Journal of Comparative Psychology
2007, Vol. 121, No. 2, 145–155

0735-7036/07/$12.00 DOI: 10.1037/0735-7036.121.2.145

Chimpanzee (*Pan troglodytes*) Anticipation of Food Return: Coping With Waiting Time in an Exchange Task

V. Dufour
Biomedical Primate Research Centre

M. Pelé
Université Louis Pasteur

E. H. M. Sterck
Biomedical Primate Research Centre and Utrecht University

B. Thierry
Université Louis Pasteur

Despite controversial expectations that animals achieve reciprocal altruism, it is unclear if nonhuman species possess the necessary cognitive abilities. For reciprocal altruism, individuals must anticipate the loss of a commodity and accept a delay before some return. The authors investigated the abilities of 5 chimpanzees (*Pan troglodytes*) to cope with increasing waiting duration in exchange tasks. Subjects had to keep a small cookie before returning it to a human partner to obtain a larger piece. For a piece 2, 4, or 8 times the size of the small piece, 3 of the 5 subjects waited for up to 4 min. For a piece 40 times larger, 4 of the 5 subjects waited up to 8 min. At long time lag, renouncement to wait occurred earlier than predicted by subjects' general waiting capacity, suggesting that the decision to wait was based on a trade-off between reward quantity and expected costs of the waiting duration. Chimpanzees could anticipate a delayed reward at a time scale of several minutes. If this reflects a cognitive limit in chimpanzees' anticipation capacity, reciprocal altruism by keeping track of costs and benefits over extended periods may be unlikely in chimpanzees.

Keywords: reciprocal altruism, delayed gratification, exchange, anticipation, chimpanzee

Reciprocal altruism has been proposed to be a mechanism that can support cooperation (Trivers, 1971). A donor who performs a costly behavior and a recipient who benefits from this behavior alternate their roles, producing delayed reciprocity. Although several studies have shown that unrelated animals may benefit from each other's behavior (Milinski, 1987; Packer, 1977; Seyfarth & Cheney, 1984; Wilkinson, 1984), research on the mechanisms involved is still scarce (Stevens, Cushman, & Hauser, 2005). In its simplest form, reciprocity is *symmetry based*. If individuals mostly direct positive behavior to close associates, reciprocal turn taking occurs in relation to the time spent in association (de Waal, 2000; de Waal & Luttrell, 1988). Another process, *attitudinal reciprocity*, has been proposed to explain some occurrences of food transfers between unrelated capuchin monkeys (*Cebus apella*). In this context, reciprocity would emerge from monkeys mirroring the behavior of the others (de Waal, 2000). The most demanding mechanism would require that partners take into account the costs and benefits of reciprocated behaviors. This *calculated reciprocity* was suggested to account for the exchanges of goods and services in chimpanzees (*Pan troglodytes*; Brosnan & de Waal, 2002). For instance, males may groom females to increase their chances of mating, or they may share meat according to the amount of help provided in hunting the prey (de Waal, 1989; Mitani & Watts, 2001), which would be in line with the reciprocal altruism hypothesis as originally formulated by Trivers (1971). Although some authors have maintained that chimpanzees keep a record of social credits and debits (Brosnan & de Waal, 2002), others argue that the correlations observed in the reciprocity of the positive behavior are not sufficient to draw conclusions about the calculation that would underlie this reciprocity (Hemelrijk, 1996).

In view of the lack of evidence for the occurrence of reciprocal altruism in nature, the cognitive prerequisites for the occurrence of calculated reciprocity have been reevaluated (Stevens & Hauser, 2005). Reciprocal altruism supposes estimating the values of goods, memorizing what has been given and received, anticipating the return of goods, and displaying a sufficient degree of self-control to accept in advance the loss of some goods. Both the ability to estimate the value of goods and memory capacities have been assessed in primates. Chimpanzees may select the largest quantity from two options when bananas had been accumulated in opaque containers over a 20-min period (Beran & Beran, 2004). A number of other experiments also point at an ability of capuchin monkeys and chimpanzees to recognize food quantity and quality; they may also attribute value to tokens and exchange goods with

---

V. Dufour, Ethology Research, Animal Science Department, Biomedical Primate Research Centre, Rijswijk, the Netherlands; M. Pelé and B. Thierry, Département d'Ecologie, Physiologie et Ethologie, Centre National pour la Recherche Scientifique, Université Louis Pasteur, Strasbourg, France; E. H. M. Sterck, Ethology Research, Animal Science Department, Biomedical Primate Research Centre, and Behavioral Biology, Utrecht University, Utrecht, the Netherlands.

We are grateful to Han de Vries for guidance and collaboration in statistical analysis of the results and to the keepers for their help and assistance in working with the chimpanzees.

