

Do chimpanzees learn reputation by observation? Evidence from direct and indirect experience with generous and selfish strangers

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Received: 20 June 2007 / Revised: 20 February 2008 / Accepted: 22 February 2008
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Abstract Can chimpanzees learn the reputation of strangers indirectly by observation? Or are such stable behavioral attributions made exclusively by first-person interactions? To address this question, we let seven chimpanzees observe unfamiliar humans either consistently give (generous donor) or refuse to give (selfish donor) food to a familiar human recipient (Experiments 1 and 2) and a conspecific (Experiment 3). While chimpanzees did not initially prefer to beg for food from the generous donor (Experiment 1), after continued opportunities to observe the same behavioral exchanges, four chimpanzees developed a preference for gesturing to the generous donor (Experiment 2), and transferred this preference to novel unfamiliar donor pairs,

significantly preferring to beg from the novel generous donors on the first opportunity to do so. In Experiment 3, four chimpanzees observed novel selfish and generous acts directed toward other chimpanzees by human experimenters. During the first half of testing, three chimpanzees exhibited a preference for the novel generous donor on the first trial. These results demonstrate that chimpanzees can infer the reputation of strangers by eavesdropping on third-party interactions.

Keywords Reputation · Social learning · Eavesdropping · Third-party interactions · Chimpanzees

Introduction

Humans, unlike other primates, regularly interact with strangers (Seabright 2005). This feature of human sociality may have favored the evolution of a cognitive system that assigns reputations to others. Reputation judgments involve the attribution of stable character traits or behavioral dispositions to specific individuals in a flexible and adaptive manner. Reputation judgments are functionally equivalent to the conjecture that the behaviors of others are predictable and consistent. There are two ways to assess reputation as operationalized here: directly (individual learning), through first-party interactions, or indirectly (social—observational—learning), by eavesdropping on third-party behavioral exchanges (McGregor and Dabelsteen 1996).¹

¹ In the animal behavior literature, ‘eavesdropping’ has been defined in terms of how individuals use ‘public information’ (Valone 2007). Our use of the term ‘eavesdropping’ in this paper is consistent with the definition of Parejo and Aviles (2007), “the behavior involving the extraction of information from signaling interactions between others” (81).

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Direct reputation judgments arguably provide the most accurate predictor of an individual's future behavior because expectations about a given individual's behavior have been verified through first-person experiences (Alexander 1987; Axelrod 1984; Hauser 1992; Hauser et al. 2003). In contrast, indirect reputation judgments might provide less accurate predictors of an individuals' future behavior because the dynamics governing the interactions of groups, such as the individual's past interactions, are not immediately accessible to the observer and may be specific to the particular group of observed participants (Alexander 1987; Axelrod 1984). However, indirect reputation judgments might serve a vital function in allowing individuals to predict the behavior of others when direct interactions may be costly (i.e., as in assessing another's fighting skill or relative dominance).

Economists have suggested that, because reputation judgments may be used to predict future behavioral interactions, they represent an essential feature of cooperative exchanges among humans (Brandt et al. 2003; Brandt and Sigmund 2005; Fehr and Fischbacher 2003; Nowak and Sigmund 1998; Sigmund et al. 2001; Wedekind and Milinski 2000). Thus a system for attributing reputation might be expected in any species in which it is critical to assess the behaviors of others and to predict the outcomes of future interactions.

A number of studies have highlighted how natural selection may favor domain-specific skills² that function analogously to reputation judgments in a variety of species (Birds: Amy and Leboucher 2007; Paz-y-Miño et al. 2004; Fish: Brosnan and de Waal 2003; Bshary and Grutter 2006; Grosenick et al. 2007; Dogs: Rooney and Bradshaw 2006). In these cases, social learning is achieved by calculating the likelihood of success/failure in a match with either conspecific A or B after eavesdropping on a confrontation between A and B (Valone 2007). In many of these cases the computations made by these animals were spontaneous and performance was at ceiling. In some of these studies, researchers required only an implicit response such as time

spent in proximity (Bshary and Grutter 2006) rather than a direct response requiring an explicit prediction of the future behavior of conspecifics. Because of this level of performance and the fact that these skills appear to exist in only one context (e.g., fighting/dominance), it is likely that they are mediated by a highly constrained domain-specific mechanism dedicated to the processing of dominance information alone. Such mechanisms, while impressive, are only analogously similar to reputation judgments, which have to be abstract in order to process a wider array of social information across different contexts.

There is evidence that primates eavesdrop and, consequently, benefit from third-party interactions (Brumm et al. 2005; Melis et al. 2006). But is learning under these circumstances mediated by the same domain-specific reputation mechanism reported in birds and fish? Or did different selection pressures acting on primates in general and chimpanzees in particular, favor a different type of reputation mechanism; one that is more abstract and, consequently, more context and information general? Consider that chimpanzees live in large fission–fusion groups where individuals (males and females) are hierarchically organized (Goodall 1986). Relationships within these groups are dynamic and dominance is frequently contested; thus individuals must negotiate group dynamics through strategic alliances. These social dynamics have aptly been referred to as 'chimpanzee politics' (De Waal 1982). Chimpanzees have also been observed to engage in a limited number of cooperative acts in the wild (Boesch and Boesch-Achermann 2002; Goodall 1986; Hohmann et al. 1999; Mitani et al. 2000; Mitani and Watts 2001; Nishida and Hosaka 1996; Watts 1998, 2002, 2004; Watts and Mitani 2001), and laboratory experiments have converged on the observation that, under controlled circumstances, chimpanzees demonstrate the capacity to cooperate with humans and conspecifics (Hirata and Fuwa 2007; Melis et al. 2006; Warneken and Tomasello 2006). Taken together, the dynamic nature of chimpanzee social structure and their dietary needs, which place a premium on cooperation, make these animals relatively unique in the animal kingdom and would certainly favor the emergence of a system for inferring reputation across a wide variety of information domains and contexts. In such animals, a mechanism that operates only in a specific information domain (e.g., fighting/dominance) would be less advantageous than a more general reputation mechanism—perhaps a part of the imitation faculty (Subiaul 2007)—that allows learning under a variety of contexts and domains (e.g., fighting, hunting, diet, tool-use).

