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Comparative economics: Responses to the Assurance game in monkeys, apes, and humans using equivalent procedures

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Abstract

There is great interest in the evolution of economic behavior. In typical studies, species are asked to play one of a series of economic games, derived from game theory, and their responses are compared. The advantage of this approach is the relative level of consistency and control that emerges from the games themselves; however in the typical experiment, procedures and conditions differ widely, particularly between humans and other species. Thus, in the current study we investigated how three primate species, capuchin monkeys, chimpanzees, and humans, played the Assurance (or Stag Hunt) Game using procedures which were, to the best of our ability, the same across species, particularly with respect to training and pre-testing. Our goal was to determine what, if any, differences existed in the ways in which these species made decisions in this game. We hypothesized differences along phylogenetic lines, which we found. However, the species were more similar than might be expected. In particular, humans who played using 'non-human primate-friendly' rules did not behave as is typical. Thus, we find evidence for similarity in decision-making processes across the Order *Primates*. These results indicate that such comparative studies are possible and moreover that in any comparison rating species' relative abilities, extreme care must be taken in ensuring that one species does not have an advantage over the others due to methodological procedures.

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Introduction

Recent advances in the study of economic decision-making have fundamentally altered how we view the science of economics. Beginning with experimental economics (1), and continuing in more recently emerging fields, such as neuroeconomics (2, 3), there has been a much more scientific approach to understanding how humans make decisions in economic contexts. Most recently, there has emerged an interest in understanding the evolution of human decision making, primarily as studied using a comparative approach. Although studies of rats and pigeons emerged many decades ago, a recent surge with additional species has provided even more data relevant to social scientists interested in decision making.

Although game theory has been used independently in behavioral ecology for decades (4), it is only recently that human economic games have been used extensively to address decision-making behavior (5, 6) and underlying neural activity (7). There are certainly reasons to think that humans and other primates might be similar in their decision-making abilities. Other primates are our closest living relatives - we share a common ancestor with chimpanzees within approximately the last 6 million years (8) – so there is a high likelihood of homology. Even though this does not mean identical decision making, it implies similarity in the underlying structures. Non-human primates also show many of the same cognitive skills, and even biases (9, 10), as humans.

Alternately though, humans are distinct from other primates, and even a few million years is sufficient for substantial evolutionary divergence. In fact, despite the use of non-human primate models as a means of understanding human cognitive evolution, some

studies have indicated differences between us (6, 11), and there remains a sense that humans are the exceptional primate (12, 13).

An often overlooked aspect of this debate, though, is inconsistent methodology. At the most basic level, procedural differences, such as in timing, reward and experimental environment, may make a difference in outcomes and imply species differences that do not necessarily exist (14). More critically, there are typically fundamental differences in procedure and format that often advantage humans. Humans can be verbally instructed on constraints, rules, and contingencies; presented with payoff matrices; and given pre-tests to verify understanding. Animals cannot. Instead, they must be trained, and investigators must infer when individuals across species possess an apparently equivalent understanding of the task. Given the differences in procedure, however, this cannot be assumed any more than can evolutionary homology. Thus, the purpose of our study was to provide a comparison that was as procedurally similar as possible across three species frequently used in studies of cooperation. Our goal was to create as fair a playing field for this cross-species assessment as possible and to see whether previously reported differences remained.

Different disciplines define cooperation differently, so it is important to clarify what we mean in this case. We define cooperation as a situation in which two individuals can increase their immediate payoffs by working together. This definition emphasizes the behaviors of the individuals involved, as measured by their decisions and the pairs' outcomes. Thus, our focus is on what the individual gains from the behavior (i.e., the proximate payoff to their decision making), rather than whether the individual understands their behavior (i.e., the cognitive or neural mechanisms underlying their

decision). This evolutionary perspective differs from both psychology and economics, which tend to have a more mechanistic focus. However, it allows for a direct comparison without assuming cognitive complexity that may not be required (15), or reliance on self-report, which may be unreliable (16).

Of course, testing multiple species with additional paradigms is not sufficient; it is also critical that all species have some ability in the chosen task. Otherwise apparent differences in ability may be instead due to differences in aptitude to the specific task. Even among closely related species, differences in ecology may lead to selection for quite different skills (17). We tested capuchin monkeys, chimpanzees, and humans, three species that show a strong tendency to cooperate across multiple domains and have demonstrated an ability to extrapolate these skills to experimental tasks in the laboratory (18, 19, 20; see SOM for additional detail).

