

Human–Grey parrot (*Psittacus erithacus*) reciprocity: a follow-up study

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Abstract In a previous study (Péron et al. in Anim Cogn, doi:10.1007/s10071-012.05640, 2012), Grey parrots, working in dyads, took turns choosing one of four differently coloured cups with differing outcomes: empty (null, non-rewarding), selfish (keeping reward for oneself), share (sharing a divisible reward), or giving (donating reward to other). When the dyads involved three humans with different specific intentions (selfish, giving, or copying the bird's behaviour), birds' responses only tended towards consistency with human behaviour. Our dominant bird was willing to share a reward with a human who was willing to give up her reward, was selfish with the selfish human, and tended towards sharing with the copycat human; our subordinate bird tended slightly towards increased sharing with the generous human and selfishness with the selfish human, but did not clearly mirror the behaviour of the copycat. We theorized that the birds' inability to understand the copycat condition fully—that they could potentially maximize reward by choosing to share—was a consequence of their viewing the copycat's behaviour as

erratic compared with the consistently selfish or giving humans and thus not realizing that they were indeed being mirrored. We suggested that copycat trials subsequently be performed as a separate experiment, without being contrasted with trials in which humans acted consistently, in order to determine if results might have differed. We have now performed that experiment, and shown that at least one Grey parrot—our dominant—responded in a manner suggesting that he deduced the appropriate contingencies.

Keywords Grey parrot cognition · Reciprocity · Non-human sharing · *Psittacus erithacus*

Introduction

Papers that review the current literature on reciprocity/sharing/prosociality in non-humans (e.g. Horner et al. 2011; Péron et al. 2012; Silk and House 2011; Yamamoto and Takimoto 2012) suggest that the presence or absence of such types of behaviour depended not only upon the species being tested, but also upon the parameters of the task being used. With respect to species, non-human primates are most often tested in an attempt to determine evolutionary precursors of such behaviour patterns and the evolutionary pressures that may have selected for these patterns (e.g. Silk and House 2011; Yamamoto and Takimoto 2012). Nevertheless, several studies have tested avian subjects (e.g. Di Lascio et al. 2013; Péron et al. 2012; Scheid et al. 2008; Schwab et al. 2012; Seed et al. 2008; von Bayern et al. 2007). The rationale has been either to provide evidence for convergent evolution of such traits or to determine their absence: lack thereof might assist in determining what ethological, ecological, and possibly

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even neurological constraints might be preconditions for their existence. With respect to task parameters, many issues—for example, apparatus complexity, visible reward options (particularly when food is the reward), physical competition and/or limited communication between subjects have all been shown to affect success or failure (again, for reviews, see Horner et al. 2011; Péron et al. 2012; Silk and House 2011; Yamamoto and Takimoto 2012).

A prior study on Grey parrots (*Psittacus erithacus*), with a token-based protocol that attempted to avoid as many confounding design parameters as possible, demonstrated a limited understanding of reciprocity (Péron et al. 2012). We were careful to discuss the task merely in terms of “reciprocity”, because it did not involve reciprocal altruism, where one subject acts in a costly manner in the expectation that such behaviour would be rewarded at a later date (e.g. as when birds assist in mobbing predators, Krams et al. 2008; rats alternating at pulling in treats where only the non-puller is rewarded, Rutte and Taborsky 2008). Nor did it involve simultaneous cooperation, where two subjects are required to work together at the *same time* (e.g. see Melis et al. 2006) so that they both could benefit immediately from their efforts. Nor were both participants competing to monopolize a reward that could potentially be shared (e.g. Cronin and Snowdon 2008); if chosen by the subject, such rewards were disbursed equally to each player by humans. Nor was our study fully comparable with the standard (even iterative) Prisoner’s Dilemma (Axelrod and Hamilton 1981; Trivers 1971) because of the reward system we used (see below).