Correspondence concerning this article should be addressed to V. Dufour, who is now at the Département d'Ecologie, Physiologie et Ethologie, UMR 7178, IPHC, Centre National pour la Recherche Scientifique, 23, rue Becquerel, 67087 Strasbourg Cedex 2, France. E-mail: valerie.dufour@c-strasbourg.fr

humans in bartering tasks (Brosnan & de Waal, 2004, 2005; Drapier, Chauvin, Dufour, Uhlrich, & Thierry, 2005; Hyatt & Hopkins, 1998; Lefebvre, 1982; Padoa-Schioppa, Jandolo, & Visalberghi, 2006; Sousa & Matsuzawa, 2001; Westergaard, Liv, Rocca, Cleveland, & Suomi, 1998, 2004). With regard to memory performances, a study showed that a chimpanzee remembered the location of food over 3 days (Menzel, 1999). In another investigation chimpanzees remembered the value of Arabic numerals over periods longer than 3 years (Beran, 2004). Melis, Hare, and Tomasello (2006) further reported that chimpanzees could choose the best partner between two, based on previous experience and success with this partner in a cooperative task. Thus, the cognitive prerequisite for calculated reciprocity such as accurate memory for food or partner quality has been described in nonhuman species.

Much less is known of the temporal dimension involved in anticipation and self-control, which are other capacities reciprocal altruism is thought to require. When bartering about food, for instance, individuals have both to anticipate an expected gain and to inhibit food consumption while waiting. In general, animals prefer immediacy of reward, as shown in studies on self-control. When given a choice between a small immediate reward and a larger delayed reward, pigeons (Mazur, 1987), domestic fowl (Abeyesinghe, Nicol, Hartnell, & Wathes, 2005), and rats (Richards, Mitchell, de Wit, & Seiden, 1997) opt for the small immediate reward when the delay surpasses a length of a few seconds. Long-tailed macaques (*Macaca fascicularis*; Tobin, Logue, Chelonis, Ackerman, & May, 1996), rhesus macaques (*M. mulatta*; Szalda-Petree, Craft, Martin, & Deditius-Island, 2004), marmosets (*Callithrix jacchus*), and tamarins (*Saguinus oedipus*; Stevens, Hallinan, & Hauser, 2005) reach an indifference point of 50% of preference for one or the other option for delays shorter than a half a minute with a similar paradigm. Other studies have explored the duration that subjects can delay gratification when they can choose the initial smaller reward at any time during the delay. Children, for example, can delay the retrieval of cookies for 5 min when the reward is visible and can wait for 18 min when the expected reward is not visible (Mischel, Shoda, & Rodriguez, 1989). In a variant of this delay-of-gratification task, chimpanzees could inhibit themselves to access preferred food for 3 to 5 min when the quantity to gain increased regularly with time (Beran, 2002; Beran, Savage-Rumbaugh, Pate, & Rumbaugh, 1999). However, in Beran's paradigm, chimpanzees did not experience costs other than refraining from accessing a favored food and they did not experience a loss. These aspects can be assessed in a context in which animals have to barter for food.

The ability to delay gratification in an exchange task was recently addressed in brown capuchin monkeys (Ramseyer, Pelé, Dufour, Chauvin, & Thierry, 2005). The subjects had to return a small piece of a cookie after a certain time lag to obtain a larger one. These capuchins did not wait for over 20 s before returning food (although 1 subject waited for 40 s in 25% of the trials), pointing at limited self-control abilities and tolerance to loss in this species. In view of chimpanzees' excellent performances in exchange and cognition tasks (Beran et al., 1999; de Waal, 1989; Hyatt & Hopkins, 1998; Mitani & Watts, 2001; Mulcahy & Call, 2006; Savage-Rumbaugh, Rumbaugh, & Boysen, 1978), we expect that chimpanzees will postpone returns on a longer time scale than capuchin monkeys. We lack evidence about chimpanzees' understanding of time when anticipating an expected valuable reward, however. To get an insight into their ability to calculate reciprocity, we need to investigate at which time scale they can anticipate the return of some food. The aim of the present study was to assess how long a chimpanzee can wait for varying amounts of returns and decide to engage in an exchange with a human partner.

In a variant of a delayed-gratification paradigm (Beran, 2002; Mischel et al., 1989), we offered 5 chimpanzees the opportunity to exchange small pieces of cookie for larger pieces. Upon receiving the initial cookie, the chimpanzee had to keep it for a given time before returning it to the human partner in order to obtain the larger one. The larger pieces of cookie remained visible from the chimpanzees throughout the trial. In a first phase, various amounts of reward were offered in exchange for the initial piece of cookie to assess the mean duration of waiting chimpanzees could reach. In a second phase, we offered a reward 40 times the size of the initial piece to assess for the maximum waiting duration.

