E., and Snowdon, C. (2010). Prosocial behaviour emerges independent of reciprocity in cottontop tamarins. *Proceedings of the Royal Society B*, 277, 3845-3851.
- David, H., and Balfour, D. (1992). *The inevitable bond: Examining scientist-animal interactions*. Cambridge, UK: Cambridge University Press.
- Deaner, R. O., Isler, K., Burkart, J., and van Schaik, C. P. (2007). Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain, Behavior, and Evolution*, 70, 115-124.
- Dugatkin, L. A. (1997). *Cooperation among animals: An evolutionary perspective*. New York: Oxford University Press.
- Fehr, E., and Fischbacher, U. (2003). The nature of human altruism. *Nature*, 425, 785-791.
- Fehr, E., and Schmidt, K. M. (1999). A theory of fairness, competition, and cooperation. *The Quarterly Journal of Economics*, 114, 817-868.
- Fletcher, G. E., Warneken, F., and Tomasello, M. (2012). Differences in cognitive processes underlying the collaborative activities of children and chimpanzees. *Cognitive Development*, 27, 136-153.
- Freeman, H. D., Sullivan, J., Schultz-Darken, N., Williams, L. E., and Brosnan, S. F. (in review). All in the family? Cooperative breeders' response to unequal outcomes provides support for the cooperative breeder hypothesis.
- Gächter, S., Herrmann, B., and Thöni, C. (2010). Culture and cooperation. *Philosophical*

- Transactions of the Royal Society B*, 365, 2651-2662.
- Goodall, J. (1986). *The chimpanzees of gombe*. Cambridge, MA: The Belknap Press of Harvard University Press.
- Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., and McElreath, R. (2001). In search of homo economicus: Behavioral experiments in 15 small-scale societies. *American Economic Review*, 91, 73-78.
- Herrnstein, R. J. (1961). Relative and absolute strength of responses as a function of frequency of reinforcement. *Journal of the Experimental Analysis of Behaviour*, 4, 267-272.
- Hillix, W. A., and Rumbaugh, D. M. (2004). *Animal bodies, human minds: Ape, dolphin and parrot language skills*. New York: Kluwer Academic/Plenum Publishers.
- Horowitz, A. (2012). Fair is fine, but more is better: Limits to inequity aversion in the domestic dog. *Social Justice Research*, 25, 195-212.
- Jensen, K., Call, J., and Tomasello, M. (2007). Chimpanzees are rational maximizers in an Ultimatum Game. *Science*, 318, 107-109.
- Kagel, J. H., Battalio, R. C., and Green, L. (1995). *Economic choice theory: An experimental analysis of animal behavior*. Cambridge, UK: Cambridge University Press.
- Kiers, E. T., Rousseau, R. A., West, S. A., and Denison, R. F. (2003). Host sanctions and the legume-rhizobium mutualism. *Nature*, 42, 78-81.
- Maestripieri, D. (2007). *Macchiavellian intelligence*. Chicago, IL: University of Chicago Press.
- Marino, L. (1996). What can dolphins tell us about primate evolution? *Evolutionary Anthropology*, 5, 81-85.
- Martin, C. F., Bhui, R., Bossaerts, P., Matsuzawa, T., and Camerer, C. (in review). Experienced chimpanzees behave more game-theoretically than humans in simple competitive interactions.
- Maynard Smith, J. (1982). *Evolution and the theory of games*. Cambridge, UK: Cambridge University Press.
- Maynard Smith, J., and Price, G. R. (1973). The logic of animal conflict. *Nature*, 246, 15-18.
- Melis, A. P., Hare, B., and Tomasello, M. (2006a). Chimpanzees recruit the best collaborators. *Science*, 311, 1297-1300.
- Melis, A. P., Hare, B., and Tomasello, M. (2006b). Engineering cooperation in chimpanzees: Tolerance constraints on cooperation. *Animal Behavior*, 72, 275-286.
- Parrish, A. E., Brosnan, S. F., and Beran, M. J. (in review). The role of the partner in achieving reciprocal behavior in capuchin monkeys (*Cebus apella*).
- Perry, S. (1996). Female-female social relationships in wild white-faced capuchin monkeys, *Cebus capucinus*. *American Journal of Primatology*, 40, 167-182.
- Perry, S. (1998). Male-male social relationships in wild white-faced capuchins, *Cebus capucinus*. *Behaviour*, 135, 139-172.
- Perry, S., Manson, J. H., Dower, G., and Wikbert, E. (2003). White-faced capuchins cooperate to rescue a groupmate from a *Boa constrictor*. *Folia primatologica*, 74, 109-111.