The previous study involved two experiments. In the first, two birds worked alternatively with each other, acting either as leader or follower; the point was to see if, given a choice among cups with differing outcomes [empty (null, non-rewarding), selfish (keeping reward for oneself), share (sharing a divisible reward), or giving (donating reward to other)] they would learn to cooperatively reward their partner at little cost to themselves—by sharing—and potentially maximize overall reward by reciprocating such sharing. Dominance–subordination issues may have come into play (only our dominant bird, as follower, was willing to share) in the first experiment; however, in the second, each bird worked alternatively with three humans with whom dominance was presumed to be unimportant. There, each human had different specific intentions (selfish, giving, or copying bird’s behaviour). In this experiment, birds’ responses tended towards consistency with human behaviour. Both birds (although to somewhat different extents) were willing to share a reward with a human who was willing to give up her reward and were selfish with the selfish human. The dominant, however, only

tended towards sharing with the copycat human, and our subordinate bird did not specifically share with the copycat. We hypothesized that the birds’ inability to understand the copycat condition fully—that they could potentially maximize reward by choosing to share—was a consequence of their viewing the copycat’s behaviour as erratic compared with the consistently selfish or giving humans, and thus of not realizing that they were indeed being mirrored. We suggested copycat trials subsequently be performed as a separate experiment, without being contrasted with trials in which humans acted consistently, to determine if results might have differed. The present study is a test of that hypothesis.

Methods

Subject and housing

A 17-year-old hand-reared male Grey parrot, Griffin, was tested between September and October 2012 with a male human trainer and between June and July 2013 with a female trainer. Griffin has been the subject of continuing studies on comparative cognition and interspecies communication (e.g. Pepperberg 1999, 2004; Pepperberg et al. 1997, 1998, 1999, 2000, 2012; Pepperberg and Shive 2001; Pepperberg and Wilcox 2000); he was the dominant subject in the prior reciprocity study (Péron et al. 2012). Details of housing conditions are in Pepperberg and Wilkes (2004). Outside of testing, he lived separately in or on a cage out of reach of another Grey parrot, Arthur, also in the previous reciprocity study. Arthur became ill, could not be re-tested in 2012, and died before testing in 2013. Griffin was never food or water deprived at any time during the experiment. We realize that the study now examines the behaviour of a single individual; however, in classic power studies (Triana and Pasnak 1981), if one or two individuals of a species demonstrate proficiency, the species is considered capable of succeeding.

Materials

Four same-sized plastic cups of differing colours (*First Years Stack N Count Cups*TM) were placed on a felt-covered tray equidistant from a parrot’s beak (see Fig. 1), and rewards consistent with each cup colour were put under each cup without Griffin observing the placement: The green cup held 2 treats, pink and orange cups held 1 each, and the violet cup held none. If a bird chose (a) green cup—sharing, he and his partner each got treats; (b) pink cup—selfish, only he got a treat, (c) orange cup—giving, only his partner got a treat, and (d) violet cup—null (spiteful/opt out), no one got treats.

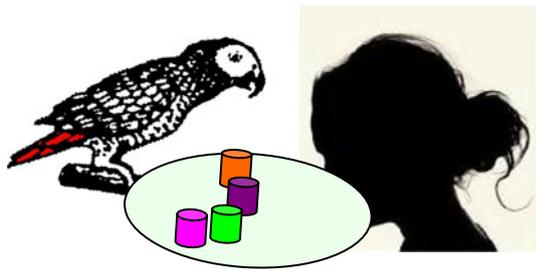


Fig. 1 Position of bird, tray, and human during trials; during trials, cups are arranged so as to be equidistant from the beak of the bird or the human's face

Notably, a human other than the social partner disbursed the treats; thus the parrot could not spar with the partner over the reward. The set-up was designed to ensure that human cuing via gaze of a particular choice of cup would not be an issue: cups were closely spaced (<5 cm) on a tray and the human head was about 30 cm away from the tray, a situation in which parrots have not previously been shown to react to human gaze direction (Pepperberg 1990, 1999), unlike that of Giret et al. (2009) in which Grey parrots did respond to human gaze when objects were 1.6 m apart and the human face was deliberately turned in the direction of one of the objects.