Method

Subjects and Breeding Conditions

Five chimpanzees (*Pan troglodytes*) of the Biomedical Primate Research Centre's colony were tested: 2 male and 1 female chimpanzee age 15 years from Group A (Tho, Juu, and Wil); a 24-year-old male chimpanzee from Group B (Ton); and a pair- and, because of the natural death of his companion, temporarily single-housed 16-year-old male (Noa). He obtained as soon as possible a new partner. Groups A and B were composed of chimpanzees from the subspecies *Pan troglodytes verus*. The 5th subject, Noa, belonged to the subspecies *Pan troglodyte schweinfurthii*. Groups A and B lived in similar conditions and were housed in a 40-m^2 indoor main room connected with individual compartments. Noa was also housed in a 40-m^2 indoor room. The study was part of a program designed to provide daily enrichment for the chimpanzees. Two prerequisites were strictly followed during this study: Only subjects willing to participate were included, and the entire study was conducted using positive reinforcement only. Subjects showed a constant willingness to participate, indicating that the tasks indeed improved the well-being of the chimpanzees.

Training Procedure

Prior to the study, Groups A and B had been involved in a cognitive task aimed at assessing their planning abilities in an exchange procedure (Dufour & Sterck, 2007). As this task relied on the immediate exchange of one nonedible token for a favored food (a peanut), both groups were familiar with immediate exchange procedures. In the current task, however, subjects had to learn to barter one food for another. In a first training phase, they were given a small piece of lettuce that they had to give back to the partner, when instructed so, to obtain a small piece of cookie held in front of them in the partner's hand. The instruction given was the word *terug* (the Dutch equivalent for *back*) that was uttered by the partner, who also showed her empty hand, palm open, in front of the chimpanzee. The other hand was holding the reward. This phase was run until chimpanzees reached a criterion of 100% of success. This training required a mean of 3 sessions (range = 1 to 5) of 12 trials each per subject. In this phase, there was no delay between the moment when subjects were given the initial item and the moment they were instructed to give it back. In a second training phase, they were required to dispose of the food they gave back in a plastic cup, but only when the cup was presented in its normal orientation in front of them by the human partner. Reverting the cup never took more than 2 s, but as long as the cup was presented upside down, chimpanzees could not give the initial food item back—they received no reward if they dropped the food item too fast out or on top of the cup. If they did so, they were given back their initial item, and the partner stepped back and waited for 30 s before starting a new trial. The same procedure was followed if chimpanzees broke, nibbled, or just touched with their lips the initial item before returning it. For this second training phase, a first step consisted in training the chimpanzees to exchange a small piece of lettuce for a piece of cookie of 2 × 4 × 0.5 cm, until they reached 80% successful returns. This step required a mean of 3.2 sessions (range = 1 to 4) of 12 trials each per chimpanzee. A second step consisted in training them to exchange a piece of cookie measuring 1 × 2 × 0.5 cm to obtain a piece 4 times the size of the initial item (2 × 4 × 0.5 cm). This second step required a mean of 3.2 sessions (range = 2 to 5) of 12 trials each. Once they reached 80% success, they entered the testing phase. In total, the chimpanzees required a mean of 9.5 sessions (range = 7 to 12) of 12 trials each to successfully master the entire procedure.

Procedure for Phase 1

Chimpanzees were separated in their familiar individual compartment. The human partner (V. Dufour and M. Pelé) gave the initial piece of cookie (1 × 2 × 0.5 cm in size) to the chimpanzee and stood in front of the cage. The partner was holding in one hand the inverted plastic cup while showing in the other hand the exchange reward that was visible during the whole delay for the chimpanzee. After a given time period, the human reversed the cup and asked *terug* to the chimpanzee. If the latter dropped the cookie in the cup, the chimpanzee received the exchange reward. The chimpanzee was required to return the first item intact; whenever the chimpanzee consumed part of it, the human partner refused the exchange and stepped back. If the chimpanzees dropped the initial small item out of the compartment, it was given back to them. During the task, the human partner looked at the timer and remained still, avoiding the gaze of the chimpanzee. If ever a subject displayed signs of excitement, the human softly said *rustig* (the Dutch equivalent for *calm down*) to quiet the chimpanzees and avoid any attempt to engage in an interaction with the human. This instruction was familiar to the chimpanzees because it was used by keepers during daily routine, for example, during feeding and/or conflicts. All chimpanzees were tested by both V. Dufour and M. Pelé, except for Juu and Noa. When tested by M. Pelé, Noa only attempted to play and did not focus on the task. Therefore, Noa was tested by V. Dufour only, and M. Pelé tested Juu instead. Other chimpanzees were tested by both human partners. The two partners each worked at the same time with 1 chimpanzee from a different group. No other people were present in the room.