We used the Assurance game, in which each individual must choose whether to coordinate for a large reward that they only receive if their partner also takes the same action. We chose this game because it is simple in that there are two symmetric strategies that result in two Nash equilibria, one risk-dominant and the other payoff-dominant. The strategy in the risk-dominant equilibrium generates a sure payoff regardless of what the partner does. The strategy in the payoff-dominant equilibrium, if both partners play it, generates a payoff that strictly dominates the risk-dominant payoff. In other words, in the payoff-dominant strategy, both individuals' objectives are aligned.

The goal of this study was to provide the first multi-species comparison of an interdependent game when the task was presented using nearly identical methodology in a nearly identical experimental environment to all species. We designed the procedure to

be particularly amenable to non-human primates, but also of sufficient interest to allow for human use. Note that by designing the study first for non-human primates and then adapting it for humans, we reversed the typical procedure. We paid careful attention to the details, including potentially ‘irrelevant’ features, such as the mechanism by which payoffs were delivered and the previous experience of the participants. This made the tasks as similar as possible, given the obvious differences among the species in terms of their housing and lifestyles. We hypothesized that we would find differences in game play, with humans outperforming the other two species, based on humans’ more developed cognitive abilities and increased cooperative tendencies. We did not have a directional prediction for the two non-human primates; chimpanzees are more closely related to humans (8), but capuchin monkeys have a similar brain-to-body ratio (21) and are known to be highly cooperative (see details above). We also predicted that the differences we found might be minimized in comparison to other studies due to the more similar procedures employed in the current experiment.

2. Methods

2.1 The Assurance Game

The game we used was a common game of coordination called the Assurance Game, sometimes referred to as the Stag Hunt game. This is a generic 2 x 2 game with the following constraints on the payoffs $w > x \geq z > y$ (see Table S1). This game has two pure strategy Nash equilibria: (*Stag-Stag*), which is the payoff-dominant equilibrium (e.g. that which maximized payoff to both individuals), and (*Hare-Hare*), which is the risk-dominant equilibrium if $x > z$ (e.g. that which minimizes risk to both individuals). This

well-known coordination game is interesting to economists because strategic uncertainty plays a key role in the selection of the equilibrium, yet the players' objectives are aligned (see 22 for a summary). In the Assurance game, the objectives may be the same (*Stag*, *Stag*), but the question of strategic interest is how sure a given player is that the other player will play *Stag* when he or she plays *Stag*. Evidence from coordination game experiments indicate that the payoff-dominant equilibrium is not a focal point with repeated interactions (as in 23), or with anonymous play with different individuals (as in 24).¹

2.2 General Method

We re-designed the typical, normal-form Assurance Game methodology specifically to work across species. Decisions were made by returning one of two tokens to an experimenter, one of which represented the *Stag* strategy and one of which represented the *Hare* strategy.² For the procedure, each subject was given one of each token. Experimenters then solicited a token from the subject (see below for details for each species). When each participant had returned a single token of their choice, they were held up so that both subjects could see which tokens were returned by each individual. Then each subject received (or not) a reward dependent upon both what they returned and what their partner returned, following the payoff structure of the assurance experiment (payoffs were standardized throughout the following experiments). If the subject returned both tokens, they were presented again without comment and solicitation continued until a single token was returned. For rewards, non-human primates received

¹ Though we should note that the former experiment involves more than two players with more than two potential actions, and the latter experiment uses a 3 x 3 coordination experiment.

² We use the word "strategy" to conform to the standard lexicon of game theory, which indicates a choice or decision, but makes no assumptions about the underlying cognitive processes or understanding which led to that decision.

small pieces of preferred food rewards (fruit) and humans received money (quarters/dollar bills). The reward structure was such that mutual *Stag* play was the most beneficial (4 units), mutual *Hare* resulted in a low payoff (1 unit each), and the uncoordinated payoff of playing *Stag* when one's partner plays *Hare* was unrewarded (however the partner that played *Hare* still got 1 unit).

2.3 Novel components of experimental design and procedures

The procedures explicitly incorporated a number of differences from the traditional normal form game to allow for direct comparison across species. First, no subject received any verbal instruction. The humans' only instruction was limited to the following six points:

- 1) Have you participated in an economic experiment before? (Both must answer "yes" to participate. This was to verify that they had previous experience in this lab making decisions that led to rewarded outcomes.)
- 2) In this experiment you will be using red and blue chips to make decisions behind a partition.
- 3) As the experiment progresses you may be paid in quarters.
- 4) Please collect the coins in the yellow cups provided.
- 5) These are the only instructions you will receive in the experiment. Once the experiment begins, the experimenter will not be allowed to answer *any* questions until the experiment is over.
- 6) Do you have any questions before the experiment begins?

Second, no species received any pre-tests designed to assess task understanding.