The same materials were used for all experimental trials. The physical set-up of cups and the tray was identical to that used in Péron et al. (2012), so that neither training nor familiarization trials were necessary. Cup positions were now changed after every human choice, with positions determined by use of the program random.org. Overall, each cup was thus in each position an equal number of times. Rewards—pieces of cashews, almonds, occasionally crackers—were special treats not available except in experimental sessions.

Protocol

Each two-choice trial consisted of the following pattern: the tray was presented to Griffin; after he chose a cup (either by picking it up or pecking it), the experimenter intervened and distributed the reward(s) according to the cup's value (NB: "Pecking" was considered a choice because sometimes Griffin's beak slipped as he tried to grip the edge of the cup; such "pecks" initially looked identical to successful grips). The tray was re-baited (out of Griffin's sight), then immediately presented to the human copycat for his/her choice (set to be identical to that of Griffin), with subsequent reward disbursement by the experimenter. Inter-choice and inter-trial intervals (i.e. time needed to re-bait and re-present the tray, approximately 12–15 s for nut rewards, somewhat longer for cracker rewards) were kept

as consistent as possible. We did ensure that Griffin was attending (e.g. not preening) before a presentation. The idea was to model what might be a feeding session in the wild, where the first bird to arrive at, for example, a fruiting tree, might have some advantage, but then feeding by the flock is more or less simultaneous, excepting various affiliative and aggressive flock interactions, where birds may share or locally defend their food (May 2004). The experiment consisted of 10 sessions of 10 two-choice trials with each of two humans, with no more than one session/day with each human. If Griffin hesitated, he was told "Go pick up cup". For each trial, we recorded Griffin's choice and noted any additional physical behaviour. The question under study was whether Griffin would attend—or learn to attend—to the human partner's actions, understand that the human was replicating his own behaviour and thus acting in a reciprocal manner, and that by choosing the green (sharing) cup, he could maximize the overall payoff, because then each individual would receive a reward on each turn.

Because our hypothesized explanation for the birds' inconclusive results in the previous experiment with the copycat humans was that they might have thought the copycat was performing erratically compared with humans who were consistently selfish or generous, we specifically did not have the humans in this study act randomly, change his/her strategy to either selfish or generous, or engage in any other alternation. Notably, although the birds previously did show clear preferences to respond to stable acts by the humans, in one case a bird changed from a generous to a selfish behaviour in the face of what appeared to be "betrayal" (absence from the experiment for an extended period of time; see Péron et al. 2012).

To ensure that the parrot was not responding to a particular human, we ran two sets of trials with two different students, the second after a delay of several months. The first set of data was collected with a male, the second with a female, to test whether human gender could influence the bird's choice. The several months delay ensured that the bird was not likely to have immediately transferred behaviour from one human to another.

Results

Cup choices

Griffin's data were similar with both humans, but more striking with the second. With the first human, LT, Griffin overall chose green 50 times, pink 32 times, orange 10 times, and violet 8 times (Fig. 2). His choices were statistically not random: $\chi^2 = 47.52$, $P < 0.001$, $df = 3$, with a preference for green and pink and clear avoidance of

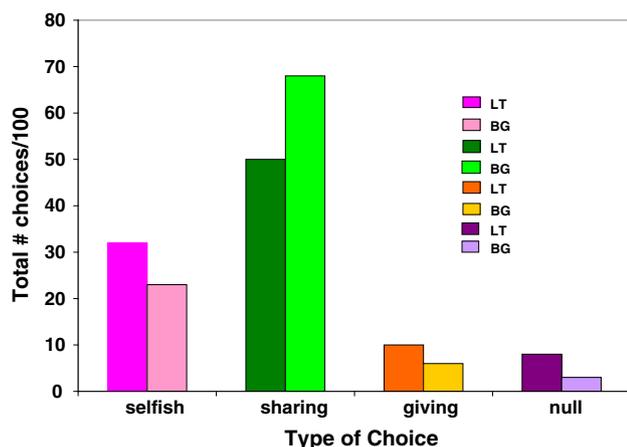


Fig. 2 Summed comparison of all Griffin's choices of the various cups over all trials