We ran the tests in a succession of stages, each stage corresponding to a specific time lag. All chimpanzees followed seven stages with increasing time lag: The first stage tested their capacity to wait for 2 s, the second stage for 7 s, and the following stages tested for 15 s, 30 s, 1 min, 2 min, and 4 min. Chimpanzees who succeeded in waiting at least once at 4 min were also tested at 8 min. Each stage was composed of four identical sessions of 12 consecutive trials. In each session, three possible sizes of cookie were presented four times, in a predetermined random order. In each trial, a chimpanzee was first given a small piece of cookie (1 × 2 × 0.5 cm), while the human partner held a cookie of a larger size—2 × 2 × 0.5 cm (2 times the initial item), 4 × 2 × 0.5 cm (4 times), or 4 × 4 × 0.5 cm (8 times)—that was visible during the whole trial. The experimenter waited for 30 s after the subject ended food consumption before starting another trial. To "inform" chimpanzees about the duration of the time lag, the human partner always maintained the cup inverted for the whole time lag in the first 3 trials of a session, even if the chimpanzee dropped or ate the cookie before the whole delay had elapsed. Failure to return the initial cookie, as well as its timing and the type of error, was recorded. Chimpanzees were tested daily during weekdays. For the first series with a relatively short time lag, it was possible to run two sessions per day and per chimpanzee, with a minimum delay of 1 hr between two sessions (mean delay between two sessions: 2.64 hr, range = 1 to 4 hr). With time lags longer than 1 min, however, only one session could be run per day and per chimpanzee. Trials were not filmed, so that no behavioral data other than success, error type, and timing of error were available for the analysis.

Procedure for Phase 2

The procedure was identical to that of Phase 1 except that chimpanzees were offered a reward 40 times the size of the initial food item: five pieces of cookie, each measuring 4 × 4 × 0.5 cm. Testing started at a 7-s time lag, and longer time lags were successively tested until the individual performance dropped to 0% of return. Because this reward represented a large quantity, sessions were reduced to 4 daily trials (2 in the morning, 2 in the afternoon), with each trial being followed by, minimally, a 15-min interval before the start of the following one. The last morning trial was separated from the 1st afternoon trial by a duration of 3 hr minimum. In the previous phase, testing long delays sometimes led to the extinction of the exchange behavior. At the end of Phase 1, some subjects (such as Ton or Tho) immediately ate the initial cookie without waiting when tested at the 2- or 4-min time lag. These time lags being the most recently tested, exchange behavior had to be refreshed before starting Phase 2. To do so, chimpanzees were asked to exchange a small piece of cookie for a cookie 4 times its size with a time lag of 2 s, and then of 7 s. This required a mean of five sessions of 12 trials per chimpanzee (two sessions minimum were given at each time lag; an additional session was given if the score of 80% successful return was not reached). Because all chimpanzees succeeded in delaying the reward for 7 s in Phase 1, this time lag was chosen as the starting delay in Phase 2.

Each subject was run in 12 trials for each time lag: 7 s, 15 s, 30 s, 1 min, 2 min, 4 min, 8 min, and 16 min. A trial ended as soon as the chimpanzee dropped, broke, or ate the cookie. If a chimpanzee succeeded in waiting at least once in the time lag, it was tested at the next longer time lag. Testing was performed by V. Dufour, who recorded, as in Phase 1, the success, timing, and type of error made by the chimpanzees. Trials were not videotaped.

Data Analysis

The results of this study were analyzed following three different steps. First, for both phases, we report the longest waiting duration observed in the chimpanzees. In addition, for Phase 1, we used a nonparametric Friedman analysis of variance (ANOVA), two-tailed test (Siegel & Castellan, 1988), to compare the percentages of successful returns for the sizes of 2, 4, and 8 times the size of the initial cookie, at each of the time lags separately. Average values are given as means and standard error of the mean. This analysis was not performed for Phase 2, because only one size of reward was tested (40 times the initial size).

Second, we analyzed for both phases the type of errors made. The various error types were analyzed by comparing their relative proportion of occurrence at each time lag using a Friedman ANOVA, two-tailed test (Siegel & Castellan, 1988).

Third, we conducted an analysis on the timing of errors, that is, the time at which chimpanzees gave up waiting before the end of the trial. We compared the distribution of observed error times with the distribution of times to be expected under the null hypothesis of a constant giving up chance during the trial. If the chimpanzees could anticipate from the start of the trial the length of the delay that remained to be waited for, they may have decided early on whether to wait or not. To test this hypothesis, we calculated the estimated (observed) probability to keep on waiting at each point of time that the chimpanzee gave up waiting by using the Kaplan Meier survival analysis. This analysis includes both the failure times and the times of successful return at the end of the trial (as censored data). In this analysis, the survival probability is expressed as percentage of chance to wait longer than the time already elapsed in the trial. Against this observed survival function, we calculated the expected (exponential) distribution of giving up times under the null hypothesis of a constant giving up chance. The two distributions, the expected and the observed one, were compared using an adjusted Kolmogorov–Smirnov test (Haccou & Meelis, 1992). A statistically significant difference between both distributions leads to the rejection of the null hypothesis that a subject has a constant chance to fail (to give up) independent of the time elapsed in the trial. We ran the analysis on Phase 1 by combining all cookie sizes: 2, 4, and 8 times the original size ($N = 48$). In Phase 2, only one size of reward was tested; therefore, the analysis was run on a smaller number of events ($N = 12$). For all analyses, the significance level was set at .05.

