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Old World monkeys are more similar to humans than New World monkeys when playing a coordination game

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48

49 **Abstract**

50 There is much debate about how humans' decision-making compares to that of other
51 primates. One way to explore this is to compare species' performance using identical
52 methodologies in games with strategic interactions. We presented a computerized Assurance
53 Game, which was either functionally simultaneous or sequential, to investigate how humans,
54 rhesus monkeys, and capuchin monkeys utilized information in decision-making. All species
55 coordinated via sequential play on the payoff-dominant Nash equilibrium, indicating that
56 information about the partner's choice improved decisions. Furthermore, some humans and
57 rhesus monkeys found the payoff-dominant Nash equilibrium in the simultaneous game, even
58 when it was the first condition presented. Thus, Old World primates solved the task without any
59 external cues to their partner's choice. Finally, when not explicitly prohibited, humans
60 spontaneously used language to coordinate on the payoff-dominant Nash equilibrium, indicating
61 an alternate mechanism for converting a simultaneous move game into a sequential move game.
62 This phylogenetic distribution implies that no single mechanism drives coordination decisions
63 across the primates, while humans' ability to spontaneously use language to change the structure
64 of the game emphasizes that multiple mechanisms may be used even within the same species.
65 These results provide insight into the evolution of decision-making strategies across the
66 primates.

67

68

69 **Introduction**

70 Along with the dispositions to trust and reciprocate and the propensity to exchange, the
71 human ability to coordinate activities is a pillar upon which the flourishing of the species is built.
72 The ability of two individuals to coordinate, literally to mutually arrange, an activity presupposes
73 firstly that two individuals cognize that the outcomes of their actions are interdependent.
74 Secondly, successful coordination assumes a shared attention and agreement on the ends to be
75 achieved by mutually arranging a pair's activities. Within the Pleistocene tribe or the modern
76 small group of family, friends and neighbors, these conditions are almost trivially met as
77 personally known individuals share the habits, knowledge, and beliefs about the methods and
78 possibilities necessary to coordinate successfully. But what happens when modern strangers face
79 a novel task of playing a simple 2 x 2 normal form game of coordination? How well can the
80 personally unknown extend to each other the assumptions of interdependent decisions and
81 agreement on the ends? As van Huyck et al. (1990) suggested, not as robustly as we might
82 hubristically expect. The question then becomes more interesting when posed of our primate
83 relatives. Do we share the ability to cognize actions as interdependent and to share attention on
84 the ends achieved?

85 There is little research addressing the question, but what there is indicates that several
86 primates may share these abilities with humans. For instance, in one Ultimatum game study with
87 chimpanzees (Jensen et al. 2007), the apes' decisions were dissimilar from human-typical
88 behavior (Camerer 2003). However a subsequent study found that the protocol designed for
89 chimpanzees led to a similar outcome in humans (Smith & Silberberg 2010). Our previous work
90 investigated the Assurance game, which is a well-known model of social interactions (Skyrms

91 2003). We found that while humans found payoff dominant outcomes more readily than did
92 either capuchin monkeys or chimpanzees, pairs of all species were able to find these outcomes,
93 indicating that selection has favored similar outcomes (if not similar cognitive mechanisms)
94 across these three primates (Brosnan et al. 2011). Moreover, we found that chimpanzees with
95 greater experience in cognitive testing found the payoff dominant outcome far more readily than
96 did chimpanzees with little or no cognitive testing experience, indicating that, as with humans,
97 experience may play a role in outcomes.

98 For the current study, we chose to investigate the Assurance Game using a computerized
99 methodology. This provided a number of advantages for further research. First, there is a long
100 history in comparative research suggesting that the format in which one presents the same kind
101 of task to nonhuman animals can have radical effects on performance. For example, spatial
102 discontinuity between response loci and stimuli was recognized as an obstacle to learning in
103 animals (e.g., McCleam & Harlow 1954; Murphy & Miller 1959; Stollnitz & Schrier 1962).
104 However, training primates to use a joystick gets past that problem of discontinuity and produces
105 markedly different patterns of results (see Beran et al. 2007; Rumbaugh et al. 1989), and the
106 same may be true for performance in economic games. Thus, comparing our previous results to
107 those from a computer task may help to highlight factors which affect decision-making.

108 Another advantage of a computerized task is the abundance of data with respect to other
109 cognitive abilities which are relevant. This allows us to not only consider a priori whether
110 species might be able to solve the task, but if our predictions are proven false to re-consider how
111 the subjects might perceive the game. Considering cognitive mechanisms, success in the game
112 seems to require, at minimum, an ability to respond flexibly (e.g., contingent upon one's
113 partner's decisions) and, related to this, an ability to inhibit (e.g., avoid the temptation of a large

114 short-term payoff). Considering first the role of phylogenetically widespread learning
115 mechanisms, a number of primate species, including the rhesus monkeys and capuchin monkeys
116 who participated in the current study, have shown substantial behavioral flexibility in responding
117 to game-like tasks presented on computer screens. These include tasks that involve behavioral
118 inhibition, tracking of relative rates of reward for different responses, and even information-
119 seeking behavior (Beran et al. 2011; Beran et al. 2008; Evans 2007; Flemming et al. 2011).
120 These skills, along with the monkeys' clear interest in maximizing their food intake during these
121 tasks, indicate that comparative assessments of cooperation using computer tasks are likely to
122 provide the most compelling data for understanding the emergence of cooperation in humans.