Perhaps the best evidence in support of the notion that chimpanzees make reputation judgments, as defined here, comes from social learning studies. Certainly, social learning is widespread in the animal kingdom (Zentall 2006), but to date only great apes and humans have evidenced

²In the cognitive and computer sciences, a 'domain' generally refers to a specific class of information. Fodor (1983), referred to mechanisms that operate on a specific domain as 'modules.' These modules are specialized (processing only certain types of information), fast and 'encapsulated,' meaning that they operate outside of conscious awareness and are not affected by learning. In contrast, here, we define the ability to make reputation judgments as an abstract social reasoning skill, meaning that judgments of reputation though social, are not limited to specific social contexts or information. Such judgments can thus be used flexibly in novel circumstances and require inferential reasoning; they may even be applied to non-social agents like computers or even vending machines with a bad 'reputation' of stealing your money. We do not believe that the claims of 'reputation' in fish and birds (Amy and Leboucher 2007; Brosnan et al. 2003; Bshary and Grutter 2006; Grosenick et al. 2007; Paz-y-Miño et al. 2004; Rooney and Bradshaw 2006) meet this more stringent criterion.

novel motor imitation (i.e., imitation learning)—where individuals execute behaviors that do not already exist in their behavioral repertoire—and have extensive behavioral traditions that range from tool-use to social and communicative conventions (van Schaik et al. 2003; Whiten et al. 1996, 1999). Apes' unique imitative abilities may allow them to infer a wide variety of rules by observation including behavioral characteristics such as reputation. For instance, chimpanzees respond differently to humans whom they observe behaving as unwilling versus unable helpers (Call et al. 2004), and to those who intentionally rather than accidentally fail to give them a food reward (Call and Tomasello 1998; Povinelli et al. 1998). In addition, Melis and colleagues (2006) have shown that chimpanzees choose to recruit the best collaborators in a cooperative task where two chimpanzees must work in tandem to secure reinforcement. The sophisticated social skills of chimpanzees suggest that they are likely to possess a system for forming reputation judgments that is likely to be a part of the primate imitation faculty (Subiaul 2007).

This data indirectly bears upon the question of whether primates can infer by observation various social rules pertaining to behavioral attributes and can make reputation judgments. Yet, none of the naturalistic observations or experiments described earlier were designed explicitly to contrast the extent to which chimpanzees make accurate predictions about the future behaviors of others following the observation of indirect versus direct exchanges.

Experiment 1

We assessed whether chimpanzees could learn, after multiple observations of an exchange between three human experimenters, which of two potential human donors was likely to give a food reward when a request was made from a third human (i.e., the 'recipient'). During these exchanges, one experimenter, "generous donor," always offered food to a familiar animal trainer—"recipient"—and another experimenter, the "selfish donor," never gave food to the recipient. During testing, chimpanzees had the opportunity to request food by begging to one of these potential donors. If they are capable of making spontaneous and accurate predictions concerning the future actions of humans from prior observations, they should prefer to beg from the generous donor on the first trial. First trial responses are important because, after the first trial, chimpanzees can make direct reputation judgments, acquired through first person interactions with the human donors on earlier trials. Consequently, this procedure sought to directly assess the relative importance of direct versus indirect reputation judgments on the responses and preferences of chimpanzees.

Methods

Subjects

Seven chimpanzees, one male and six females ranging in age from 15.9 to 16.8 and housed in a single social group at the New Iberia Primate Research Center participated in this experiment. All of the chimpanzees had been living together for at least 13 years and had participated regularly in cognitive and behavioral tests since they were 3–4 years (for further details on the rearing history and testing environment of the chimpanzees, see Povinelli 2003). Studies were conducted between January 2006 and July 2006.

Procedure

Observation

Chimpanzees were individually tested inside an indoor testing room with a Lexan divider separating the chimpanzees from the human experimenters. Three evenly spaced holes in the divider (10 cm in diameter each) located 30.5 cm above the floor could be covered and uncovered selectively, allowing the chimpanzees to respond by gesturing through these response holes. Human experimenters sat on small gray benches 65 cm from the Lexan divider in front of these response holes facing the chimpanzee. The human recipient always stood equidistant between the two donors at the start of the trial. Two familiar humans played the role of recipient across an equal number of trials for each chimpanzee in randomly presented order within 8-trial blocks. Two unfamiliar humans played the roles of generous and selfish donors. One individual of the pair *always* played the role of a generous donor and the other individual *always* played the role of a selfish donor for individual chimpanzees; donors did not change roles for individual chimpanzees. However, the role of each individual was counterbalanced between chimpanzee subjects. The position of the generous and selfish donors was counterbalanced within 8-trial blocks in random order with the constraint that the generous/selfish donor did not appear in front of the same response hole for more than three consecutive trials.

All exchanges between the recipient(s) and the donors began once the chimpanzee touched a symbol in the middle of the Lexan wall and directly in front of the recipient that signified the chimpanzee's readiness to respond. This response forced the chimpanzee to face the experimenters and attend to the interactions. In the observation phase, chimpanzees observed a familiar human recipient gesture to two unfamiliar human donors, one who always gave food to the recipient ('generous donor') and another who always refused to do so (i.e., 'selfish donor') (see Fig. 1). On these

Fig. 1 Example of behavioral exchanges observed by chimpanzees in Experiments 1 and 2 involving a recipient and two donors. **a** Generous donor, who always gave food to the recipient; **b** selfish donor, who never gave food to the recipient



trials, each donor faced the chimpanzee and held a piece of fruit in the palm of their hand. When the recipient gestured to the generous donor, that donor placed the food in the recipient's hand. When the recipient gestured to the selfish donor, that donor abruptly turned 180° away from the recipient while huddling over the piece of food. Once the recipient gestured to the donor(s) present, a response barrier (that prevented chimpanzees from making a response) was lowered, uncovering a response hole located directly in front of the recipient. At this point, the chimpanzee was allowed to make a response—defined as breaking the plane of the response hole. The human recipient then placed the piece of food he had collected from the generous donor on the chimpanzee's outreached palm. Reinforcement consisted of various types of foods: quarter pieces of bananas, apples, plain vanilla wafers or cookies with peanut butter filling. Donors (generous and selfish) always held identical pieces of food to avoid any preference based on the perceived size or type of food reward. Throughout this observation phase chimpanzees could observe but could not receive food directly from the donors, thus limiting their observations of the donors to that of indirect, third-party exchanges.