Results

Percentage of Success in Delaying Gratification

In Phase 1, the results showed that the chimpanzees failed to return the initial cookie at the time lag of 8 min but that they succeeded for shorter time lags (see Figure 1). At the 15-s time lag, 1 chimpanzee (Tho) stopped to exchange, then systematically consumed or discarded the initial item when tested at longer time lags. The success percentage of a 2nd chimpanzee (Ton) dropped to 0% at the 30-s time lag. The last 3 chimpanzees still delayed rewards at the 4-min time lag, albeit at very low rates. The longest time lag before renouncing was displayed by chimpanzee Wil, who waited once for 5 min before consuming the initial item.

The time lag sustained by the subjects did not exceed 4 min in this first phase of tests. It could be that the subjects estimated that the payoff was not worth the wait. In Phase 2, we dramatically increased the subjects' gains to 40 times the size of the initial cookie. The results showed that all subjects reached high levels of success at the 4-min time lag (see Figure 1). Performances decreased at 8 min, but 4 of the 5 chimpanzees still returned food at low rates for this delay. Of interest, the chimpanzee (Tho) who could not wait for more than 15 s in the previous phase was 1 of these subjects. None of the subjects reached the time lag of 16 min. It is worth mentioning, however, that Wil (after 14 consecutive failures) and Noa (after 4 consecutive failures) once waited for 11 min 48 s and 10 min 25 s, respectively, which were the longest waiting times observed in this study (see the Appendix).

In Phase 1, chimpanzees could receive three different amounts of cookie that were either 2, 4, or 8 times the size of the initial item. We observed that the cookie had an effect on the success rate at both the 1- and the 4-min time lag (see Figure 2). For these time lags, a Friedman ANOVA, two-tailed test (Siegel & Castellan, 1988), revealed that the percentage of return for larger cookies is significantly higher than for cookies of smaller size. (For the 1-min time lag, for the cookie size that was 2 times the initial size the percentage of return was 26.25%, for the cookie size that was 4 times the initial size it was 32.5%, and for the cookie size that was 8 times the initial size it was 38.75%, $p < .05$, $N = 5$. For the 4-min time lag, for the cookie size that was 2 times the initial size the percentage of return was 0%, for the cookie size that was 4 times the initial size it was 3.75%, and for the cookie size that was 8 times the initial size it was 13.75%, $p < .05$, $N = 5$.) Despite a

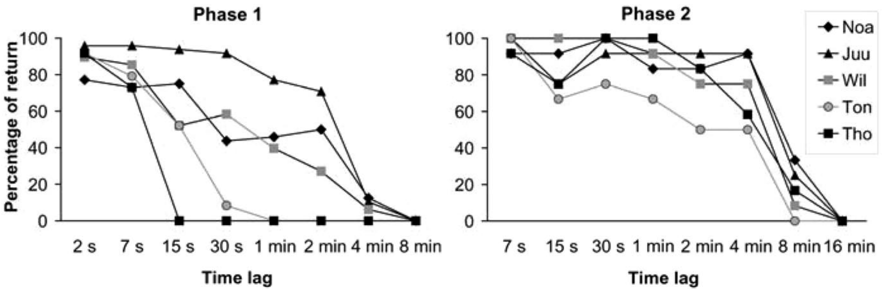

Figure 1. Percentage of successful returns for the 5 chimpanzees in Phase 1 (all sizes of cookies combined) at each time lag (from 2 s to 8 min; left panel). Percentage of successful returns for the 5 chimpanzees in Phase 2 when the reward was 40 times the size of the initial item at each time lag (from 7 s to 16 min; right panel).

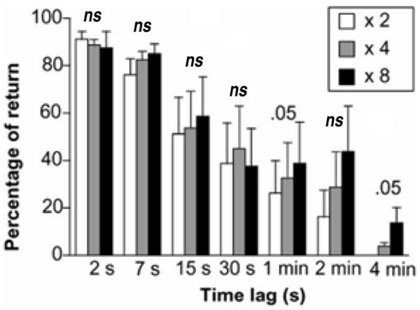

Figure 2. Percentage of successful returns for each size of cookie (2, 4, and 8 times the size of the original cookie) at each time lag (from 2 s to 4 min) in Phase 1. The percentage of return increased significantly with the size of the cookies for the time lag of 1 and 4 min (Friedman test for each time lag, $N = 5$, $^{*}p < .05$, $^{**}p < .01$). Error bars represent standard errors of the mean.

similar pattern for the 2-min time lag, the effect of size on the proportion of returns did not reach significance. (For the cookie size that was 2 times the initial size the percentage of return was 16.25%, for the cookie size that was 4 times the initial size it was 28.75%, for the cookie size that was 8 times the initial size it was 43.75%, *ns*, $N = 5$.) Together, these data indicate that chimpanzees match waits to expected gains at long time lags. No such effects were found for shorter time lags.