123 However, despite equivalent performance on basic learning tasks (e.g., two choice
124 discrimination and learning set tasks), not all primates are equally adept at performing higher-
125 level cognitive tasks. Relevant to this task, rhesus monkeys, but not capuchin monkeys, show
126 evidence for metacognitive monitoring during psychophysical judgment tasks (Beran et al. 2009)
127 and information-seeking paradigms (Beran & Smith 2011). Thus suggests a species difference in
128 monitoring ongoing performance. Thus emerges a potentially important way to determine which
129 cognitive mechanisms are important; it is possible that rhesus and capuchins would do equally
130 well on games of coordination where contingencies for responses are clearly presented, that is, in
131 a situation similar to a basic learning task, while diverging in performance when immediate cues
132 are not present. Finally, it is possible, although we think unlikely, that even higher-order
133 cognitive mechanisms are involved, such as theory of mind, which could be activated in this case
134 due to the social nature of the task. If this is the case, we expect humans to outperform the other
135 species (Penn & Povinelli 2007), despite some basic perspective abilities which have been seen
136 in rhesus monkeys (Flombaum & Santos 2005). Thus, testing these species on the Assurance

137 game may shed light on not only performance levels, per se, on the game, but also the nature of
138 the game itself from the perspective of the individuals playing it.

139 To explore these issues in more detail, we here investigated the role of information in
140 coordination decisions amongst three primate species, humans (*Homo sapiens*), rhesus monkeys
141 (*Macaca mulatta*), and capuchin monkeys (*Cebus apella*). We re-designed the typical, normal-
142 form (NFG) Assurance Game methodology (Cooper et al. 2003; Ochs 1995; Smith 1982; van
143 Huyck et al. 1990) specifically to work across species, holding the methodology as constant as
144 possible (see Methods for details). We had two hypotheses for the current work. First, based on
145 our prior results with the exchange version of the task, we expected all species to be capable of
146 successfully navigating the task, but we predicted that a higher percentage of human pairs would
147 find the payoff dominant outcome as compared to the monkey species. Our second hypothesis
148 was that outcomes would change as the task parameters varied. Specifically we predicted that if
149 pairs could see each other's choices prior to making a decision, the task could be solved by a
150 cognitively simpler matching rule, meaning that all species would perform equally well. On the
151 other hand, we predicted that in the situation in which their partners' choices were not available,
152 higher-order mechanisms might be required, separating the species based on their aptitude at the
153 tests of cognitive abilities we proposed above as relevant to this task, that is, humans performing
154 better than the other primates.

155

156 **Methods**

157 *General Methods*

158 *The Assurance Game*

159 The game we used was a common game of coordination called the Assurance Game,
160 sometimes referred to as the Stag Hunt game. The reward structure was such that mutual *Stag*
161 play was the most beneficial (4 units), mutual *Hare* resulted in a low payoff (1 unit each), and
162 the uncoordinated payoff of playing *Stag* when one's partner plays *Hare* was unrewarded, while
163 the individual who played *Hare* received 1 unit. This game has two pure strategy Nash
164 equilibria: (*Stag-Stag*), which is the payoff dominant equilibrium (the outcome that maximizes
165 payoff to both individuals), and (*Hare-Hare*), the outcome which is payoff dominated. This well-
166 known coordination game is interesting to economists because strategic uncertainty plays a key
167 role in the selection of the equilibrium, yet the players' objectives are aligned (for a summary see
168 Ochs 1995). In the Assurance game, the objectives may be the same (*Stag, Stag*), but the
169 question of strategic interest is how sure a given player is that the other player will play *Stag*
170 when he or she plays *Stag*². Evidence from coordination game experiments with humans indicate
171 that the payoff dominant equilibrium is not a focal point with repeated interactions as in (van
172 Huyck et al. 1990) , or with anonymous play with different individuals as in (Cooper et al.
173 1990)¹.

174 We explicitly incorporated a number of features common to non-human studies but
175 different from traditional NFG experiments with humans to facilitate cross-species comparisons.
176 First, subjects received no verbal instruction or pre-testing so that individuals had to discover the
177 payoff structure during the course of the game (note that there were only two options from which
178 to choose, and thus four possible outcomes). Second, all subjects, including humans, had
179 participated in other experiments in the laboratory prior to this study so they were aware that
180 decisions would result in tangible rewards (e.g. food or cash). Third, subjects were paid on a

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.

181 trial-by-trial basis, in case the immediacy of receiving rewards on each trial affected behavior.
182 Fourth, for most treatments (see exception, below), subjects sat directly next to one another and
183 were not anonymous, so subjects could potentially communicate (Brosig 2002; Fetchenhauer et
184 al. 2010; we saw no attempts to communicate between the primates). Fifth, neither humans nor
185 rhesus monkeys received any pre-tests designed to assess Assurance game understanding, so all
186 subjects, including humans, had to discover the payoff structure during the course of the game.
187 Capuchins had previously participated in an exchange-based version of the task (Brosnan et al.
188 2011), but had no additional training. Finally, we manipulated whether or not they could see
189 their partners' decisions to investigate how information affected decision-making.

190 *General computerized design*

191 Decisions were made by choosing one of two icons on each side of a split computer
192 screen, one of which represented *Stag* (a red square) and one of which represented *Hare* (a blue
193 circle). Icons were presented in a vertical distribution, with the order of presentation randomized
194 both across trials and across individuals within the same trial. Subjects of all species made a
195 choice using a joystick. We chose to study their behavior as naturally as possible, and so did not
196 constrain the order of play or the timing of decisions. Once both subjects had made a choice,
197 each subject received (or not) rewards dependent upon both what they chose and what their
198 partner chose, following the payoff structure of the assurance experiment.

199 There were two conditions, *Synchronous*, in which subjects did not know what their
200 partner had chosen until both choices were complete, and *Asynchronous*, in which decisions
201 were revealed as they were made (e.g., subjects potentially had information about their partners'
202 responses). To block any information transfer in the *Synchronous* condition, the joystick itself
203 was occluded and the cursor did not move; when they joystick was manipulated, both options

204 and the cursor disappeared simultaneously, and both subjects' choices were displayed
205 simultaneously once both decisions had been made. Thus it was, to our knowledge, impossible
206 to determine the partner's behavior by observation in this procedure, other than knowing that
207 their partner had made a choice. In the *Asynchronous* game, the procedure was identical, except
208 that choices were displayed as they were made, so that their partner could see their choice and
209 potentially use the information when making their decision.