On 24 trials, both donors were present. On an additional 24 trials, only one donor was present (12 trials with the selfish donor alone and 12 trials with the generous donor alone). Single donor trials were identical to trials described earlier, except that only one donor was present and no food was given to the chimpanzee following the observation.

Testing

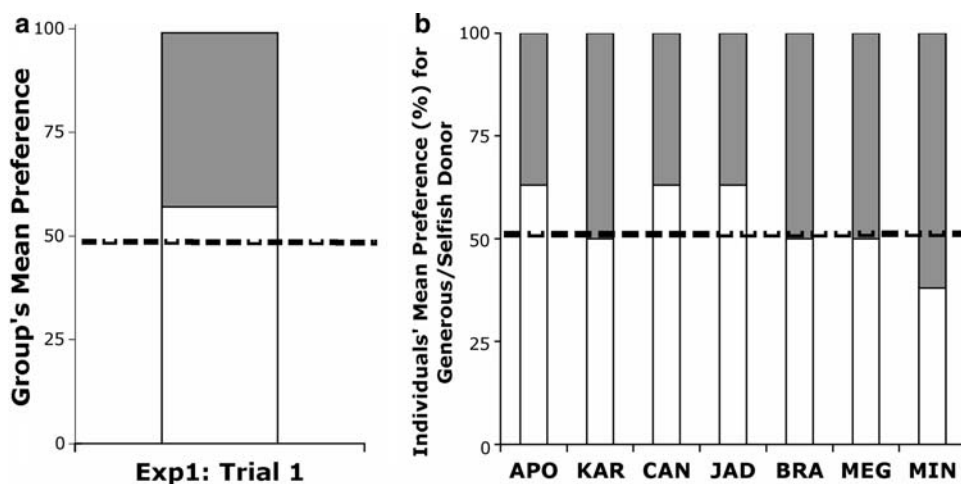
The procedures used during testing were the same as those used during observation except for the following: (a) Testing

consisted of eight 2-trial sessions to guarantee that all subjects would be tested on the same day; (b) both donors were always present; (c) once the recipient had gestured to each of the donors (and received food from the generous donor), he walked to the back of the test unit and stood behind an occluder without giving a piece of food to the chimpanzee; (d) both donors faced the chimpanzee and picked up a piece of food hidden underneath their benches. The selfish donor—who still had a piece of food—picked up only *one* piece of food; The generous donor—who had given his food to the recipient—picked up *two* pieces of food; (e) Once both donors visibly held two pieces of food in the palm of their hands and were facing the chimpanzee, the response barrier was lowered uncovering a response hole directly in front of each of the donors, allowing the chimpanzee to gesture through a hole to one of the two donors. If the chimpanzee gestured to the generous donor, that donor placed both pieces of food in the chimpanzee's hand. If the chimpanzee gestured to the selfish donor, that donor turned away from the chimpanzee while huddling over the food.

Data coding

All responses were recorded by two experimenters and archived on videotape. The chimpanzees' responses—defined as gesturing through a response hole to one of the two donors on the first opportunity to respond—were recorded by two human independent raters, the recipient and the observer who recorded the trials on video from a separate video control room and was unaware of the rationale of the study. The two observers were in near perfect agreement (Cohen's Kappa value of 0.98). A third party resolved all disagreements by observing the trials in question on video.

Fig. 2 Experiment 1. The *open bars* represent the preference for the generous donor. The *shaded bars* represent the preference for the selfish donor. **a** Groups' mean preferences on trial 1, **b** individual's mean preferences in the first 8 trials



Statistical analysis

First trial data was analyzed using non-parametric tests because the data was bivariate (selfish or generous). When first trial data was averaged across donor pairs, one-sample *t*-tests were used as these tests have more power for small samples and chimpanzees' averages represented continuous data. Sign tests were used when comparing two dichotomous variables within chimpanzees. Exact *P*-values were computed to account for the small sample size and the failure to meet assumptions of normality and homogeneity. Directional (one-tailed) tests were used when the a-priori expectation was that chimpanzees would show a preference for only the generous donors. The alpha level was set to $\alpha = 0.05$ for all tests.

Results

As can be seen in Fig. 2a, chimpanzees, as a group, chose the generous donor on average 57% (SD = 0.09) of the time on the very first trial; a result that was not statistically significant (Binomial Test, $n = 7$, $P = 0.25$). The group's mean preference for a generous donor across the first 8 trials of testing was not significant (One-Sample *t*-test, $t^6 = 1.0$, $P = 0.17$). Individual responses are summarized in Fig. 2b. There were no significant changes in performance after 16 trials; no individual showed a significant preference for the generous donor (all $n = 16$, APO: $P = 0.11$, KAR: $P = 0.11$, CAN: $P = 0.23$, JAD: $P = 0.40$, BRA: $P = 0.50$, MEG: $P = 0.50$, MIN: $P = 0.50$).

Discussion

There are several possible explanations for the failure of our chimpanzees to demonstrate a preference for the generous donor during testing. First, at a very low level, chim-

panzees may have great difficulty discriminating between two unfamiliar humans.³ Second, during the observation phase, chimpanzees always received a food reward from the human recipient, who was absent during the testing phase. This methodological feature of our study might have inadvertently resulted in chimpanzees focusing exclusively on the human recipient who always gave them a food reward, disregarding the interactions between the human actors. Third, chimpanzees may have failed to make a connection between the behaviors of human donors directed towards another human and the future behaviors of those same humans directed towards them. Failure to perceive a correspondence between third-party interactions involving humans and future behaviors toward chimpanzees does not preclude the ability of chimpanzees to observe and respond to such correspondences involving their own species, or to predict the behaviors of strange humans toward other humans. Fourth, chimpanzees may have failed to infer reputation after few observations, or after repeated observations involving few potential recipients. Even when humans form judgments of another's character, we often reserve judgment for future interactions until a long history of such behavior has been revealed. Perhaps repeated exposure to unfamiliar humans displaying consistent behavioral interactions is necessary for chimpanzees to make indirect reputation judgments. Finally, it is possible that chimpanzees require multiple, direct, first-party interactions with the donors to verify the accuracy of their reputation judgments. Potentially, given such an experience, the chimpanzees would subsequently display the ability to generalize from the familiar donors' behaviors to those of novel donors and thus utilize these reputation judgments to anticipate which of the two donors is likely to give them food.