Error Type

An analysis of the type of error revealed four different categories of error: "Eat directly" the initial cookie (Ed), "Eat" the initial cookie after some time had elapsed (Et; this category includes error due to contact between the cookie and the lips of the subjects even if the subject further attempted to give the cookie back), "Drop, Break, or Give back" the initial cookie before the end of the delay (Db), and refuse to take the initial cookie (R). Figure 3 shows the mean of error type (on a maximum of 48 trials) per time lag observed in Phases 1 and 2. A Friedman ANOVA, two-tailed test (Siegel & Castellan, 1988), was used to compare the mean of error type occurring at each time lag. As the last type of error, R, occurred only four times in the course of Phase 1 (two times for Tho and 1 time for Noa and Ton), it was not included in the analysis. In Phase 1, no significant differences were observed between the means of error type at the 2-, 7-, 15-, and 30-s time lags (Friedman test; at 2 s, mean Et = 3.6, mean Ed = 0.6, mean Db = 1, *ns*; at 7s, mean Et = 4.2, mean Ed = 1.6, mean Db = 3.2, *ns*; at 15 s, mean Et = 7.8, mean Ed = 8.8, mean Db = 4.8, *ns*; at 30 s, mean Et = 6.6, mean Ed = 14.8, mean Db = 7, *ns*). At the 1-min time lag, there was a nonsignificant trend that error type Ed occurred more frequently than other error types (Friedman test; mean Et = 7.4, mean Ed = 21.8, mean Db = 3.2, $p < .07$, $df = 2$). At the 2- and 4-min time lags, error type Ed occurred significantly more often than other error types (Friedman test; at 2-min time lag, mean Et = 7.8, mean Ed = 24.2, mean Db = 1.8, $p < .05$, $df = 2$; at 4-min time lag, mean Et = 3.8, mean Ed = 39.8, mean Db = 1.6, $p < .01$, $df = 2$). For this phase, chimpanzees ate the initial piece of cookie at the start of the trial more often when they had to wait for long time lags (over 1 min) than when they had to wait for shorter time lags.

In Phase 2, error types encountered were Ed, Et, and Db (see Figure 3). None of the chimpanzees refused to take the initial item. A Friedman ANOVA, two-tailed test (Siegel & Castellan, 1988), conducted on the mean of occurrence for each error type reveals that error type Db was encountered significantly more often than other error types at the 2-min time lag and had a trend to be more frequent than other error types at the 4-min time lag (Friedman test; at 2 min, mean Et = 0.6, mean Ed = 0.2, mean Db = 2.2, $p < .05$, $df = 2$; at 4 min, mean Et = 0.4, mean Ed = 0.4, mean Db = 2.4, $p < .05$, $df = 2$). Contrary to Phase 1, chimpanzees' main errors in longer time lag were not caused by early renouncement but by failures to keep the initial cookie intact without dropping it until the end of the trial.

Timing of Error

The amount of food and the duration of the delay affected the waiting time of subjects. Chimpanzees might consider that a rather small food item is not worth waiting for. If they anticipated the time duration before they could exchange and receive the second cookie, they may have decided early on whether to wait or to give up. Such a hypothesis is suggested by the results of the errors analysis. In the current analysis, we compared the distribution of observed error times with the distribution of times to be expected under the null hypothesis of a constant giving up chance during the

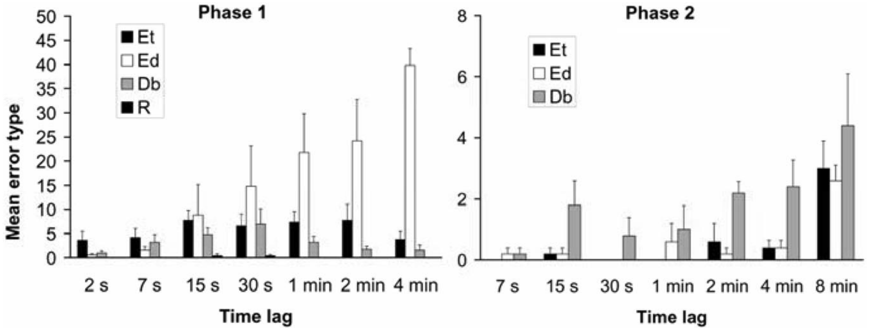

Figure 3. Mean occurrences and standard error of each error type for Phase 1 (left) and Phase 2 (right). Et = eat the initial item after waiting for some time; Ed = eat the initial item directly; Db = drop or break the initial item; R = refuse to take the initial item. Error bars represent standard errors of the mean.