210 *Non-human primates*

211 All non-human primates were socially housed at the Language Research Center of
212 Georgia State University. Rhesus monkeys were all adult males who were moved to a specially
213 designed paired testing area. Capuchin monkeys were socially housed in multi-male, multi-
214 female social arrangements and voluntarily separated in an adjacent cage for testing, to limit
215 distractions. Only adults were tested with members of their social group, and in multiple
216 pairings from within the same social group whenever possible. No individual was ever food or
217 water deprived for testing. During test sessions, pairs did not always finish a trial block, and
218 pairs completed different numbers of blocks during each testing session. Thus the number of
219 trials varied across both pairs and sessions.

220 The capuchins and the rhesus monkeys were used to somewhat different testing
221 schedules, so to avoid changing their schedules and causing unnecessary stress, we initially
222 proceeded using their typical schedules. Rhesus monkeys were given 6 hour testing sessions
223 consisting of 60-trial blocks with a 30 minute interval between blocks. Pairs could complete as
224 many trial blocks as they chose. Capuchins were initially given a single 40-trial session per day,
225 as per their norm, but of four pairs, only one achieved the *Stag-Stag* outcome in the
226 *Asynchronous* version, and even this pair did not maintain it. We then implemented a more

227 rhesus-like schedule, except with two hour test sessions (they became agitated if left in their
228 testing cages for any longer), at which point all reached the *Stag-Stag* outcome. For more detail,
229 see SOM.

230 The non-human primates did require some training to learn to use the split screen (a
231 novel experimental feature) and to make choices within the same time frame. This occurred
232 through a two-stage training process. First, two monkeys worked together to learn that they had
233 to both hit a single, solitary target on their side of the screen before both would receive a food
234 pellet. Then, they had to progress to a point where they would make those same responses
235 within a 5 second window from the initial presentation of a trial. Note that these training stimuli
236 were not those used in the Assurance game, and there was no choice behavior on the part of the
237 primates. There was only one icon on the computer screen which could be contacted with the
238 cursor. This training was used to teach them which half of the screen presented their choices
239 (and outcomes), and to teach them that they needed to respond relatively quickly when a trial
240 was presented. This training assured that, at minimum, subjects knew that 1) rewards were not
241 given without both individuals making a response and 2) they could control only their cursor.
242 Although of course we cannot know how the monkeys actually interpreted the task, we do know
243 they at least understood how to generate responses that might bring rewards, and what
244 limitations had been imposed.

245 *Capuchin monkeys* Based on our previous research (Brosnan et al. 2011), we knew that
246 the capuchins would have more difficulty with the task than did the humans. Thus, we started all
247 capuchins with the *Asynchronous* version of the task, and once they had learned it, gave them the
248 *Synchronous* version. The subjects had far more difficulty with this, so to verify that they were

249 still able to do the basic task, we repeated the *Asynchronous* version. Finally, we repeated the
250 *Synchronous* version to see if the extensive experience had increased their skill level.

251 *Rhesus monkeys* Half of the rhesus monkeys were started on the *Synchronous* and half
252 with the *Asynchronous* version. All of the subjects on the *Synchronous* version succeeded, and
253 so we did not return them to the *Asynchronous* version (see Results and Table 2). Subjects that
254 started on the *Asynchronous* version were subsequently run on the *Synchronous* version.

255 *Humans*

256 Undergraduate subjects were recruited from the general student body at Chapman
257 University, Orange, CA, USA. Subjects were randomly recruited via an electronic email system
258 and paid \$7 for showing up on time, plus what they earned in the experiment. Each subject had
259 participated in at least one economic experiment sometime prior to this session (participating in a
260 previous study involving Normal Form game experiments or the Assurance Game disqualified
261 individuals as a participant) so that they had experience with receiving actual payment for their
262 decisions in this laboratory. No subject participated in more than one pairing or more than one
263 version of the task.

264 The humans' only instruction the *Synchronous* treatment was limited to the following six
265 points:

266 1) Have you participated in an economic experiment before?

267 (Both must reply with a "yes" to participate.)

268 2) In this experiment you will be making decisions using a joystick attached to a computer.

269 Use the *left* thumb pad to make a decision.

270 3) As the experiment progresses you may be paid in quarters by the machines next to your
271 computer.

- 272 4) Please collect the coins in the yellow cups provided so as to not clog up the machines.
- 273 5) These are the only instructions you will receive in the experiment. Once the experiment
- 274 begins, the experimenter will not be allowed to answer *any* questions until the experiment
- 275 is over.
- 276 6) Do you have any questions before the experiment begins?

277 Subjects initially began with the *Synchronous* task, as described above. Pairs of

278 participants, who were the only two individuals in the room, sat next to one another at a single

279 computer and used a joystick. The lack of anonymity enhances the likelihood of achieving the

280 Pareto dominant outcome. Pairs received payment in quarters (from a coin dispenser, an

281 analogue to the primates' pellet dispenser) and payoffs were in the same ratios as those of the

282 monkeys (accumulated coins were converted into large bills at the conclusion of the experiment).

283 However, the results of this game indicated that language was an important characteristic in

284 determining the pairs' outcomes (see Results for details), thus a true comparison between the

285 conditions could not be done. While we could have simply asked participants not to talk with

286 each other during the game, this differed from the other primates, who could communicate to the

287 fullest extent of their abilities, and may have led to an awkward social environment. Thus, we

288 instead investigated the *Synchronous/Asynchronous* comparison using an alternate procedure.