orange and violet. Concentrating on selfish versus sharing, his choice of green over pink was statistically different from chance, $\chi^2 = 3.95$, $P = 0.047$, $df = 1$. With the second human, BG, Griffin overall chose green 68 times, pink 23 times, orange 6 times, and violet 3 times (Fig. 2). His choices again were statistically not random: $\chi^2 = 107.92$, $P < 0.001$, $df = 3$, again with a clear preference for green, somewhat of a preference for pink, and a clear avoidance of orange and violet. He chose green (sharing) more than twice as many times as he chose pink (selfish), and the difference was clearly statistically significantly different: $\chi^2 = 22.253$, $P < 0.001$, $df = 1$.

He was fairly consistent over all trials. A plot of individual sessions (Figs. 3, 4) shows that, with few exceptions, he consistently favoured green for both humans. He did not change his behaviour over time; his choices did not differ significantly from the first half to the second half of the study. For LT, $\chi^2 = 1.73$, $P = 0.632$, $df = 3$. For BG, change does appear to exist from the first to second half of the study, but the difference just misses significance: $\chi^2 = 7.53$, $P = 0.057$.

Interestingly, he did have somewhat of a position preference with LT, $\chi^2 = 9.09$, $P = 0.028$, $df = 3$. The distinction was not between choice of inner versus outer positions (those possibly easier to access on the edges vs. those in the middle; $\chi^2 = 3.60$, $P = 0.058$, $df = 1$). Rather, he seemingly chose the first position somewhat more often (36/100) and the third position somewhat less (15/100); he did not seem either to prefer or avoid the second or fourth positions (21/100, 28/100, respectively). Chi square statistics are consistent with such an analysis. For position 1 versus 3, $\chi^2 = 8.0$, $P = 0.005$, $df = 1$ (significant even with Bonferroni correction, requiring $P < 0.007$); Chi square values for 2×2 position comparisons other than first with third are non-significant (for 1

vs. 2, $\chi^2 = 3.5$, $P = 0.061$, $df = 1$; for 1 vs. 4, $\chi^2 = 0.78$, $P = 0.38$, $df = 1$; for 2 vs. 3, $\chi^2 = 1.0$, $P = 0.317$, $df = 1$; for 2 vs. 4, $\chi^2 = 1.0$, $P = 0.317$, $df = 1$; for 3 vs. 4, $\chi^2 = 3.93$, $P = 0.047$, $df = 1$; the last does not survive Bonferroni correction). All cups were equally placed in all positions and the distribution of choices for individual colours were, however, statistically random: For pink, $\chi^2 = 1.25$, $P = 0.741$, $df = 3$, for green, $\chi^2 = 7.57$, $P = 0.057$, $df = 3$, for orange, $\chi^2 = 6.80$, $P = 0.079$, $df = 3$, and for violet, $\chi^2 = 3.0$, $P = 0.392$, $df = 3$. A two-way ANOVA to check for an interaction between position and colour choice was not significant: $F(9,144) = 1.084$, $P = 0.378$. However, looking at his specific choices for orange and violet and the low power of the statistics given the few choices of these colours, the data suggest that, had he not had such a preference, his choices with respect to cup colour might have been even more striking. Specifically, although he mostly avoided choosing violet and orange (null and giving), half of his