trial. Figures 4 and 5 present for Phase 1 and 2, respectively, the difference in percentage between the observed and expected distribution at each tested time lag. A positive value indicates that the expected chance to keep on waiting is higher than the observed percentage of trials where chimpanzees waited longer than the time already elapsed. Therefore, it indicates that the chimpanzees renounced earlier than predicted, whereas a negative value indicates that chimpanzees waited longer than expected. In Phase 1, the adjusted Kolmogorov–Smirnov test was used to assess whether the difference between both distributions (expected and observed) was significant (see Table 1). The results show that at the 15-s time lag Noa and Tho renounced earlier than predicted (see Figure 4). These 2 chimpanzees also renounced earlier than expected when tested at the longer time lags. At the 30-s time lag, an additional chimpanzee, Ton, renounced significantly earlier than predicted, and this was also the case when he was tested at the 1-, 2-, and 4-min time lag. For the 2- and 4-min time lag, 5 chimpanzees renounced waiting earlier than expected. Renouncement for Tho at the 4-min time lag could not be assessed statistically because he ate the cookie from the start of the trials.

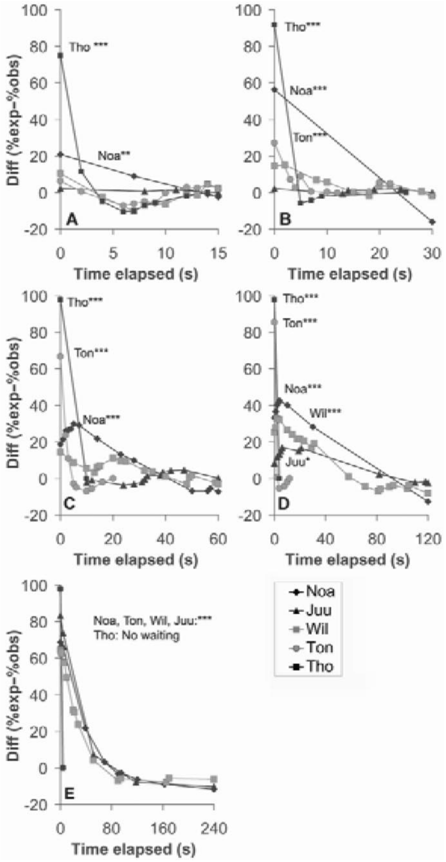

Figure 4. Phase 1: Difference between the distribution (in percentages) of expected and observed error time at each tested time lag. A: 15-s time lag; B: 30-s time lag; C: 1-min time lag; D: 2-min time lag; E: 4-min time lag. A positive value means that the expected chance to keep on waiting is higher than the actual percentage of trials where chimpanzees waited longer than the time already elapsed. It indicates that renouncement occurred earlier than predicted by a constant chance to give up through the trial. A negative value means that chimpanzees waited longer than expected, considering the time already elapsed in the trial. The statistics indicate whether the difference was statistically significant for a given chimpanzee as estimated by the adjusted Kolmogorov–Smirnov test. $^{*}p < .05$. $^{**}p < .01$. $^{***}p < .001$.

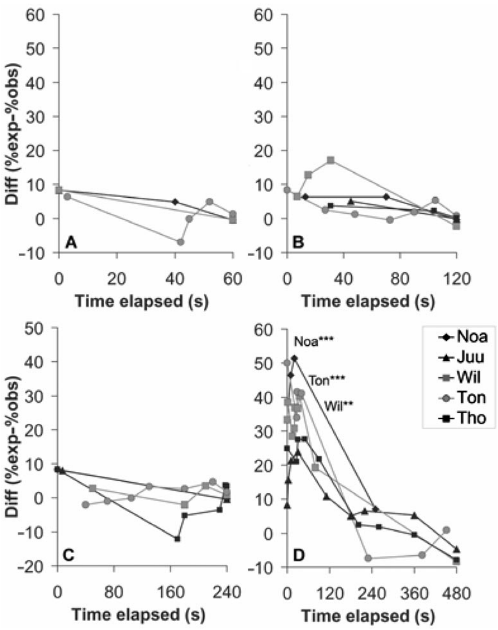

Figure 5. Phase 2: Difference between the distribution (in percentages) of expected and observed error time at each tested time lag. A: 1-min time lag; B: 2-min time lag; C: 4-min time lag; and D: 8-min time lag. Earlier time lags are not represented because of the very low percentage of failures. A positive value means that renouncement occurred earlier than predicted by a constant chance to give up through the trial. A negative value means that chimpanzees waited longer than expected considering the time already elapsed in the trial. The statistics indicate whether the difference was statistically significant for a given chimpanzee as estimated by the adjusted Kolmogorov–Smirnov test. $^{*}p < .05$. $^{**}p < .01$. $^{***}p < .001$.