289 This procedure was based on a typical Normal Form Game (NFG) procedure with a 2 x 2

290 matrix of payoffs and strategies. For the *NFG* treatments, the game and payoffs were the same,

291 however participants were isolated at individual study carrels playing on their own computer

292 against an anonymous opponent drawn from amongst the other participants in the room. To hide

293 who was partnered with whom, rewards accumulated and were paid out at the end of the session,

294 rather than using a coin dispenser after each decision (the noise from coin dispensers would have

295 served as a cue). As with the monkeys, in the *NFG Synchronous* version, both partners' choices
296 were displayed simultaneously to both players after both decisions had been made, while in the
297 *NFG Asynchronous* version choices were displayed to both players as they were made. As an
298 additional benefit, having results in a traditional NFG procedure allowed us to see how our
299 *Synchronous* results with humans compared to typical NFG experimental procedures (e.g.
300 involving instruction).

301 *Synchronous version*

302 Fifty-two undergraduate subjects participated in the study in pairs (i.e., in 26 separate
303 sessions).

304 *NFG Synchronous and NFG Asynchronous versions*

305 One hundred eighteen undergraduate subjects were recruited by the same protocols
306 above, except that 12-24 people participated at the same time. Fifty-eight people in three
307 sessions of 22, 24, and 12 participated in the *NFG Synchronous* treatment and 60 people in three
308 sessions of 24, 24, and 12 participated in the *NFG Asynchronous* treatment. The subjects were
309 simultaneously seated in a computer laboratory at visually-isolated carrels and instructed not to
310 talk to one another. They then read self-paced instructions on how to participate in the
311 experiment. These subjects were privately paid their total accumulated earnings at the
312 conclusion of the experiment; they did not receive payment as they made each decision to avoid
313 possible cuing to one's partner's identity.

314 *Statistics*

315 Statistics are non-parametric due to small sample sizes. Primate results are based on
316 individual analyses, while for humans we include both individual analyses and inferential
317 statistics that allow generalizations about the population. This difference in approach is because

318 fewer monkeys were available for the study, as few are sufficiently well trained for computerized
319 testing. All statistics are two-tailed.

320 Note that in many cases both chi-square and Fisher's exact tests were impossible due to
321 the large number of cells with zero values. Thus, to determine whether a pair showed a pattern
322 in their decision-making, we considered it meaningful if the subject showed an 80% or greater
323 preference for one of the four options (for the pair; chance was actually 25% in this case) or one
324 of the two options (for the individual; chance is 50%). This percentage is significant for a
325 binomial test for 20 trials and, as all of our subjects had at least 40 trials (and for pairs, chance
326 was 25%, not 50%), this represented a conservative estimate for what constituted a significant
327 pattern to their decision-making.

328

329 **Results**

330 *Non-human primate results*

331 Both monkey species did very well in the *Asynchronous* task. All capuchins began with
332 the *Asynchronous* version due to previous results indicating that they would have trouble finding
333 the payoff dominant outcome (Brosnan et al. 2011). One pair reached the payoff-dominant
334 outcome in our initial 40-trial sessions and the other three did so when switched to 60-trial
335 sessions (see Methods, above). Three of the rhesus monkey pairs (composed of four unique
336 individuals) first played the *Asynchronous* game. Two reached the 80% *Stag-Stag* criterion
337 within a single session (see Table 2) and the third pair did so in the second session.

338 Despite this similarity, the monkeys differed in their outcomes in the *Synchronous* task.
339 None of the capuchin pairings showed any preference for playing *Stag-Stag* (or any other
340 outcome) when tested in a novel pairing on the *Synchronous* task. To see if this was due to a

341 lack of understanding of the task, we re-ran the *Asynchronous* version with the capuchins. Eight
342 monkeys were paired in multiple pairings (range: 1-3; see Table 1) for a single session consisting
343 of as many trials as they chose to complete in 2 hours (mean=253 trials). All but one pair chose
344 *Stag-Stag* at least 80% of the time (range: 80.6%-96.1%; see Table 1) and the exceptional pair
345 chose *Stag-Stag* 71% of the time. Nonetheless, when retested on the *Synchronous* task,
346 outcomes remained poor. *Stag-Stag* was maintained in only one of the five pairs which had been
347 tested together previously (see Table 1). Intriguingly, the exceptional pair showed the lowest
348 frequency of *Stag-Stag* outcomes in the *Asynchronous* test, and the pair which had not previously
349 been tested together also most often played the *Stag-Stag* outcome (see Table 1). Note that
350 capuchins' poor performance occurred despite both previous experience with the Assurance
351 game and introductory experience in the presumably easier *Asynchronous* version of the game.

352 On the other hand, the two pairs of rhesus monkeys that were tested first on the
353 *Synchronous* version quickly found the *Stag-Stag* outcome. Although it took them slightly
354 longer to reach the 80% criterion than did the pairs that played the *Asynchronous* version first,
355 both pairs did so within 4 trial blocks, and at the same frequency as those pairs which first played
356 the *Asynchronous* version (see Table 2). Note that they accomplished this despite never having
357 had the opportunity to match a partner's play after having seen it, ruling out this simple
358 associative mechanism.

359 Finally, the two rhesus pairs which showed the highest frequency of *Stag-Stag* choices in
360 the *Asynchronous* game were subsequently given the opportunity to play the *Synchronous*
361 version. One pair maintained a preference for playing *Stag-Stag*, while the other started at a
362 lower level of *Stag-Stag* choices and subsequently declined further. This seemed to be primarily
363 due to one individual who began preferentially choosing *Hare*. Thus, unlike with the capuchins,

364 at least one pair was able to maintain the *Stag-Stag* outcome when switched to the *Synchronous*
365 task.