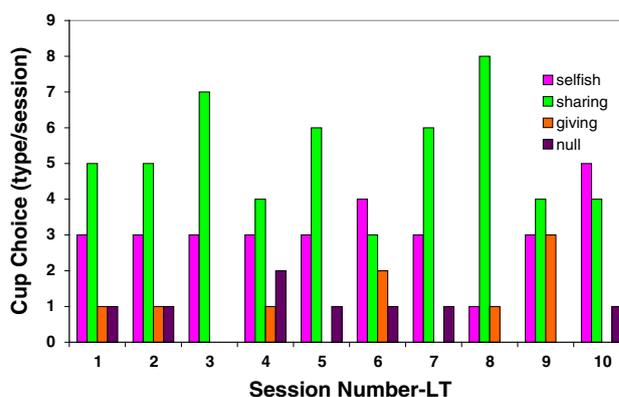


Fig. 3 Summation of Griffin's choices for each type of session with LT, 10 trials/session

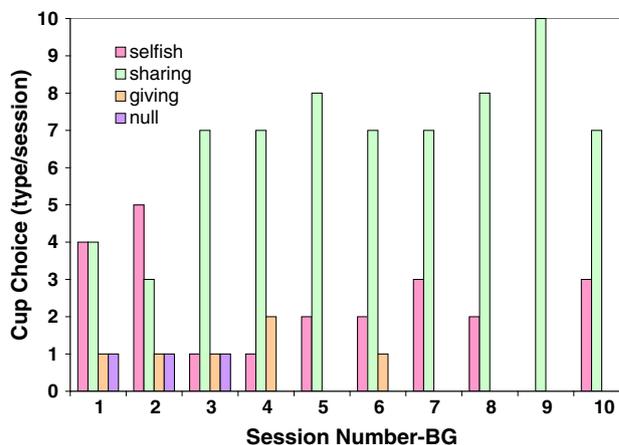


Fig. 4 Summation of Griffin's choices for each type of session with BG, 10 trials/session

choices of violet were when the cup was in the first position, and 4 of his 10 choices of orange were when that cup was also in the first position.

When working with BG, Griffin did not demonstrate any position preference, $\chi^2 = 2.70$, $P = 0.441$, $df = 3$. Furthermore, a two-way ANOVA to check for an interaction between position and colour choice was not significant: $F(9,144) = 1.375$, $P = 0.205$.

As in the earlier study, Griffin did not equivocate or dither on any of his choices, and all were clear to observers (e.g. Supplemental Video 1). A sample of his choices were videotaped and scored by IMP, who never participated in any sessions; agreement on Griffin's choices was 100 %.

Discussion

When the copycat partners were the only ones participating in the sessions, Griffin seemed to understand the parameters of the study; that is, that each person was mirroring Griffin's own behaviour and not acting erratically. Although Griffin had had some refresher trials on the task in the summer of 2010, no other trials had occurred in almost 2 years before his work with LT; nevertheless, he seemed to retain knowledge of the task and seemed to understand fairly quickly that choice of green led to maximizing the rewards he could obtain. He began his choices with LT roughly at the same place he ended in the previous study (Péron et al. 2012), with 50 % choices of green, although he began with fewer choices of pink. He thus may have brought some knowledge from the previous study to the present one. He clearly was avoiding aversive choices: giving up the reward (orange) or choosing the cup without any reward (violet). He did, however, pick pink—acting selfishly—with LT about one-third of the time. The difference between his choices of green and pink showed a clear trend towards green (50 % of all choices). His work with BG began 7 months later and, as seen from Fig. 4, although he began with approximately equal choices of pink and green, he again seemed to retain a general sense of the task and quickly began choosing green on most trials. His shift in behaviour from the first to second half of the trials was not statistically significant. The underlying rationale for Griffin's behaviour cannot be definitively determined, but various possibilities can be discussed.