³ After all, we, as humans, often have grave difficulty initially discriminating between members of other species, even chimpanzees.

Experiment 2

Having established that our chimpanzees did not spontaneously predict the future actions of humans, given the opportunity to indirectly observe exchanges, we now sought to determine whether chimpanzees could eventually learn to make this discrimination, given prolonged exposure to *direct* interactions with the same two donors. If they could, we then examined whether they could transfer what they had learned to novel pairs of unfamiliar donors, after observing them in a single *indirect* interaction. In other words, having learned which of the two familiar donors were likely to give them food, would chimpanzees generalize this social rule to make inferences about the responses of novel donors?

Methods

Subjects

The same seven chimpanzees who participated in Experiment 1 participated in Experiment 2 immediately after the completion of Experiment 1. The experiment took approximately 2 months to complete.

Procedure

Training

All seven chimpanzees received extensive training (Table 1) with the same two donors engaged in the same “generous” and “selfish” acts as in Experiment 1 (Fig. 1). Chimpanzees were continuously tested in blocks of eight “criterion” trials (criterion training) until they gestured to the familiar generous donor in seven out of eight trials for two consecutive 8-trial blocks. Left/right position of the donors was counterbalanced in blocks of eight trials.

Table 1 Training with familiar donors during Experiments 1 and 2

Subjects	Did subject meet criterion?	Number of trials to meet criterion	Total number of trials with familiar donors
APO	Yes	15	55
KAR	Yes	15	55
CAN	Yes	71	143
JAD	Yes	75	111
MEG ^a	Yes	47	89
BRA	No	N/A	180
MIN	No	N/A	177

^a Subject was excluded because she failed to maintain a preference for the familiar generous donor

Transfer testing

Four chimpanzees (APO, KAR, CAN and JAD) met this criterion and were advanced to transfer testing, during which they were presented with a series of novel pairs of human donors (henceforth, novel donor pairs), consisting of unfamiliar humans. Donor pairs were always matched for gender. The procedure was identical to that used in testing of Experiment 1, except that, during these transfer sessions, the chimpanzees observed the recipient’s (i.e., animal trainer) gesture to each of the familiar donors for a single observation trial and then were given the opportunity to beg to one of these two familiar donors themselves (criterion trial). If the chimpanzee gestured to the familiar generous donor in this criterion trial, they participated in a single 8-trial session involving a novel donor pair (one selfish, one generous). This procedure allowed us to directly compare chimpanzees’ preferences for the familiar generous donor with their preferences for the novel generous donor on the very first trial. We repeated this procedure four times for a total of five novel (transfer) pairs of strangers (10 strangers in total). Thus, the chimpanzees participated in five transfer testing sessions, each with novel donor pairs.

If a chimpanzee did not gesture to the familiar generous donor on the criterion trial the transfer session was aborted, and the chimpanzee was required to meet criterion once again before transfer testing was resumed. Chimpanzees were never presented with a novel donor pair unless they displayed a significant preference for the familiar generous donor. The position of the novel generous donors on the very first trial was counterbalanced across transfer sessions within chimpanzees. In addition, the position of the familiar and the novel generous donor on the first transfer trial was counterbalanced such that, in half of the first transfer trials (involving a novel donor pair), the position of the familiar donors (during the criterion trial) was the same as the position of the novel donors. On the remaining half of first transfer trials the positions of the familiar and the novel donors were reversed.

Data coding

All responses were recorded by two experimenters and archived on videotape. The chimpanzees’ responses—defined as gesturing through a response hole to one of the two donors on the first opportunity to respond—were recorded by two raters, the recipient and the observer who recorded the trials on video from a separate video control room. The two observers were in near perfect agreement (Cohen’s Kappa value of 0.98). Once again, a third party who was not a co-investigator resolved all disagreements by observing the trials in question on video.

Results

Training

After more than four blocks or 32 trials (range: 32–184 trials) with these familiar donors, four chimpanzees [Apollo (APO), Kara (KAR), Candy (CAN), and Jadine (JAD)] met the criterion and maintained a significant preference for the generous donor throughout the study. One chimpanzee, Megan (MEG), who initially responded to the generous donor in 7/8 trials for two consecutive blocks was excluded from Experiment 2 because she subsequently failed to show a consistent preference for the familiar generous donor on the first criterion trial of each session.

Transfer testing

As can be seen in Fig. 3a, chimpanzees significantly preferred to gesture to the novel generous donors on the very first trial (One-sample *t*-test, $t^3 = 3.46$, $P = 0.02$). Individuals' preferences on the first 8-trials of testing are summarized in Fig. 3b. An analysis of the chimpanzees' performance revealed that there was only a 10% difference between chimpanzees' preference for the novel generous donor (mean = 0.70, SD = 0.12) and the familiar donor in immediately preceding criterion trials (mean = 0.80, SD = 0). When average preference for all five novel generous donors on the first trial with those donors was computed for each chimpanzee and compared to average preference for the familiar generous donor on all five criterion trials the difference did not reach statistical significance (paired *t*-test, $t^3 = 1.7$, $P = 0.18$).

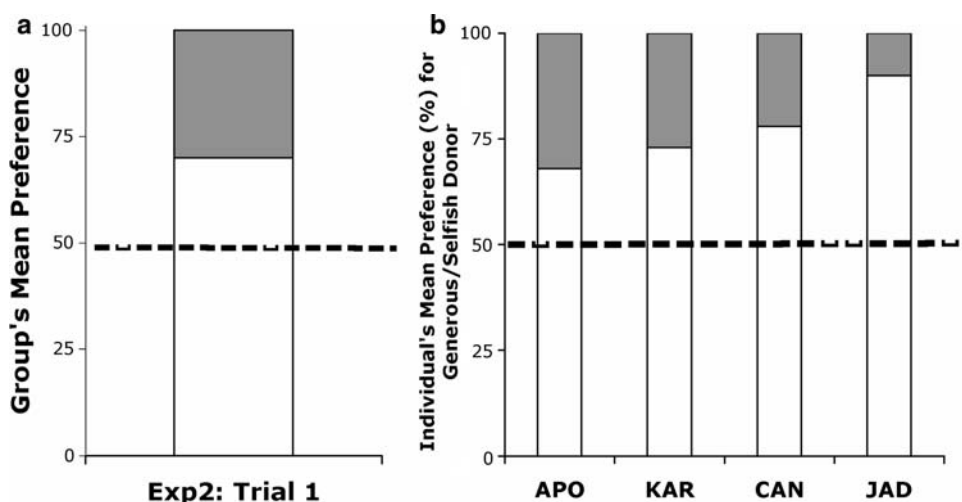
To assess whether this preference for generous donors emerged as a result of extended testing, we compared our chimpanzees' preferences in each 8-trial block with all five novel donor pairs and found no significant effect of testing block across chimpanzees. As a group, chimpanzees' mean

preference for the novel generous donors did not change from the first transfer session to the last [Friedman test, $X^2(6) = 2.91$, $P = 0.85$].