366 *Human Results*

367 Among 27 human pairs in the *Synchronous* condition, 22 ultimately settled on *Stag-Stag*
368 and 5 settled on *Hare-Hare*. What was notable was the perfect correlation between outcomes
369 and pairs' discussions. Although all pairs spoke to each other, textual analysis of video
370 recordings revealed that not every pair spoke about the game. Amongst the 5 pairs who settled
371 on *Hare-Hare* (range: 34-36 *Hare-Hare* choices in 40 trials; see Table 3), not a single pair spoke
372 about the game (henceforth, non-communicators), while among the 22 pairs who did so
373 (henceforth, communicators), every pair ultimately settled on *Stag-Stag*, choosing it in at least
374 seven of the last 10 choices (13 pairs did so on every one of these choices). One-third of
375 communicators chose *Stag-Stag* a minimum of 80% of the time overall (range: 32-39 *Stag-Stag*
376 choices) and more than half (55%) did so at least 70% of the time. No non-communicators ever
377 played *Stag-Stag*, indicating that they did not explore the decision space as thoroughly as did the
378 other pairs (or the monkeys).

379 Given the larger human sample size, we can consider variation using inferential statistics.
380 The overall payoff between communicators and non-communicators differed by a factor of 3
381 (Independent samples Mann-Whitney U test: $p < 0.001$, mean \pm SE payoff per trial for pairs of
382 communicators: $\$1.48 \pm .08$; non-communicators: $\$0.47 \pm .002$). Moreover, among
383 communicators, there was an increase in payoff between the first quartile and last quartile
384 (Wilcoxon Signed-ranks test, $p < 0.001$, quartile 1 mean \pm SE: $\$0.98 \pm .11$; quartile 4: $\$1.89 \pm .03$).
385 On the other hand, among non-communicators, the payoffs increased across these quartiles only
386 because the decrease in number of *Stag* choices stabilized payoffs at one quarter for each

387 individual by the fourth quartile (Wilcoxon, $p=0.039$; quartile 1 mean \pm SE: $\$0.44\pm.01$; quartile 2:
388 $\$0.50\pm.00$). Thus, sociality is not synonymous with coordination; humans had to actually
389 discuss the game in order to benefit from language. Moreover, humans were not intrinsically
390 better than the other primates at the *Synchronous* condition. They appeared to use
391 communication to turn the *Synchronous* game in to an asynchronous game, giving humans an
392 additional mechanism for coordination.

393 Based on these results, humans played the *NFG Synchronous* and *NFG Asynchronous*
394 versions using a more traditional normal-form game set-up that prohibited discussion (see
395 Methods). One third (10 of 30) of the pairs in the *NFG Asynchronous* game chose *Stag-Stag* at
396 least 80% of the time. Intriguingly, an additional four of these pairs chose *Hare-Hare* 80% or
397 more (and one other did so 78% of the time), an outcome that we never saw in either of the
398 monkey species. This could indicate the non-human primates are more likely to explore the
399 decision space than are humans, or that humans are more likely to persevere on responses that
400 are rewarding. In the *NFG Synchronous* game, only four (14%) pairs chose *Stag-Stag* this often,
401 while ten (35%) pairs chose *Hare-Hare*. Thus the frequency of *Stag-Stag* and *Hare-Hare*
402 choices flipped between the two conditions.

403 Considering the data quantitatively, the overall payoffs do not differ between the games
404 (Mann-Whitney, $z=1.47$, $p=0.14$), although there is a non-significant trend for the players in the
405 *NFG Asynchronous* game to earn more by the fourth period than do players in the *NFG*
406 *Synchronous* game (Mann-Whitney, $z=1.85$, $p=0.0643$). Moreover, the number of *Stag-Stag*
407 choices was greater in the *NFG Asynchronous* treatment than *NFG Synchronous* treatment
408 (Mann-Whitney, $z=1.9$, $p=0.0574$), and twice as many partnerships failed to ever play *Stag-Stag*
409 in the *NFG Synchronous* as compared to the *NFG Asynchronous* treatment (10/29 vs 5/30).

410 Considering the games individually, participants showed a trend towards playing *Stag-Stag* more
411 often than *Hare-Hare* in the *NFG Asynchronous* game (Wilcoxon, $z=1.86$, $p=0.0624$), but not
412 the *NFG Synchronous* version (Wilcoxon, $z=0.46$, $p=0.6818$). Subjects improved over the
413 course of both treatments, earning more money in the fourth quartile than in the first (*NFG*
414 *Asynchronous*: Wilcoxon, $z=4.26$, $p<0.001$, *NFG Synchronous*: $z=3.42$, $p=0.0006$). Nonetheless,
415 as with the other two primate species, humans were better at finding the payoff dominant
416 outcome when an opportunity to coordinate was presented (e.g., sequential play).

417 Finally, comparing humans' results from the nonhuman primate format (which was the
418 *Synchronous* treatment) to the *NFG Synchronous* format, the pairs' payoffs were higher when
419 they could talk (mean payoffs for the *Synchronous* treatment: \$1.63; *NFG Synchronous*
420 treatment: \$1.07; Mann-Whitney, $z=2.62$, $p=0.0087$). On the other hand, by the end of the game,
421 subjects did equally well when they could see each other's decision as it was made as when they
422 could talk (comparing fourth quartile payoffs in the *Synchronous* and *NFG Asynchronous*
423 treatments; Mann-Whitney, $z=1.00$, $p=0.3179$; see Table 3). Thus, subjects were equally able to
424 use language or sequential moves without language to coordinate on the *Stag-Stag* outcome and
425 achieve the same level of payoffs across procedures.