Thus all subjects, including humans, had to discover the payoff structure during the

course of the game. However, since there were only two options, there were only four possible outcomes and the parameter space was limited and easy to explore. All species easily perform similar kinds of tasks with varied response strategies that must be retained in memory (e.g., conditional discrimination tasks).

Third, all subjects, including humans, were paid in the actual currency (food or cash) on each trial, rather than rewards accumulating and being awarded at the end. This is a common procedure for non-human primates, and it is possible that the immediacy of obtaining the reward, rather than seeing a number accumulate, alters responses. While we cannot verify that these rewards have equivalent subjective value for each species, or indeed, for each individual within a species, we chose rewards that are highly valued in such testing situations. Humans' decisions ranged from \$0 to \$1 for each round, so each decision was valuable and they had the opportunity for a large payoff (\$40 + \$7 show-up payment for 10-15 minutes of participation, or \$0.50 to \$2 per minute). In addition, the use of qualitatively different rewards does not substantively impact human or non-humans' choice behavior (25).

Finally, all subjects sat immediately next to their partner, again common in non-human primate, but not human, studies. This had two direct impacts on the study. First, subjects were not anonymous, and it was clear that they were playing together without having been told this. The lack of anonymity enhances the likelihood of achieving the Pareto dominant outcome. Second, subjects had the capability to communicate with each other to whatever degree they were able to, given their species. This might include direct communication, including vocalizations, gestures, and, in humans, speaking (only two pairs of 26 human pairs spoke), or indirect communication, including unconsciously

communicating their intentions through body posture, facial expression, or gesture, behaviors that humans are known to utilize (26, 27).

2.3.1 Non-human primates

All non-human primates were socially housed in multi-male, multi-female social arrangements with extensive indoor and outdoor living space complete with environmental enrichment. For details on species' housing, see SOM. Nonhuman primates received 30 trials per session, excepting the LRC chimpanzees, who tended to lose interest and so received 20 trials per session. All test sessions were videotaped for later analysis.

Although in a typical Assurance Game choices are made simultaneously (or functionally simultaneously), we were unable to separate some individuals in such a way that they could see each other and not the tokens. Thus, we initially tested all non-human primates without a visual barrier, and hid the tokens as they were returned. Nonetheless, subjects may have been able to view what the other subject was doing while, or before, making their own choice, meaning that they might have been playing an extensive form game (see below for details). Our plan was to then incorporate a divider and see if the animals' behavior remained the same. However, given the results, this option was pursued in only one group of chimpanzees (see below for details).

2.3.1.1 Capuchin monkeys Capuchin monkeys lived at the Language Research Center of Georgia State University (hereafter LRC) in two multi-male, multi-female social groups of 5-8 individuals with offspring present (2M, 2F subjects from one group and 3M, 1F from the other).

2.3.1.2 *Chimpanzees, MD Anderson* Subjects included 20 chimpanzees housed in social groups at the Michale E. Keeling Center for Comparative Medicine and Research of The University of Texas MD Anderson Cancer Center, Bastrop, TX, USA (hereafter MDA). There were two changes to the protocol from the capuchins. First, the chimpanzees could not be separated, so to keep them from stealing each other's tokens, we used "T" shaped PVC pipes that could be placed through the mesh of the caging, but were held in place by the top of the T. Second, we used two experimenters, one for each ape, as it was difficult for one experimenter to interact with both subjects simultaneously. The experimenters simultaneously provided each chimpanzee with one of each token and, after both subjects had returned their tokens, the experimenters simultaneously held them both up and proceeded to give the appropriate rewards. Neither experimenter was aware of what token the other chimpanzee returned to the other experimenter, and therefore the potential for cuing a given response was minimized.

2.3.1.3 *Chimpanzees, Language Research Center* We tested four additional chimpanzees (2M, 2F) who lived at the LRC. The experimental procedure at the LRC was identical to that at MDA, except that the chimpanzees were separated into different cages for testing. There was additional testing for two pairs that chose the payoff-dominant outcome (*Stag-Stag*). For the first test, we added a partition to block their view of the other's choice (all other procedures were identical). This partition extended only up to the chimpanzees' shoulder height, so that they could identify each other, and extended approximately 18 inches in front of the caging, to eliminate the possibility that they saw what the experimenter accepted. Since the T shaped tokens could not be moved in such a way that their partner could see them, the game was functionally simultaneous. The

second test was identical to the barrier procedure, but used two new tokens, a purple token (*Stag*) and a green token (*Hare*), to see if they could extrapolate their behavior to novel tokens used in the same game. This allowed us to verify that any consistencies in behavior between the original and barrier tests were due to active choices rather than established preferences for one or the other token.