Discussion

Two important findings emerged from Experiment 2. First, after extended experience in which the chimpanzees were required to reach a criterion preference for the familiar generous donor, as a group they significantly preferred the novel generous donor on the very first trial, indicating that they based this preference on observations of third-party interactions. Second, for two of the chimpanzees (APO, KAR) this preference for novel generous donors did not differ numerically from that for the familiar generous donor. For the other two chimpanzees, (CAN, JAD), there was a 20% decrement in preference for the novel generous donor compared with their preference for the familiar generous donor. Some decline in performance on transfer tests is entirely expected, given that responding to familiar stimuli may become somewhat automatic, whereas responding to novel stimuli requires an additional inference that the consequences of responding will be identical to the consequences learned through direct experience with the familiar donors. The finding that group performance did not statistically differ between familiar and novel pairs, and did not numerically differ for half of our chimpanzees, is striking given that at the beginning of transfer testing the chimpanzees had interacted directly with the familiar donors for more than 30 trials (range 33–182) and not at all with the novel donors. The only knowledge that could guide their responses in the initial trials of transfer testing was derived from a single observation of an indirect, third-party interaction. This result indicates that chimpanzees can make equivalently valid predictions of future behaviors (or at the very least develop equivalent preferences for interacting with particular others) based on indirect as well as direct reputation judgments.

Fig. 3 Experiment 2. The *open bars* represent the preference for the generous donor. The *shaded bars* represent the preference for the selfish donor. **a** Groups' mean preferences on trial 1, **b** individual's mean preferences in the first 8 trials



Their ability to make use of information acquired indirectly is consistent with research in children demonstrating that direct (operant) and indirect (vicarious) reinforcements have equivalent reinforcing effects (Bandura 1977).

However, an alternative explanation for these results is that chimpanzees simply avoided the person who abruptly turned their back during the observation portion of the trial. In this case, they could have avoided approaching the side on which that individual sat, in effect, tracking the location where an aversive behavior occurred in observation, rather than using a reputation judgment to guide their responses. Another possibility is that chimpanzees may have been making judgments about the consequences following very specific, observable behaviors (e.g., no food given when experimenter turns away; food given when experimenter gives to human and does not turn away) rather than about reputations *per se*. However, if the chimpanzees were merely making a behavioristic association between observed behaviors and reward outcomes, it is surprising that some required over 100 trials with familiar donors to reach criterion, and others did not meet criterion. Humans use patterns detected in the observed behaviors of others to draw inferences of underlying dispositions, which can then be used to predict the occurrence of similar behaviors in both similar and novel contexts. Thus, for humans, reputation judgments allow for flexible predictions of future behaviors and dispositions to be generalized from single or multiple observations with both familiar individuals and strangers (Maass et al. 2001; Winter and Uleman 1984). In effect, chimpanzees inferred that because these novel individuals ‘behaved’ as the familiar donors did, they should respond to these novel individuals in the same way that they learned to respond to the familiar individuals, to their advantage: rejecting the selfish donor and gesturing to the generous donor. Whether individuals additionally make attributions of unobservable dispositional states that underlie the target behaviors is not testable in the current study but is a matter of interest for future experiments. However, it was of importance to extend the findings in Experiment 2 to a different context, further separating the behaviors in observation and testing, which would require the chimpanzees to make a more abstract generalization, precluding a simple generalization of a behavioral rule learned during Experiments 1 and 2. Under such conditions, any transference is best explained by the generalization of a more abstract concept of ‘generous’ (or ‘gives food’), selfish (or ‘doesn’t give food’) or both.

Experiment 3

In a third experiment we sought to extend the results reported in Experiment 2 to a novel experimental context

using chimpanzee conspecifics rather than human experimenters as recipients of the human donors’ selfishness or generosity. To this end, the same four chimpanzees tested in Experiment 2 were given the opportunity to observe novel human donors interact directly with the other three conspecifics from their peer group (MEG, MIN, BRA). Using conspecific rather than human recipients might increase the attention and relevance that our chimpanzees attributed to the potential donor’s actions.

In addition, the procedures differed from those used in Experiments 1 and 2 in order to exclude the possibility that context effects or the use of behavioral rules could facilitate responses. Specifically, testing procedures for Experiment 3 differed from those used in Experiments 1 and 2 in the following ways. First, human donors wore distinctive t-shirts differing in both color and pattern; diminishing the possibility of confusion between the identities of donors (a potential confound in Experiment 1). Second, Experiment 3 consisted of an observation phase executed in an outdoor enclosure and a testing phase executed in the indoor testing unit; eliminating the possibility of tracking ‘aversive’ or ‘rewarding’ spatial locations. Third, for each novel donor pair, there was a single observation session consisting of 12 trials, two trials with each of the novel donors individually interacting with three chimpanzees (BRA, MEG, and MIN); making interactions between donors more ecologically valid. Fourth, the generous and selfish acts differed from those used in Experiments 1 and 2; eliminating the possibility of generalizing from previously learned ‘patterned behaviors’. Finally, when chimpanzees responded to the selfish donor, there was no response, rather than a potentially aversive 180° turn away from the chimpanzee, as was the case in the previous experiments; reducing the possibility of behavioral associations between the observation and testing phases.

Methods

Subjects

Only the four chimpanzees (APO, KAR, CAN, JAD) who passed the training phase and completed the testing phase of Experiment 2 participated in the current experiment, immediately following Experiment 2. Experiment 3 took approximately 2 months to complete.