426 *Does finding Stag-Stag mark a change in behavior?*

427 The above results assess individuals' tendency to find the cooperative, *Stag-Stag*,
428 solution. That is, to what degree do they explore the problem space and encounter *Stag-Stag* as
429 an option? A second way to consider these data is to determine the frequency with which they
430 played stag-stag after having found it for the first time. Considering first the monkeys, there is
431 no evidence that finding *Stag-Stag* was sufficient to alter their behavior. Amongst capuchins, no
432 pair ever had a single trial block (60 trials) in which they did not play *Stag-Stag* at least once (see

433 Supplemental Results for details), yet despite this not a single pair was able to successfully solve
434 the Synchronous version of the task. Rhesus similarly played *Stag-Stag* in every trial block, yet
435 it was rare for a pair to settle on *Stag-Stag* before the third trial block (see Supplemental Results
436 for details).

437 Humans showed a similar pattern. In the *Asynchronous* task, most players who found
438 *Stag-Stag* did so quickly (within the first 4 trials), yet only three (12%) of these pairs played
439 nothing but *Stag-Stag* after finding it. In the *Synchronous* task, no pair ever exclusively played
440 *Stag-Stag* after finding it (for details of both conditions, see Supplemental Methods). Thus we
441 find clear indication that in neither of the two computerized conditions do pairs' payoffs change
442 meaningfully after finding the first *Stag-Stag* outcome, indicating that these results cannot be
443 explained by a lack of knowledge about the payoff matrix. Similarly, sitting next to one's partner
444 did not affect the frequency with which individuals stayed on the *Stag-Stag* payoff. Of the 22
445 pairs that played *Stag-Stag* at some point, only one played nothing else after finding that
446 outcome. Four additional pairs played *Stag-Stag* all but one or two times, possibly indicating
447 that they were either jointly exploring the parameter space, or individually exploring potentially
448 increased outcomes (see Supplemental Results).

449

450 **Discussion**

451 Our results indicate that generalizing the decision-making outcomes of primates into one
452 in which species are 'better' or 'worse' than others is not sufficiently nuanced. Instead, we find
453 that the results vary in interesting ways depending upon context. Considering our second
454 hypothesis first, all species were able to more easily solve the task in the *Asynchronous* than in
455 the *Synchronous* conditions. Although these studies were explicitly designed to investigate

456 outcomes, not mechanism, we are able to use these results to posit necessary mechanisms. Thus
457 it seems likely that this boost in performance was due to the availability of simple rules, such as
458 matching-to-sample (e.g., Cumming & Berryman 1961) which could not be used in the
459 *Synchronous* task since the partner's behavior was hidden. This indicates that it is possible to
460 solve this task with a suite of fairly simple behavioral mechanisms. We also note that, without
461 other data, this would indicate phylogenetic continuity amongst the primates, and thus, when
462 considered with the *Synchronous* results, emphasizes the utility of using multiple methods to
463 assess behavior and cognition.

464 On the other hand, not all species were able to solve the *Synchronous* task. No pair of
465 capuchin monkeys ever solved this task, even after experience (successfully) solving the
466 *Asynchronous* task. Thus, the monkeys' inability in the *Synchronous* pairing was not due to a
467 failure to understand the task outcomes. Instead, we think that the best explanation for the
468 decline in performance in the *Synchronous* task is likely related to the fact that they could no
469 longer see their partners' decisions and use a simple strategy such as matching. These results
470 also imply that the one pair's success in the previous, exchange version (Brosnan et al. 2011)
471 was likely due to the fact that they could see their partners' choices. On the other hand, some
472 rhesus monkeys and humans found the payoff dominant outcome in the *Asynchronous* task, and
473 required very few trials in order to do so. Thus, Old World primates outperformed New World
474 primates, rather than humans outperforming nonhumans.

475 This has several very important implications when considering the mechanisms required
476 to solve the Assurance game. First, of course, the task can be solved using fairly simple
477 learning-based mechanisms when appropriate cues are available (e.g., the *Asynchronous* task).
478 Second, the high performance of both rhesus and humans implies that the presence of theory of

479 mind is not required. Although one can see how the ability to predict one's partners' behavior
480 would be useful, it seems the task can be solved without it. It will be interesting to see whether
481 this remains true in more complex games which lack a mutually beneficially payoff dominant
482 outcome. Finally, in the absence of cues, it seems likely that other more complex cognitive
483 abilities are required to solve the task. We note that these results are particularly strong given to
484 our choice of a New World monkey species. Capuchins have an unusually large (for a monkey)
485 brain-to-body ratio (Rilling & Insel 1999), a general high ability in cooperative tasks (e.g., de
486 Waal & Berger 2000; Mendres & de Waal 2000), and equal rhesus in many learning tasks (see
487 Introduction). Any of these might have led to the prediction that capuchins would cluster with
488 the Old World monkeys, even if uniquely amongst New World primates. On the other hand,
489 despite the capuchins' apparent advantages (for solving this task) over other New World
490 monkeys, cognitive differences favoring rhesus monkeys over capuchins have been seen in other
491 recent tasks involving higher-order cognitive abilities, such as metacognition (Beran et al. 2009;
492 Hampton 2001).

493 Our final intriguing result is that outcomes in these games, and in particular the
494 inefficiencies in decision-making, were based on an inability to coordinate on the payoff-
495 dominant outcome, not an inability to locate it due to a lack of exploration of the problem space.
496 None of our subjects, including humans, immediately reverted to the payoff dominant choice
497 after having first experienced it. This was true whether they could or could not see their
498 partners' choice when it was made or, in the case of humans, whether or not they could talk to
499 their partner. This observation is clearly contrary to what would be expected if finding the
500 payoff dominant solution is the only thing required to solve this game. Moreover, this result
501 indicates that there are really two aspects involved in successful performance. First is exploring

502 the parameter space, and locating the payoff dominant outcome. In this, we saw great variability
503 within each species, as indicated in our analysis of their overall results. Second is the ability of
504 pairs to coordinate on that outcome once they have found it. This is explored in our analysis of
505 the choices following the first *Stag-Stag* play. The data indicate that both of these aspects of the
506 Assurance game present challenges to all three species; obviously individuals who do not fully
507 explore the parameter space may never find the payoff dominant outcome, but even after this has
508 been found, coordination is not assured.