2.3.2 *Humans*

Fifty-two undergraduate subjects were recruited from the general student body at Chapman University, Orange, CA, USA. Subjects were randomly recruited via an electronic email system and paid \$7 for showing up on time, plus what they earned in the experiment. Each subject had participated in at least one economic experiment prior to this session so that they had experience with receiving actual payment for their decisions in this laboratory. This was necessary for a direct comparison, as all non-human primates had previous experience making decisions during experiments to receive food rewards. Accumulated coins and dollar bills were converted into large bills at the conclusion of the experiment. No subject participated in more than one pairing.

Upon hearing the limited instructions listed above, the humans were seated in desk chairs next to one another in front of a 4' circular table. On the table was a T-shaped partition that horizontally separated the experimenter from the subjects, and prevented direct eye contact. The partition also vertically split the table into two halves, one for each subject. The partition separating the subjects did not extend to the edge of the table (it stopped approximately 4" from the edge) so that they could comfortably make eye contact with each other (as could the non-human primates). Subjects could have leaned

around to watch each other submit their token, but video analysis revealed that none did so.

The barrier separating the subjects from the experimenter had a 2" x 5.5" slot at the bottom of each side through which the experimenter slid the two tokens (one red and one blue poker chip) at the beginning of each trial. The experimenter also passed their earnings through this slot at the end of each trial. At the top, the partition also included a 1" x 5" slot for each subject, outlined in green, through which they could submit tokens. The experimenter held a ceramic bowl under each slot to collect the tokens, which allowed the subjects to hear whether their counterpart had made a decision. After receiving a single token from each subject, the experimenter held up the tokens above the barrier, with each token in front of the subject who submitted it. He then put down the tokens, held up the appropriate payoff (quarter or dollar bill), or raised an open hand on that side if there was nothing, and then slid the token and payoff to the respective subject through the bottom slot of the barrier. If a subject slid two tokens through the green slot, the experimenter returned them both through the bottom slot (with no comment from the experimenter) until the subject returned a single token. If a subject slid money through the slot, it was immediately returned to the subject through the bottom slot. During no session did a subject try to talk to the experimenter. Due to the constraints of subject recruitment, humans received only a single session, so they were given 40 trials.

Statistics

Pairs' outcomes were compared to chance using chi-squared tests, including the Yates continuity correction for observations less than 40 (28). In cases in which there were fewer than five occurrences within a cell, the Fisher test was used instead, and when

there were no occurrences in multiple cells, proportions were reported in lieu of statistics. In all cases, the unit of analysis was the pair. Note that these statistics are intended to determine whether that pair's behavior differed from chance, not whether these results generalize to the species as a whole.

In addition to comparing overall outcomes, we examined changes in individuals' behavior that may have indicated a non-random strategy in making decisions (28). To do this, we first examined individuals' choices using the binomial (proportions) test, to see whether there was an overall preference for either *Stag* or *Hare* choices. Second, we used the nonparametric runs test, which determines if the distribution of a series of binary events is random. A run is defined as a sequence within a series in which one of the two alternatives occurs on consecutive trials. The null hypothesis is that the series is generated randomly, i.e., there are neither too few nor too many runs. Finally, we used the nonparametric change-point test to determine if there was a change in the binomial process that generates a series of binary events. Note that the test does not assume *a priori* when a change occurred. The null hypothesis is that there is no change at any point in the sequence. All statistics were two-tailed and significance was at the $p < 0.05$ level.

Results

Capuchin Monkeys

Among the six capuchin pairs, only one (16%) chose *Stag-Stag* more often than by chance ($\chi^2 = 4.57$, $df = 1$, $p < 0.05$; see Table 1). We also considered the possibility that the capuchins would perform better given extended opportunities to participate (although five of the eight individuals participated in more than one pair). Thus, we ran two pairs for additional sessions. After a total of 32 sessions, one of these pairs matched each

other's choice, but showed no preference for *Stag-Stag* or *Hare-Hare* (last 10 sessions: $\chi^2=5.38$, $df=1$, $p<0.05$).

Individual capuchins made non-random choices. One monkey preferred to return the *Stag* token (binomial test, $p=0.024$), five showed more or fewer runs than anticipated (all $ps\leq 0.002$), and two changed their decision-making strategy during game play (change-point test: $ps<0.05$). Among individuals tested in multiple pairings, some changed their behavior between partners. Two monkeys showed non-random behavior (as measured by the runs test) with one partner, but not the other.