Procedure

Observation

Over the course of 12 observation trials, each chimpanzee (APO, KAR, CAN and JAD) observed two unfamiliar human donors (a generous donor who extended a tray baited with food within reach of a recipient chimpanzee and

a selfish donor who lifted a baited tray above their head, away from the recipient chimpanzees' reach) in an adjacent outdoor cage. They observed a total of eight pairs of novel donors either give (generous) or refuse to give (selfish) food to three of their conspecifics (MIN, MEG, and BRA). Each chimpanzee observed each donor interact individually with each of the three conspecifics in their outdoor enclosures during six trials (36 total observations). Throughout observation, an experimenter (FS) recorded the observing chimpanzees' attention, defined here as a subjective measure of amount of time spent looking through the Lexan window in the direction of a human donor and a chimpanzee recipient. If the experimenter did not see the chimpanzee peer through the partition, they were given a score of 1 ("did not look at donor"). If chimpanzees looked at the donor briefly (<5 s), they were given a score of 2. If the chimpanzee looked at the donor from more than 5 s or on more than one occasion, they were given a score of 3. This measure was critical, as we did not train chimpanzees to attend to the third-party interactions. Consequently, chimpanzees were free to attend or to ignore the interactions in the adjacent chamber between their conspecifics and the novel human donors. Because the interactions in this experiment did not take place in the more confined testing area in which testing stimuli are typically presented, we could not guarantee the attention of our chimpanzees to the interactions as reliably as we could in Experiments 1 and 2. Thus, we recorded these admittedly "rough" measures of attention simply to validate that chimpanzees did observe the critical interactions. Table 2 summarizes each chimpanzee's mean attention during "selfish" trials, "generous" trials, and "overall" attention score throughout testing.

At the start of the observation phase, chimpanzees were placed in the outside enclosure connected to the testing unit, while one of the three recipient chimpanzees (BRA, MEG, MIN) was placed in the adjacent outside enclosure. The shuttle door separating the two outdoor enclosures was made of Lexan, allowing the observer chimpanzee to look into the adjacent enclosure. Both human donors stood out of view of the participating chimpanzees. For each observation, donors took turns interacting with one recipient chimpanzee at a time in the presence of the observing chimpanzee. The other recipient chimpanzees were in a separate enclosure.

Donors sat on a wooden stool located in front of the enclosure and held a white food tray (30 × 30 cm²) which was baited with a piece of food equivalent to a half portion. (A bowl of fruit was hidden underneath the bench.) The selfish donor never gave their food to the chimpanzee recipient and looked at the recipient for a total of 1 min. At approximately 3–5 s intervals they lifted a piece of food, placed it on the tray, and lifted the tray above their heads (out of the recipient's reach). The generous donor sat in front of the recipient and always extended their tray in the

Table 2 Chimpanzees' mean attention scores (SE) during 'selfish' and 'generous' trials as well as overall attention

	APO	KAR	CAN	JAD
Selfish				
1	1.333 (0.21)	1.333 (0.33)	1.000 (0)	2.000 (0.37)
2	2.167 (0.40)	1.167 (0.17)	1.500 (0.22)	2.167 (0.31)
3	2.333 (0.42)	1.167 (0.17)	1.000 (0)	2.167 (0.31)
4	1.833 (0.40)	1.000 (0)	1.000 (0)	2.333 (0.33)
5	1.333 (0.33)	1.333 (0.33)	1.333 (0.33)	2.500 (0.22)
6	1.000 (0)	1.000 (0)	1.000 (0)	2.000 (0.26)
7	<i>2.667 (0.33)</i>	<i>1.167 (0.17)</i>	<i>2.333 (0.33)</i>	<i>2.000 (0.45)</i>
8	<i>1.500 (0.22)</i>	<i>1.667 (0.33)</i>	<i>1.333 (0.21)</i>	<i>1.000 (0)</i>
Mean	1.667 (0.22)	1.167 (0.06)	1.139 (0.09)	2.194 (0.08)
Generous				
1	1.667 (0.34)	1.500 (0.34)	1.000 (0)	1.667 (0.33)
2	2.500 (0.34)	1.167 (0.17)	1.167 (0.17)	2.000 (0.37)
3	2.333 (0.42)	1.000 (0)	1.500 (0.34)	2.500 (0.22)
4	1.167 (0.17)	1.667 (0.33)	1.000 (0)	2.167 (0.40)
5	1.167 (0.17)	1.000 (0)	1.167 (0.17)	1.833 (0.40)
6	1.000 (0)	1.333 (0.33)	1.000 (0)	2.833 (0.17)
7	<i>3.000 (0)</i>	<i>1.167 (0.17)</i>	<i>2.500 (0.34)</i>	<i>2.667 (0.33)</i>
8	<i>2.167 (0.40)</i>	<i>2.000 (0.26)</i>	<i>1.667 (0.33)</i>	<i>2.000 (0)</i>
Mean	1.639 (0.26)	1.278 (0.11)	1.139 (0.08)	2.167 (0.18)
Overall				
1	1.50 (0.24)	1.42 (0.28)	1.00 (0)	1.83 (0.29)
2	2.33 (0.31)	1.17 (0.14)	1.33 (0.17)	2.08 (0.28)
3	2.33 (0.35)	1.08 (0.10)	1.25 (0.22)	2.33 (0.23)
4	1.50 (0.28)	1.33 (0.24)	1.00 (0)	2.25 (0.21)
5	1.25 (0.22)	1.17 (0.20)	1.25 (0.22)	2.17 (0.29)
6	1.00 (0)	1.17 (0.20)	1.00 (0)	2.42 (0.24)
7	<i>2.83 (0.20)</i>	<i>1.17 (0.14)</i>	<i>2.42 (0.28)</i>	<i>2.33 (0.35)</i>
8	<i>1.83 (0.29)</i>	<i>1.83 (0.25)</i>	<i>1.50 (0.24)</i>	<i>1.50 (0.29)</i>
Mean	1.653 (0.20)	1.222 (0.04)	1.139 (0.06)	2.181 (0.07)

Scores in italics represent sessions where experimenters attempted to increase subject's attention. These attention scores from these sessions are not included in the subject's mean

direction of the chimpanzee when the chimpanzee gestured to the donor, stood before them or whenever the chimpanzee stared at the food. The generous donor remained seated in front of the recipient and continuously gave her food for a total of 1 min. For half of the novel pairs, the generous donor interacted with the recipient first, followed by the selfish donor. The order of interaction was reversed for the other half of the novel donor pairs. Thus, order was counterbalanced across novel donor pairs within chimpanzees and counterbalanced across chimpanzees for each donor pair ($n = 8$ novel donor pairs). The same two novel donors were used within sessions and within a given testing day. The roles of each novel donor were stable and did not change within sessions or across chimpanzees.