509 While we are strongly in favor of testing additional primates (and non-primates) of all
510 taxa, given these data we predict that evidence will continue to favor a New World/Old World
511 split in decision-making outcomes. We are also enthusiastic to see how the inclusion of different
512 game features which may require other abilities, such as theory of mind, will affect species' play.
513 We predict that such studies will serve to illuminate not only the phylogeny of decision-making,
514 but also the cognitive requirements of different decision-making situations, as illustrated by
515 various economic games. In particular, some rhesus monkeys were notable for their success, a
516 pattern of results which clearly deserve additional investigation. One possibility for
517 investigating these mechanisms is to see whether humans and rhesus monkeys differ in the
518 flexibility with which they can switch between strategies. This question is more than academic;
519 if humans and rhesus monkeys are using similar mechanisms (e.g., a cognitive homology), then
520 we know that humans' abilities are built on shared foundation that extends back at least as far as
521 the split with Old World monkeys. On the other hand, if humans and rhesus monkeys have
522 converged on similar outcomes despite using different cognitive mechanisms to reach those
523 outcomes, then we can begin to investigate what shared social or ecological factors in humans'
524 and rhesus' environments selected for these outcomes.

525 Finally, uniquely among the primates, language is an important mechanism for solving
526 coordination tasks in humans, much as additional information was used by all species in the
527 *Asynchronous* task. In other words, we hypothesize that humans may use communication to
528 transform a *Synchronous* task into an *Asynchronous* one by providing information about future
529 moves. This may indicate that some underlying mechanisms, such as the ability to increase
530 performance when cues are present, are conserved between humans and other primates, albeit
531 with differing specific mechanisms. We also think the most likely explanation for the humans
532 who did not communicate about, and thus did not solve, the task is not that they were incapable
533 of doing so. Even subjects who did not solve the task spoke to one another. Instead we propose
534 that they thought that they *had* solved the task, did not see the necessity of exploring other
535 options, and so did not converse about it. Future research aimed at determining which factors
536 cause these different reactions may help to clarify both individual (e.g., personality) and
537 contextual (e.g., social) factors which affect humans' ability to coordinate in such situations.

538 The picture that is emerging makes it clear that humans are not alone in our ability to find
539 efficient, pay-off maximizing outcomes in a coordination game. Moreover, other species'
540 behaviors can be measured using the same experimental mechanisms common in humans, that is,
541 economic games, and results can be made comparable when procedures are equalized across
542 species, including humans. Future work should be done to investigate how cognitive
543 mechanisms interact with game structure, and whether there is homology in the underlying
544 cognitive mechanisms or instead whether similar outcomes are reached in analogous ways.
545 Finally, it will be interesting to see whether this similarity in outcome remains in other more
546 challenging decision-making situations.

547

548

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560

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Table Captions

Table 1: Comparing the capuchin pairs' performance on the second asynchronous and synchronous games (note some pairs had previous experience on both the asynchronous and synchronous games; see Results for details).

	Asynchronous Game (second)		Synchronous Game (second)					
	% <i>Stag-Stag</i>	# trials (1 session)	Overall		First Session		Second Session	
Pairings	% <i>Stag-Stag</i>	# trials (1 session)	% <i>Stag-Stag</i>	# sessions/trials	% <i>Stag-Stag</i>	# trials (1 session)	% <i>Stag-Stag</i>	# trials (1 session)
Drella Wren	80.6	201						
Griffin Drella	93.0	196						
Griffin Wren	96.1	360	33.1	8/3042	34	300	24.2	355
Lily Wren	85.2	240	38.9	7/2176	81.1	180	43.8	420
Griffin Lily	81.7	68	28.4	6/2864	36.1	540	36.7	414
Liam Logan	71.3	240	78.1	6/1467	88.2	170	93.1	29
Logan Gabe	89.2	240						
Nala Logan	93.5	420	34.6	5/2260	74.2	360	31.4	420
Nala Liam			60.1	4/1437	78.3	300	64.0	417

Table 2: Comparing rhesus performance by trial.

	Game	Overall		% <i>Stag-Stag</i>				
		% <i>Stag-Stag</i>	# sessions/trials	Session 1	Session 2	Session 3	Session 4	Session 5
Obi Han	Asynchronous	74.6	5/1483	53.7	77.9	84.6	76.7	81.0
Luke Obi	Asynchronous	94.5	5/1876	90.9	95.3	96.1	93.9	96.4
	Synchronous	65.7	2/824	76.7	54.8			
Chewey Han*	Asynchronous	87.8	5/1440	85	94.2	85.3	87.2	87.3
	Synchronous	72.2	3/360	66.7	68.8	81.3		
Hank Gale	Synchronous	84.0	2/720	74.5	93.4			
Willie Murph	Synchronous	88.1	3/472	31.6^	81.3	95.7		

*Both pairs which played both games played Asynchronous first, followed by synchronous.

^This represented only a single trial block; in actuality Willie and Murph reached 90% *Stag-Stag* preference in their third trial block, which was in their second session. Hank and Gale did not reach 90% until their fifth trial block, which was in their first session.

Table 3: Human preferences across the three games. Earnings measure the mean earnings per trial for the pair, and so range from 0.25 (one individual earned a quarter from playing *Hare* and their partner earned nothing from playing *Stag*) to 2.0 (both earned a dollar from playing *Stag*). An average of 0.5 means that both played *Hare* on every trial. A mean of 1.825 indicates a single *Hare* play and a mean of 1.85 indicates a single *Hare-Hare* trial.