Chimpanzees

MD Anderson: Eight of the 10 pairs' choices deviated from chance. Six pairs 'matched', with both partners choosing the same token (all $\chi^2>27.69$, $df=1$, all $p<0.001$). However, none of these pairs preferentially chose either the *Stag-Stag* or the *Hare-Hare* options, despite extensive experience with both payoffs. Both of the remaining pairs were more likely to choose the option opposite to what their partner chose (e.g. *Stag-Hare* or *Hare-Stag*: $\chi^2=6.25$, $df=1$, $p<0.05$; $\chi^2=183.05$, $df=1$, $p<0.001$).

The above analyses were done using the entire data set of 20 sessions. To more directly compare the chimpanzees to the capuchin monkeys, we repeated the analysis using only the first 10 sessions each pair completed (partners did not switch). Five of the six pairs that matched across 20 sessions were doing so already in the first 10 sessions (all $\chi^2>4.39$, $df=1$, $p<0.05$). Of the two subjects that chose oppositely from their partner, one did so in the first 10 sessions ($\chi^2=17.25$, $df=1$, $p<0.001$). Remaining analyses are done on all 20 sessions to include as much data as possible.

The matching outcomes seen in six pairs could emerge in two contexts. First, one partner may have ‘understood’ the task and matched (or not) their partner’s choice. Second, both individuals may have understood the need to match, but failed to recognize that one outcome provided higher payoffs than the other. Thus, we investigated the frequency with which one individual spontaneously made the first choice among all 10 pairs (we decided to record these data after commencing the study, so we have data on all 20 sessions for 6 pairs and the last 15, 14, 11, and 10 sessions, respectively, for the remaining pairs). In six of the 10 pairs, one individual was more likely to make the first move than the other (binomial tests, all $p \leq 0.003$). In four of these cases, the pair matched and in one case the pair played oppositely. Looking at it another way, among the pairs that matched, in four of them (66.7%) one subject typically went first. Among the pairs that chose oppositely, in one of them (50%) one subject typically went first. Finally, among the two pairs that showed no consistent response, in one pair (50%) one of them typically went first. Thus, there is no evidence that a spontaneous consistent order to sequential play affected outcomes.

Only four subjects of the 20 showed a preference for one token over the other (binomial test, all $p < 0.05$). These four apes either matched ($n=3$) or played oppositely ($n=1$) to their partner. All 20 chimpanzees showed more runs than anticipated (runs test: all $p < 0.001$). Five of the 20 chimpanzees switched strategies more than 500 times in 600 trials, possibly indicating a side bias. No chimpanzee changed their decision-making strategy during the game (change-point test, all subjects NS).

Language Research Center: Four pairs of subjects were initially tested. Of these, two pairs preferentially choose the *Stag-Stag* option ($\chi^2=23.79$, $df=1$, $p < 0.001$; 97%

preference for *Stag-Stag*, no statistic calculated due to empty cells). Of the remaining two pairs, one failed to settle on a strategy ($\chi^2=0.16$, $df=1$, $p>0.05$). The other preferred *Stag* ($\chi^2=24.61$, $df=1$, $p<0.001$), but due to the female choosing *Stag* predominantly, while the male chose randomly. Thus, we performed additional testing only on the two pairs that showed a robust preference for the *Stag-Stag* option.

To test whether the subjects understood the game or were visually matching their partners, we erected a barrier between the individuals so that they could not see their partners' choice (see Methods). One pair continued choosing the payoff-dominant outcome (99% preference for *Stag-Stag*), while the other did not ($\chi^2=0.05$, $df=1$, $p>0.05$), although the male in the latter pair chose *Stag* more than *Hare* (binomial test, $p<0.001$). However, when novel tokens were introduced, both pairs were more likely to play *Stag-Stag* than any other option ($\chi^2=78.2$, $df=1$, $p<0.001$; $\chi^2=62.6$, $df=1$, $p<0.05$), although again in the latter pair this appeared to emerge primarily because of the male's preference for *Stag* ($p<0.001$).

Considering their individual behavior, in the pair that always chose the payoff-dominant outcome, both chimpanzees preferred *Stag* (binomial test, both $ps<0.001$) and showed fewer runs than anticipated, likely because of their preference for *Stag*. However, both showed more runs than anticipated on the novel token test ($ps=0.002$) and one did so on the barrier test ($p=0.002$), possibly because they were new situations. Both also showed a change in strategy in the novel token test (both $ps<0.05$), the test for which they initially showed the most *Hare* choices.

Since these four chimpanzees played in multiple pairings, we were also able to investigate whether their behavior changed with different individuals. Only one

chimpanzee, the one who showed the least evidence for non-random behavior, did not alter his behavior. The two individuals who showed the most evidence of understanding changed strategy in all conditions with their other partners, but only in the novel token condition with each other. The remaining female showed a change in behavior with one partner, but not the other.