As noted in our previous study (Péron et al. 2012), we did not expect dominance/subordination issues to have affected the Griffin's choices when interacting with human partners. Griffin likely had no dominance issues with respect to humans in the laboratory, and in daily interactions did not appear to favour LT over BG or vice versa. Although humans provide his care (e.g. prepare his food, preen him, move him around the laboratory), he controls

some of these interactions via vocal requests (“Want grape”, “Wanna go back”, “Tickle?” etc.); for those reasons, he probably sees himself as of relatively equal status than as either dominant or subordinate to the various students with whom he interacts. Nevertheless, the possibility of dominance/subordination must be examined. If Griffin did view himself as dependent upon the humans for his well-being—that is, as somewhat subordinate—then acting in a generous manner suggests he might have intended to “play nice” so that the human would continue his care. Finding that the human reciprocated in kind likely maintained that interaction. In contrast, had Griffin seen himself as dominant (in charge of ordering students to do his bidding), then acting in a somewhat generous manner follows explanations presented by researchers such as Zahavi (2004); that is, possibly as a way of advertising his fitness to retain his dominant position [note, too, Grant and Dutton (2012), who suggest that at least for humans, giving/sharing may increase one's identity as a capable individual, promoting the well-being of the group]. An explanation of his selfish choices is more difficult to derive with respect to dominance/subordination. Previously (Péron et al. 2012), Griffin became selfish only when in the dominant, leader position and when his partner was or became selfish; here such behaviour occurred less than sharing. Although Griffin could possibly have viewed the so-called selfish behaviour not specifically as “selfish”, but rather as a turn-taking process (“I get a treat, then you get a treat...”), inspection of the videotaped trials (Supplemental Video 2) suggests that when the student chose selfishly, Griffin did not appear willing to await his turn patiently. Unlike in the previous study, however, he did not vocally protest the selfish choice of the human (Péron et al. 2012). Thus, although choosing pink (selfish) would have presented the same immediate reward as choosing green (sharing), Griffin did not act in that manner; he seemed to figure out, fairly quickly, that his choice of pink meant that he would miss a reward when the human subsequently made the choice; such behaviour occurred with both LT and BG.

Interestingly, although choosing orange (giving) would have ultimately presented the same overall reward as choosing pink (selfish) via a pattern of reciprocal altruism, Griffin did not act in that manner. The rationale for his action cannot be conclusively determined, but he may not have entirely trusted the human, or, alternatively, realized that green was optimal. Notably, in the earlier study (Péron et al. 2012), when a human consistently chose orange, Griffin evolved to consistently choose green; that is, he was willing to share with someone who consistently donated treats, but did not act altruistically.

One might argue that in our lab Griffin has been previously extensively trained by humans via the Model/Rival method (Pepperberg 1981) and thus expects humans to

demonstrate behaviour patterns he is to learn; that is, that Griffin was simply copying the behaviour of the human, rather than realizing he was being copied. Two points argue against such an explanation. First, in this study Griffin always got to choose first within a session, and in our previous study, he showed by differences in his behaviour that he was keeping track of who went first despite multiple rounds within a session (for details, see Péron et al. 2012). Second, in the same previous study, when the giving human always picked orange, Griffin predominantly reciprocated with sharing rather than giving; that is, he did not replicate the action of the human, and we would see no reason for him to react differently in the current study.

It may be possible that, like humans (van den Bos et al. 2011), Griffin matured somewhat in the intervening 2 years, and that brain changes were responsible for his ability to engage in more reciprocal behaviour with the copycat human in this study, unlike our previous findings (Péron et al. 2012). Little is known about Grey parrot behaviour in the wild, but in captivity these birds can reach sexual maturity when about 3 years old, and Griffin was seventeen at the beginning and eighteen at the end of the study. Given that the lifespan of these birds can, however, be up to 50 years in captivity, it is possible, although unlikely, that Griffin had undergone maturation processes.

Interestingly, Griffin's data differ somewhat from those of ravens (Di Lascio et al. 2013); the latter birds clearly did not engage in reciprocal behaviour with humans whereas Griffin did tend towards such behaviour. A critical difference between the raven study and ours, however, is that in our study, the food reward was not apparent at the moment of choice. Data demonstrate that the presence of food may override cognitive processes in apes (Boysen et al. 1996) and such may also occur in tasks involving reciprocity (e.g. Warneken et al. 2007).