- Perry, S., and Rose, L. (1994). Begging and transfer of coati meat by white-faced capuchin monkeys, *Cebus capucinus*. *Primates*, 35, 409-415.
- Price, S. A., Beran, M. J., Wilson, B. J., and Brosnan, S. F. (2012). *Responses to an anti-coordination game in capuchins (Cebus apella) and humans (Homo sapiens)*. Paper presented at the 35th meeting of the American Society of Primatologists, Sacramento, CA.
- Price, S. A., and Brosnan, S. F. (2012). To each according to his need? Variability in the responses to inequity in non-human primates. *Social Justice Research*, 25, 140-169.
- Proctor, D., Williamson, R., de Waal, F. B. M., and Brosnan, S. F. (2013). Chimpanzees play the ultimatum game. *Proceedings of the National Academy of Sciences, USA*, 110, 2070-2075.
- Raihani, N. J., Grutter, A. S., and Bshary, R. (2010). Punishers benefit from third-party punishment in fish. *Science*, 327, 171.
- Raihani, N. J., and McAuliffe, K. (2012). Does inequity aversion motivate punishment? Cleaner fish as a model system. *Social Justice Research*, 25, 213-231.
- Raihani, N. J., McAuliffe, K., Brosnan, S. F., and Bshary, R. (2012). Are cleaner fish (*Labroides dimidiatus*) inequity averse? *Animal Behavior*, 84, 665-674.
- Range, F., Horn, L., Viranyi, Z., and Huber, L. (2008). The absence of reward induces inequity aversion in dogs. *PNAS*, 106, 340-345.
- Range, F., Leitner, K., and Viranyi, Z. (2012). The influence of the relationship and motivation on inequity aversion in dogs. *Social Justice Research*, 25, 170-194.
- Rekers, Y., Haun, D., and Tomasello, M. (2011). Children, but not chimpanzees, prefer to collaborate. *Current Biology*, 21, 1756-1758.
- Rilling, J. K., and Insel, T. (1999). The primate neocortex in comparative perspective using magnetic resonance imaging. *Journal of Human Evolution*, 16, 191-233.
- Rose, L. M. (1997). Vertebrate predation and food-sharing in *Cebus* and *Pan*. *International Journal of Primatology*, 18, 727-765.
- Rumbaugh, D. M., and Washburn, D. A. (2003). *Intelligence of apes and other rational beings*. New Haven, CT: Yale University Press.
- Salwiczek, L., Prétôt, L., Demarta, L., Proctor, D., Essler, J., Pinto, A. I., . . . Bshary, R. (2012). Adult cleaner wrasse outperform capuchin monkeys, chimpanzees, and orangutans in a complex foraging task derived from cleaner-client reef fish cooperation. *PLoS ONE*, 7, e49068.
- Seabright, P. (2004). *The company of strangers*. Princeton, NJ: Princeton University Press.
- Silk, J. B. (2005). The evolution of cooperation in primate groups. In H. Gintis, S. Bowles, R. Boyd, and E. Fehr (Eds.), *Moral sentiments and material interests: On the foundations of cooperation in economic life* (pp. 43-73). Cambridge, MA: MIT Press.
- Skyrms, B. (2003). *The stag hunt and the evolution of social structure*. Cambridge, UK: Cambridge University Press.
- Smith, A. (2000 [1776]). *The wealth of nations*. New York: Random House.
- Smith, P., and Silberberg, A. (2010). Rational maximizing by humans (*Homo sapiens*) in an ultimatum game. *Animal Cognition*, 13, 671-677.
- Smith, V. L. (1987). Experimental methods in economics. In J. Eatwell, M. Milgate, and P.

- Newman (Eds.), *The new palgrave: A dictionary of economics* (pp. 241-248). London, UK: Macmillan.
- Smith, V. L. (1989). Theory, experiment and economics. *Journal of Economic Perspectives*, 3, 151-169.
- Smith, V. L. (2008). *Rationality in economics: Constructivist and ecological forms*. Cambridge, UK: Cambridge University Press.
- Stander, P. E. (1992). Cooperative hunting in lions: The role of the individual. *Behavioral Ecology and Sociobiology*, 29, 445-454.
- Washburn, D. A., Beran, M. J., Evans, T. A., Hoffman, M. L., and Flemming, T. E. (in press). Technology with non-human participants. In L. L'Abate and D. A. Kaiser (Eds.), *Handbook of technology in psychology, psychiatry and neurology: Theory, research and practice*. New York: Nova Science Publishers.
- Wheeler, B. C. (2009). Monkeys crying wolf? Tufted capuchin monkeys use anti-predator calls to usurp resources from conspecifics. *Proceedings of the Royal Society B*, 276, 3013-3018.
- Wilson, B. J. (2012). Contra private fairness. *American Journal of Economics and Sociology*, 71, 407-435.
- Yamagishi, T., Horita, Y., Takagishi, H., Shinada, M., Tanida, S., and Cook, K. S. (2009). The private rejection of unfair offers and emotional commitment. *Proceedings of the National Academy of Sciences*, 106, 11520-11523.