One of the animal trainers was in charge of transferring the recipient chimpanzees into and out of the outdoor enclosures. The outdoor video recorder documented the amount of time that the donors spent in the presence of a recipient chimpanzee and indicated to the donors when the trial was complete. A second experimenter judged whether the observer chimpanzee had witnessed any of the exchanges. Ratings were assigned as described earlier.

During sessions 7 and 8, when the observer chimpanzee's attention had been frequently judged as 1 (i.e., not looking) in the preceding session (see Table 2), the animal caretaker attempted to increase the chimpanzee's motivation to look in the direction of the donors and recipient chimpanzees by holding a piece of food while standing immediately behind each of the novel donors. This was done to ensure that chimpanzees at least had the opportunity to see the critical exchange on which to base the possible reputation judgment. Chimpanzees were variably reinforced for looking through the window in between novel donor pairs (selfish and generous) after the completion of a trial; Chimpanzees were never reinforced in the presence of a novel donor.

Testing

Following this observation period, the human donors proceeded to the indoor testing unit and sat in front of each response hole with a baited tray. However, no additional observations were provided. The chimpanzee was allowed to enter the testing unit and respond by gesturing to one of the two donors, who either gave them food or did not, depending on whether they were designated as generous or selfish donors, for six consecutive trials. Testing procedures were similar to those used for Experiments 1 and 2 with the exception that there was no observation period within the testing unit prior to a response by the chimpanzee. Chimpanzees entered the test unit, indicated readiness to respond and, if they gestured to the novel generous donor, they received reinforcement from the donor, but if they gestured to the selfish donor they did not.

There were a total of eight 6-trial sessions (one session per novel donor pair). Within each session, the donors were counterbalanced for position (on half of the trials each donor sat in front of the response hole on the chimpanzee's left). The chimpanzee had the opportunity to gesture to one of the two novel donors whom they had just observed interacting with a conspecific. Immediately following the last observation prior to each session, the two novel donors were seated inside the testing unit, facing the chimpanzee (without making eye-contact), who entered once they were in position. Donors held a tray with a food reward, equivalent to a half portion of a fruit, on their lap. The response barrier was in the raised position, covering the response holes, at the beginning

of each trial. An animal trainer was positioned at the back of the test unit behind the partition to open the shuttle door to begin a trial. The chimpanzees had 1 min to enter the test unit once the shuttle door was fully open. As soon as the chimpanzee entered the test unit, the shuttle door closed behind them. Chimpanzees had 1 min to initiate the trial and 1 min after the response barrier was lowered to make a response. As soon as the chimpanzee entered the test unit, and showed a readiness to respond, the response holes were opened. When the chimpanzee gestured to the generous donor, that donor moved their baited tray within the chimpanzee's reach. If the chimpanzee gestured to the selfish donor, that donor looked at the chimpanzee but did not move their tray, remaining still. A response was defined as gesturing to one of the two donors through the response hole.

Results

Across eight sessions the chimpanzees' mean preference for the novel generous donor on the very first trial was 53% (SD = 0.51). However, during the first four counterbalanced trials of testing (sessions 1–4), APO, KAR and CAN gestured to the novel generous donor 75% (SD = 0) of the time during the first half of testing (i.e., sessions 1–4). The lack of variance precluded the use of a one-sample *t*-test. Nevertheless, during the first half of Experiment 3 (pairs/sessions 1–4), APO, KAR, and CAN had a strong preference for the novel generous donor (mean = 0.75, SD = 0.45) on the very first trial; more than during the second half of Experiment 3 (pairs/sessions 5–8) (mean = 0.25, SD = 0.45, $Z = -1.36$, $P < 0.05$, Wilcoxon Test; Fig. 4). This pattern of response is consistent with the hypothesis that chimpanzees are capable of spontaneously making indirect reputation judgments.

However, these results revealed important differences between JAD and the other three chimpanzees. Unlike the

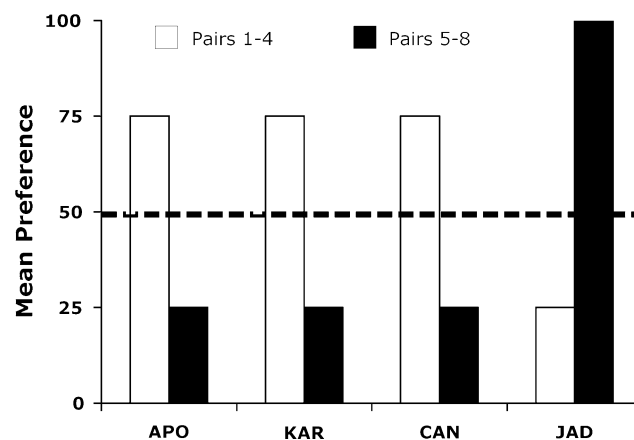


Fig. 4 Experiment 3. Individual chimpanzees' overall preference during testing and for the generous donor during the first half (white bars) and second half (black bars) of testing

other three chimpanzees, JAD developed a preference over time to the novel generous donor. Specifically, JAD gestured to the novel generous donor on 25% of the first four sessions, whereas, during the second half of testing she gestured to the novel generous donor 100% of the time. The other chimpanzees demonstrated the opposite pattern of response, showing spontaneous preferences for the novel generous donor starting in the first session. This pattern of performance suggests that although APO, KAR and CAN spontaneously inferred from the first session that the donor who gave food to a conspecific would give food to them, JAD did not. The fact that JAD's preference for the novel generous donor developed with successive testing, suggests the possibility that JAD learned during earlier sessions of testing who among the two donors was most likely to give her food based on their interactions with their conspecifics. Differences in performance between our chimpanzees cannot be readily explained by differences in perceived degree of attention to the interactions. JAD appeared equally attentive throughout testing, whereas CAN's attention appeared to increase and APO and KAR's attention appeared to decrease from the first to the second half of testing (see Table 2.)