An intriguing possible explanation for Griffin's behaviour may be derived from two papers on primates devoted to this topic. Recently, Yamamoto and Takimoto (2012) have argued that various forms of reciprocal behaviour in non-human primates can be explained as a balancing act between fairness and empathy; Silk and House (2011) present a somewhat similar interpretation but argue for welfare rather than empathy. Notably, welfare does not require putting oneself in the mindset of the other participant or perspective taking, and thus may be more easily studied in non-humans. The basic idea in both papers is that the choice of group members to reciprocate in kind derives from the interplay among selfishness, some level of concern for the well-being of others, and some sense of fairness. Such cooperative behaviour apparently depends on long-term (or at least more than single shot) interactions with the involved parties. Silk and House (p. 10911), for

example, state that "Conditional cooperators follow cooperative norms as long as other group members cooperate but stop cooperating if others defect". One might imagine a scenario for Greys in the wild in which the welfare of individuals is important to the welfare of a flock: A weak (possibly malnourished) individual could attract a predator to the flock, and any member of the flock could then be attacked. A consistent free-loader, however, might be driven from the flock, which is tantamount to a death sentence (a single bird cannot forage and simultaneously watch for predators). This balancing act might explain Griffin's tendency towards reciprocity: Griffin learned that if he defected, his partner likewise defected, but if he shared (gave up part of what could appear to be a bonus, as the green cup contained two rewards), so did his partner so that they both fared well. His acts of selfishness might have been tests to see what would happen after such behaviour. Thus, his sharing may have been less an act of goodwill than of maintaining a functional status quo. The latter does require a protocol (such as ours) involving multiple, repeated interactions with both partners taking both roles. We can, of course, merely report Griffin's actions; we cannot claim that he was deliberately acting in a "tit-for-tat" manner.

Another possible explanation may derive from the concept of "group service", an idea suggested by Burkhardt and van Schaik (2012). These researchers designed a fairly complicated experiment to separate various behaviour patterns related to prosociality and reciprocity; we merely borrow the term to suggest one reason why a Grey parrot might engage in reciprocal behaviour. In the wild, Greys (as well as other parrots) engage in sentinel behaviour: birds take turns watching for predators while the others forage (e.g. May 2004; note Snyder et al. 1987; Yamashita 1987). In the wild, such turn-taking, including delay of eating, to perform a group service might well be a learned behaviour, but provides a rationale as to why a Grey might learn to engage in reciprocal behaviour in a laboratory (again, note Grant and Dutton 2012).

One might argue that other conditions should also have been tested to ensure that Griffin actually understood what he was doing; that is, for example, by changing the payoff values of the cups by using novel colours and seeing how long it took to relearn the appropriate strategy. We expect that changing cup colours or patterns would have required a fairly long response adjustment, and would have tested a separate issue from that of understanding the mirroring/copying act of the human partner. Such an alteration would be an interesting topic for a subsequent study.

One might also argue that the human could have varied his/her behaviour randomly. As noted earlier, such a procedure would not have allowed us to test our specific hypothesis. Moreover, in support of our paradigm, we note

that in a review of models of human behaviour on cooperation, Rivas (2013) argues that imitation is a critical factor in the survival of cooperative behaviour. He explains how, in a situation involving fixed pairs of interacting subjects who work together iteratively, cooperation may evolve as the stable strategy when the subjects respond to each other in an imitative manner. Although his paper is based on the classic Prisoner's Dilemma, the conditions of the models he describes can be set to reflect the conditions of our study.

Our data suggest that some level of reciprocity can be demonstrated in at least one avian species, whatever the underlying mechanisms. The bases for such behaviour may be a consequence of the same evolutionary pressures that were exerted to develop advanced cognitive and communicative abilities in both avian and primate lineages (e.g. Emery 2004; Pepperberg 1999). Given the results of our prior study (Péron et al. 2012), however, such behaviour appears, as we noted earlier, to be heavily dependent upon the specific context in which it is examined.

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