Humans

Among human subjects, five of the 26 pairs matched *Stag-Stag* on 75% or more of the trials (e.g. ≥ 30 of the 40 trials; an additional two pairs matched on 29 of 40 trials). Ten matched *Hare-Hare*, and 3 matched their partner, with an equal number of *Stag-Stag* and *Hare-Hare* choices. Intriguingly, eight of the 26 pairs (31%) never matched *Stag-Stag* a single time, and all of these pairs preferentially matched *Hare-Hare*. Only one pair never matched *Hare-Hare*. Thus, humans who found *Hare-Hare* were less likely to explore alternate possibilities.

Of the 52 participants, all but seven showed significant preferences for one token over the other over the course of the 20 trials (binomial test, all $p < 0.05$). Twenty participants more often chose the *Hare* option while 25 more often chose *Stag*. For the seven participants that showed no preference, four participants showed more or fewer runs than anticipated ($p < 0.05$; two additional subjects showed a non-significant trend in this direction; $p \leq 0.10$). Twenty subjects showed no change in the decision making process (change-point test; $p > 0.05$). Fourteen of these preferred the *Stag* option throughout (thus 56% of those who preferred *Stag* did so from the beginning) while three chose *Hare* throughout. In the final three cases, the subjects never settled on a strategy. Thus, the majority of subjects (49 of 52) showed non-random behavior.

Discussion

We found that while there were differences in the degree to which each species could achieve payoff-dominant outcomes, there was continuity in behavior across species. Specifically, there was a phylogenetic ordering with respect to the primates' decision outcomes, with more efficient, payoff-dominant outcomes achieved more frequently in human pairs than in those of other species, and with chimpanzees doing so more frequently than capuchins. However, when procedures were equalized, only a subset of humans achieved these efficient outcomes, and pairs of both other species did so as well. Thus, when tested in similar conditions, other primates reached similar behavioral outcomes to humans more often than might have been expected based on the typical normal-form economics experiment. Consequently, we found support for both of our predictions, and potentially evidence of evolutionary continuity in decision-making.

Considering this in more detail, the capuchin monkeys, who are phylogenetically most distant from humans, showed the least structured behavior. Only one pair chose *Stag-Stag* more often than chance, and only five of the eight subjects demonstrated behavior that indicated non-random choice behavior. Note, too, that despite statistical significance, the pair that achieved the payoff-dominant outcome did so less frequently than the chimpanzees and humans who found the same outcome. Chimpanzees were intermediate, and the most frequent strategy was unanticipated. Although only two pairs of chimpanzees consistently reached the payoff-dominant outcome (see below for more details), the majority matched their partner. This strategy leads to rewards for each individual on each trial, yet *Hare-Hare* was not as efficient as *Stag-Stag*. It is not clear why they did not alter their behavior. However, the fact that the dominant strategy

seemed positional (they showed a side bias in their choices, a common behavior in primates) may indicate that despite finding a solution, they did not attend to the interaction in the same way as did the humans. Finally, despite being the species for which the highest frequency of pairs achieved the payoff-dominant outcome, even among humans fewer than 20% of pairs did so (this increases to 27% if two borderline pairs are included). An additional 38% of pairs achieved the risk-dominant outcome (*Hare-Hare*), and 12% matched their partner. It is worth reiterating that despite humans' success as compared to the other primates, a nontrivial proportion of the pairs *failed* to achieve the payoff-dominant outcome. This underscores the difficulty of finding outcomes when the typical human procedures (instructions, payoff matrices, pre-tests for understanding) are absent, common handicaps for non-human species. Nonetheless, even when the field is leveled, humans are more likely than other primates to achieve these most efficient outcomes.

With respect to the chimpanzees, it is interesting, although not diagnostic with only a single pair, that the pairs that achieved the most efficient outcome even in a functionally simultaneous design (e.g. the barrier condition) with novel tokens had a substantially different rearing history. They were cognitively enriched from infancy and are accustomed to these kinds of interactive tasks. The one who subjectively seemed to understand it first had previous experience exchanging with a partner to obtain tools (29), and this particular pair was the most successful in a recent barter task requiring them to exchange tokens with each other (30). It may be that previous experiences had led this pair to expect that interaction with the partner and the experimenter could provide rewards. These chimpanzees also may be more like humans in how they perceive these

kinds of tasks, for instance understanding it as an opportunity for rewards in a way the others do **not**, or perhaps even enhancing their interest in the task. Thus some chimpanzees can achieve maximizing outcomes in economic games that are equivalent to those of humans, yet they may require specialized background experience to do so (31). Such variation also reinforces the need to, whenever possible, test a large number of primates with varied backgrounds (e.g. multi-facility collaborations) to fully unearth the extent of their abilities and the extent of intra-specific variation within each species.