Because we were also interested in potential differences in the way chimpanzees learned from indirect and direct experiences with others, we conducted sign tests comparing each chimpanzee's performance on the first three to the last three trials within each novel donor pair. These tests revealed no differences between the first and last half of testing, $Z = -0.82$, $P = 0.41$), indicating that direct experience with the novel donors did not notably alter the responses chosen following only indirect experience.

Discussion

APO, KAR and CAN spontaneously made accurate predictions regarding the novel donor's likelihood to offer food based on only indirect observations in a new testing context. JAD learned to make accurate predictions during the experiment. During the second half of testing, JAD's learning (like that of the other three chimpanzees during the first half of testing) is best explained by vicarious reinforcement (Bandura 1965), rather than by a traditional association between a specific response and a reward. Furthermore, chimpanzees in the present study privileged indirect information as much as direct information. Thus, the results of Experiment 3 provide further evidence that chimpanzees are just as capable of attributing reputation to strangers by eavesdropping on third-party exchanges, as they are following direct experience. Regardless of whether the results represent an accurate prediction of future behaviors (sharing vs. not sharing food), the learning of a (social) rule by observation (e.g., Subiaul et al. 2004) or an overall prefer-

ence for an individual who has behaved generously in the past, all explanations rest upon the ability to infer stability in an individual's character or behavior over time—an inference that underlies the ability to make reputation judgments.

General discussion

The performance of the chimpanzees in the present study is consistent with the work of other researchers who have reported that chimpanzees (1) recruit the best collaborators (Melis et al. 2006), (2) track social exchanges (Goodall 1986; Mitani and Watts 2001; Mitani et al. 2002; Wrangham 1999) and (3) actively monitor group politics (deWaal, 1982). Although social learning is widespread in the animal kingdom as evidenced by transitive social inference in fish (Grosenick et al. 2007) and birds (Amy et al. in press; Pazy-Miño et al. 2004), and evidence of 'image scoring' in cleaner fish (Bshary and Grutter 2006), the great apes are the only animal taxa that have evidenced novel motor imitation or imitation learning (Russon and Galdikas 1993; Stoinski et al. 2001; Whiten 1998; Whiten et al. 1996, 2004, 2007) and exhibit extensive behavioral traditions that include communicative and social conventions in addition to a varied tool 'culture' (van Schaik 2003; Whiten et al. 1999; but see Perry and Manson 2003) that resembles human cultures (Subiaul 2007). Because of these unique social learning capabilities, we suspect that chimpanzees, and perhaps other primates, are capable of abstract indirect reputation judgments. This conclusion is buttressed by chimpanzees' ability, as well as that of other primates, to learn many different types of rules by observation (Apes: Horner and Whiten 2005; Sugiyama 1994; Visalberghi et al. 1995; Monkeys: Subiaul et al. 2004; Voelkl and Huber 2007). However, it remains an open question whether the ability to make reputation judgments, as defined here, transfers to other tasks and other problems such as tasks that may elicit altruistic punishment when confronted with a 'selfish' donor (Fehr 2002) or, conversely, elicit prosocial behaviors when in the presence of a 'generous' donor. At the moment, such skills may represent a human cognitive specialization.

Economists have reported that reputation is a necessary feature of cooperative exchanges among humans (Seabright 2005). Given recent experimental evidence (e.g., Hirata and Fuwa 2007; Melis et al. 2006; Warneken and Tomasello 2006); the same may be true for chimpanzees.⁴ The results reported here, while preliminary, suggest that chimpanzees

⁴ However, see Jensen et al. (2006); Silk et al. (2005); Vonk et al. (2008) for results which suggest that chimpanzees are not prosocial and so unlikely to cooperate.

are capable of making indirect reputation judgments because (1) in Experiment 2, chimpanzees showed a spontaneous preference for the novel generous donor on the very first trial across five sessions, (2) the preference for the familiar generous donor did not differ from their preference for the novel generous donors despite the many direct experiences with the familiar donors, and (3) during Experiment 3, three of the four chimpanzees' performance was better in the first half than in the second half of sessions, a result that cannot be explained by learning/conditioning accounts, which would predict the reverse pattern. Although it is possible to interpret the findings of Experiments 1 and 2 via a more basic mechanism of learning to associate particular behaviors or spatial locations with reward, the same mechanism does not explain the results of Experiment 3 for two reasons: First, the behaviors were different from the 'patterned behaviors' chimpanzee may have learned to associate with rewards in Experiments 1 and 2. And, second, the observation and testing phases occurred in different locations, precluding any type of immediate feedback. But, while the performance of three of the four chimpanzees during the first half of testing was consistent with the results of Experiment 2, during the second half of testing there was no significant preference for the novel generous donor. This outcome limits any strong conclusion on whether or not chimpanzees are capable of making indirect and abstract reputation judgments as defined here and calls for caution when interpreting these results. Nevertheless, our hope is that these results both inspire and challenge comparative scientists to extend the findings reported here to a larger number of individuals in both naturalistic and laboratory settings to develop a more complete understanding of the mechanisms mediating indirect reputation judgments that are context- and domain-general in non-human populations.

Although the ability to predict future behavioral interactions based on indirect information may be limited to the hominoid clade, we suspect that the more general ability to infer social rules from observing the behavior of others is widespread in the primate order. Consequently, this ability may have served as a catalyst to the evolution of various uniquely human traits such as shared intentionality (Tomasello 1999), language (Dunbar 1986) and reasoning about mental states among other unobservables (Subiaul et al. 2006; Povinelli 2003, 2004; Vonk and Povinelli 2006).

Acknowledgments We would like to thank S. F. Brosnan, F. deWaal, E. Fehr, and D. J. Povinelli, for their comments on earlier versions of this manuscript. We would also like to thank A. Rideaux, L. Loston, T. LaVergne and J. Reaux as well as all the volunteers that served as donors for their assistance throughout this project. This research was supported in part by a Centennial Fellowship from the James S. McDonnell Foundation to DJP and a Research Award from the James

S. McDonnell Foundation to H.S. Terrace, J. Metcalfe and F. Subiaul. All studies were reviewed and approved by the Institutional Animal Care and Use Committee of the University of Louisiana, Lafayette.

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