	Talking?	Spoke about symbols?	Number of pairs	Number of trials	Ever played <i>Stag-Stag</i>	Mean # <i>Stag-Stag</i>	Mean # <i>Hare-Hare</i>	Mean Q1 earnings	Mean Q4 earnings
Paired	Yes	Yes	22	40	ALL	27.7 (69%)	6.2	0.98	1.89
	Yes	No	5	40	NONE	0 (0%)	35.2	0.44	0.5
Synchronous	No		30	40	25 (83%)	20.27 (51%)	10.83	0.93	1.43
Asynchronous	No		29	40	19 (66%)	13.48 (34%)	16.28	0.77	1.07

SUPPLEMENTAL MATERIAL

Brosnan, Wilson & Beran

Supplemental Methods

Non-human primate housing details

All non-human primates were socially housed at the Language Research Center of Georgia State University. Rhesus monkeys were all adult males, individually housed in rooms with 1 to 2 other individuals for testing and each spent time outside in various social arrangements. Rhesus monkeys were moved to a specially designed paired testing area where they could share a single monitor between the two subjects. Capuchin monkeys were socially housed in multi-male, multi-female social arrangements with extensive indoor and outdoor living space complete with environmental enrichment. All capuchins were adults who lived in the same social group and, when possible, multiple pairings within the same social group were tested. For testing, capuchin pairs were separated from the remainder of the social group into a testing cage located in the indoor colony room to limit distractions. All separation was voluntary (i.e., subjects were only tested if they entered the testing area freely). Both species received a combination of primate chow, fruits, and vegetables as well as additional enrichment foods.

Rhesus testing schedule

Rhesus monkeys were given 6 hour testing sessions. During these sessions, pairs could complete as many trial blocks as they chose. Sessions consisted of 60-trial blocks with 30 minute long intervals between each trial block during which the program was unavailable.

Capuchin testing schedule

Capuchins were initially given a single 40-trial session per day, which reflected their typical testing pattern and the general trend that they complete fewer daily trials than do rhesus monkeys. However, only one of four unique pairs repeated achieved the *Stag-Stag* outcome in the *Asynchronous* version, and even this preference peaked at 67.5% and dropped off over the next 6 sessions to only 45% (not different from *Hare-Stag* at 40%). At this point, we implemented a more rhesus-like schedule, except that their test sessions were only two hours long (they became agitated if left in their testing cages for longer than this amount of time). Using this longer format, all three showed a 90% preference *Stag-Stag* by their first (2 pairs) or third (1 pair) session. Given these results, 60 trial sessions were used throughout the remainder of the testing.

Supplemental Results

Does finding Stag-Stag mark a change in behavior?

Of the four conditions for the capuchin monkeys, not a single pair ever had a single trial block (60 trials) in which they did not play Stag-Stag at least once (First trial block mean \pm SEM percent Stag-Stag choices, Asynchronous first time: 30.2 \pm 4.5, Asynchronous second time: 78.8 \pm 4.6, Synchronous first time: 14.1 \pm 7.0, Synchronous second time: 58.3 \pm 10). Thus for all test blocks (and sessions) following their first test block in the first Asynchronous condition, subjects had previously experience Stag-Stag, making it unlikely that the challenges the capuchins faced were due to not recognizing Stag-Stag as an option. In fact, in their second Synchronous condition (that is, the fourth condition chronologically), the capuchins did significantly better on the first trial block than they did overall (overall mean: 45.58 \pm 4.0;

Wilcoxon, $T=10$, $n=12$, $p=0.008$), indicating that previous exposure to Stag-Stag was not sufficient for them to solve the task.

All pairs of rhesus monkeys played Stag-Stag during the first trial block (First trial block mean \pm SEM percent Stag-Stag choices. Asynchronous: 59.6 ± 15.2 , Synchronous: 41.7 ± 8.4). Nonetheless, it was rare for pairs to reach 80% Stag-Stag outcomes in the next trial block (Asynchronous: mean=10, range = 1-28 trial blocks; Synchronous: mean=3, range = 2-5 trial blocks; note that the 80% criterion was reached more rapidly in the Synchronous condition, but no pair found it on the first trial block). Thus simply having experience with the Stag-Stag outcome was insufficient to settle upon that strategy.

In the *Asynchronous* computerized task, 43% (13 pairs) of humans played *Stag-Stag* on their first move and 17% (5 pair) never played it (the remaining players averaged 4.5 trials, range 2-17). Of the pairs who found the *Stag-Stag* payoff, only three (12%) pairs subsequently played nothing but *Stag-Stag* after finding it. In the *Synchronous* condition, 11 of 29 human pairs never played Stag-Stag, and only one pair (3%) played it on the first trial. The remaining pairs found the Stag-Stag outcome in a mean of 3.8 trials (range 2-12). No pair played nothing but Stag-Stag after finding it. In fact, while the overall mean payoffs increased by definition when any trials prior to a Stag-Stag choice are excluded, the mean payoff increased from 1.14 to 1.19, a very modest increase (non-parametric statistics based on rank are, again by definition, significant, but we think meaningless in this case). Thus we find clear indication that in neither of the two computerized conditions do pairs' payoffs change meaningfully after finding the first Stag-Stag outcome, indicating that these results cannot be explained by a lack of knowledge about the payoff matrix.

The primate version of the human game produced the same general results. Of the 22 pairs that played Stag-Stag at some point, they found the Stag-Stag outcome in a mean of 6.7 trials (range 1-32). Only one pair played nothing but Stag-Stag after experiencing the outcome; the rest took a mean of 21.6 trials (range 3-39) to settle on all Stag-Stag choices. Several pairs had only one or two non-Stag-Stag choices after finding the outcome, indicating that either one individual tried cheating (n=4) or they tried the Hare-Hare outcome, presumably after discussion (n=4; two pairs in both measures). If these pairs are counted from the time they went mostly to Stag-Stag, then 5 pairs (all but one of them) immediately preferred Stag-Stag.