Although in most cases subjects played only with one other individual, in several cases with chimpanzees and capuchin monkeys we were able to re-pair individuals with more than one partner. Interestingly, in some of these cases, we found differences in behavior amongst different partners. Among capuchins, two of the three individuals tested with multiple partners behaved differently with different partners, and three of the four LRC chimpanzees did the same. These data do not allow us to determine which feature was important in changing the primates' behavior (e.g. relationships, the different distribution of choices amongst different partners), but the fact that they were present indicates sensitivity to the changing conditions created by playing with a new partner. Although similar data are not available for humans, we anticipate that this would also be the case with them.

What leads to the underlying similarity in decision outcomes between humans and other species? A first hypothesis is that there is similarity in the underlying decision-making architecture across the primates. This would indicate that while humans may possess additional traits which allow more complex problems to be solved, such as narrative language, these additions support, but do not fundamentally alter, our basic

primate decision structures. In fact, while all three species have large brain-to-body ratios and cooperate extensively in both natural and laboratory conditions, the species' ecologies are consistent with our results. Humans live in an environment with ample opportunities to coordinate, particularly among out-group members, which might have led to selection on enhanced tendencies to do so beyond that seen in other species. Chimpanzees also coordinate to a greater degree than capuchins, for instance taking complementary roles in group hunts (32). These ecological differences may have increased selection pressure differentially across species, leading to differences in degree, if not kind, in decision-making. The similarity of the cognitively enriched chimpanzees, whose rearing history and behavior were both similar to humans', supports this contention.

However, there are alternative explanations. In particular, this hypothesis fails to explain humans' unexpectedly low level of success in the current game. This is difficult to explain by motivation, as rewards were quite high (approximately \$0.50 to \$2 per minute). In interpreting our results we note that our procedures differed nontrivially from the traditional study of strategic behavior of humans in the laboratory. Providing common information on all the payoff contingencies is simply not feasible for non-human primates, but the human cognitive ability to internalize the interdependency of the payoffs may be key for distinguishing human performance in this game from non-human primate performance. In ongoing research we are implementing this game with computerized interactions, and for humans we are comparing results from the 'primate format' to those which more closely follow traditional normal form game format.

Having considered the similarities, it is interesting to speculate on the differences in behavior among the three primates. Although we equalized many aspects of the experimental design, we were not able to do so for all factors. One of these may have influenced results. We were able to test all individuals, including humans, in a setting in which only that pair and the experimenter were present. Moreover, all had previous experience in the lab in which they were tested, all rewards were paid out in the actual currency (cash or fruit) by the experimenter on a trial-by-trial basis, no pairings were anonymous, and all subjects of all species lived day-to-day in multi-male, multi-female social groups. Nonetheless, only humans were tested with strangers (unfamiliar primates do not peacefully interact) and humans used a partition which blocked their view of their partners' choice. While we do not know whether the primates made use of their ability to see their partners' rewards, they may have done so (excepting the LRC chimpanzees tested with the barrier). Finally, contrary to most such comparisons, this game was designed for non-humans and adapted to humans, which may have made the task unusual for humans. All of these differences should have made the task more difficult for humans, if anything minimizing the difference between humans and other primates.

Differences in behavior may reflect less about strategic decision-making and more about how each species comes to understand the nature of the task. Although humans faced challenges in this particular task, non-human primates, too, may need different procedures or additional time and experience in order to come to understand the contingencies of the task. Thus, as with the humans, their responses may say more about their ability to understand the experimental procedure (or the underlying structure of the task) than whether they can coordinate responses to maximize reward. Second, species

may reach the same functional outcome using different mechanisms. For instance, the simplest explanation for matching behavior when partners can see each others' responses is visual matching, which would functionally result in successful coordination and, hence, reward maximization. However humans and some chimpanzees matched without observing their partners' outcomes. Moreover the fact that humans can utilize more advanced understanding of the tasks does not necessarily mean that they do so. These differences should be investigated through replication, particularly those involving different formats (e.g., on computerized tasks, for which all species have shown comparable abilities in other kinds of cognitive tests). With additional experience or procedures, we expect that more pairs of each of these species, but in particular the non-humans, might show coordinated behavior. These kinds of manipulations in future studies will better illustrate the nature of the species differences reported here, and will clarify how coordination behavior can emerge.

We find that when conditions are held as similar as possible, humans outperform other primates in finding maximizing solutions to a non-contingent economic game, but the differences in performance are not as great as might be anticipated. Rather, individuals in all species may find efficient outcomes, and the difference lies in the proportion of pairs within a species that do so. These results provide initial evidence that, as with other behaviors, humans' behavior in cooperative economic games may be part of an evolutionary continuum in which our decision-making strategies emerged from those of our common ancestors. Nonetheless, humans are superior at coordination as compared to other species, a fact that may be due to other sorts of behaviors, such as narrative language, and cognitive capacities that have emerged in the interim.

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Table Legends

Table 1: Frequencies of different strategies across species.

Numbers in parenthesis beside species indicate the number of pairs. LRC chimpanzees participated in three conditions (see Methods for details). Some non-human primates participated in greater than 10 sessions. For an equal comparison, results are reported from only the first 10 sessions first, and results considering all sessions tested are indicated in parentheses. Matching for the MDA Chimps includes two pairs which matched against their partner's play.

	<i>No Strategy</i>	<i>Matching</i>	<i>Risk-dominant</i>	<i>Payoff-dominant</i>
<i>Capuchins (6)</i>	5(4)	0(1)	0(0)	1(1)
<i>MDA Chimp (10)</i>	2(4)	8(6)	0(0)	0(0)
<i>LRC Chimp (4)</i>	2(1)	0(0)	0(0)	2(3)
<i>LRC Barrier (2)</i>	1	0	0	1
<i>LRC Novel (2)</i>	0	0	0	2
<i>Human (26)</i>	8*	3	10	5

*This includes 2 pairs who played the Payoff-dominant strategy on 29 trials of 40. These two pairs are *not* included in the Payoff-dominant column.

Supplemental Online Material

Supplemental Introductory Material

All three tested species show cooperative behavior in the laboratory and in the field. Among capuchins, In mutualistic ‘bar-pull’ tasks in which individuals work together to obtain food rewards, capuchins both visually coordinate and understand the role of their partner (33). They also understand reward contingencies. They are reciprocal (34), and do not cooperate when one member of the pair can dominate the rewards (35) or when their partners do not equitably share outcomes (36). Notably, cooperation occurs only when the monkeys understand the task (37), underscoring the importance of appropriate methodology. In the wild, monkeys collaborate (38) and may even hunt together (39).

Chimpanzees are similarly skilled at cooperation. In similar bar-pull tasks, chimpanzees cooperate at higher levels when paired with tolerant partners than with those who do not share (40), and actively choose tolerant partners when given the option (19). In the field, chimpanzees collaborate on group hunts, even taking complementary roles (41). They also exchange goods and services reciprocally (42, 43) and engage in coalitions and alliances (44, 45).

Humans are the most cooperative species. In laboratory settings, humans routinely achieve mutual gains in payoffs through trust and reciprocity by outperforming the rational predictions of game theory, even when the game is only played once, and with an anonymous stranger (for a summary, see 18). Human cooperation includes similar activities as the other two primates, including cooperative hunting of game and subsequent food sharing (e.g. 46).

Supplemental Methods

1. Non-human primates

All species received a combination of primate chow, fruits, and vegetables, as well as additional enrichment foods. No individual was ever food or water deprived for testing. Subjects were adults who lived in the same social group and, when possible, multiple pairings within the same social group were tested. Pairs were separated from the remainder of the social group into their indoor dens (chimpanzees) or their testing cage located in the indoor colony room (capuchins) to limit distractions during testing. All separation was voluntary (i.e., subjects were only tested if they entered the testing area freely).

For testing, the experimenter then held out one hand in a stereotypical “begging gesture” to request the return of a token. When a subject returned a token, the experimenter closed her hand over it (capuchins) or placed it behind her back (chimpanzees). After both subjects had returned their tokens, the experimenter held them up, with the token each subject returned in front of them. Experimenters then added the food rewards (if any) to their hand and held up the food rewards, with the tokens, for each subject. After the subjects took the food rewards, the next trial commenced. Tokens were PVC pipes painted either red (*Stag*) or blue (*Hare*). PVC pipes were sized appropriately for the species to easily manipulate.

1.1 Capuchin monkeys

In pilot testing with a single pair there was no change in either individual’s behavior (i.e., both subjects chose randomly between the tokens). Thus we conducted the experiment with one white token (*Hare*) and one black and white patterned token (*Stag*) to eliminate

the possibility that the capuchins could not distinguish between the colors (although see 47).

1.2 MDA Chimpanzees

Due to the large number of available subjects, each of the 20 subjects was used in only a single pair. A subset of chimpanzees required training in token exchange prior to the experiment, using standard procedures for training exchange (48). All training was done with a single token and invariant rewards to avoid the risk of inadvertently training a behavior; subjects learned the contingencies of the payoffs during the experiment.

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