In Phase 2, when the reward was 40 times the size of the initial item, we conducted a similar analysis. For all time lags between 15 s and 4 min, none of the chimpanzees renounced significantly differently from the expected error times (see Table 1; see Figure 5 for an illustration at the 1-, 2-, and 4-min time lags). At the 8-min time lag, however, Noa, Wil, and Ton renounced significantly earlier than expected.

The early renouncement suggests that chimpanzees estimated early whether the reward was worth waiting for and decided accordingly whether to wait or to give up. This effect was more pronounced in Phase 1, where cookies were of smaller size than in Phase 2.

Discussion

We found that chimpanzees can wait for up to 4 min when the delayed reward is 2 to 8 times the size of the original item and that they can wait for up to 8 min when the delayed reward is 40 times its size. By offering rewards 40 times the size of the initial item, we aimed at testing the maximum duration for which chimpanzees delayed reward. Indeed, this seemed to increase the chimpanzees' motivation in the task and thereby increased their capacity to wait.

Table 1

Maximum Values Obtained From the Kolmogorov–Smirnov Statistical Test Used To Compare the Expected and Observed Distribution of Giving Up Times

Subject–variable	15 s	30 s	1 min	2 min	4 min	8 min	16 min
Phase 1							
Noa	1.44^{**}	3.9^{***}	2.07^{***}	2.95^{***}	4.76^{***}	6.95^{***}	
Juu	0.14	0.14	0.32	1.17^{*}	5.77^{***}	6.78^{***}	
Wil	0.72	1.04	1.01	2.26^{***}	4.47^{***}	5.62^{***}	
Ton	0.49	1.88^{***}	4.61^{***}	5.91^{***}	NW	NT	
Tho	5.2^{***}	6.35^{***}	6.78^{***}	6.78^{***}	6.78^{***}	NT	
Mean no. of errors per subject	22.6	28.8	32.4	33.8	44.5	48	
Range	0–48	5–48	11–48	14–48	42–48	48	
Phase 2							
Noa	0.29	S	0.29	0.22	0.29	1.78^{***}	3.17^{***}
Juu	0.18	0.24	0.29	0.18	0.29	0.83	2.31^{***}
Wil	S	S	0.29	0.59	0.12	1.4^{**}	2.6^{***}
Ton	0.76	0.28	0.24	0.29	0.16	1.73^{***}	NT
Tho	0.31	S	S	0.13	0.42	0.96	0.74
Mean number of errors per subject	3	2	2.5	2.8	3	10	12
Range	1–5	1–3	2–4	1–6	1–6	8–12	12

Note. A statistically significant effect was observed when maximum values surpassed the critical values as follows. Phase 1, $N = 48$: Critical value = 1.07 for $p < .05$, critical value = 1.26 for $p < .01$, critical value = 1.45 for $p < .001$. Phase 2, $N = 12$: Critical value = 1.03 for $p < .05$, critical value = 1.22 for $p < .01$, critical value = 1.43 for $p < .001$. NW = no waiting; NT = not tested; S = 100% success. Mean no. of errors does not include NW individuals nor S individuals.

$^{*}p < .05$. $^{**}p < .01$. $^{***}p < .001$.

Brown capuchin monkeys tested using the same task were able to sustain 10 to 20 s to receive a larger reward, and only one monkey managed to wait for 40 s, that is, the next duration interval, to obtain a food amount 40 times the size of the initial one (Ramseyer et al., 2005). Similar tolerance to delay of gratification was reported in a tool-using task for this species (Evans & Westergaard, 2006). Therefore, chimpanzees were able to postpone a payoff for a duration 24 times longer than that measured in capuchin monkeys. This also contrasts with humans, for whom tolerance for delay of gratification can be measured in months or years (Rachlin, Raineri, & Cross, 1991). However, the delays observed make the chimpanzee results comparable to reports of a maximum tolerance for 5-min delays in children tested using a similar paradigm (Mischel et al., 1989).

Animals do not have at their disposal the conceptual and technological means that humans use to estimate time intervals or to cognitively travel in time (Roberts, 2002; Suddendorf & Corballis, 1997). Not only is their time understanding rather limited compared with that of humans, it is also strongly asymmetrical. Whatever their perception of temporal distance from the present, it is a common finding that animals can remember specific events for months or years. In comparison, their representation of the future appears considerably shorter. In experiments, rats anticipated a future reward at a time scale of about half an hour (Roberts, 2002). Monkeys planned travel routes of hundreds of meters, meaning some minutes in advance, when looking for food sites (*Macaca tonkeana*, Chauvin & Thierry, 2005; *Cebus apella,* Janson, 1998). Chimpanzees spontaneously saved tokens to use them in the near future, indicating that they anticipated a delayed opportunity to exchange them for food (Sousa & Matsuzawa, 2001). However, it was suggested that tokens may have become secondary reinforcers in the task. In the wild, chimpanzees walked hundreds of meters in dense vegetation to pick up and transport tools necessary to crack nuts open (Boesch & Boesch, 1984), and a bonobo (*Pan paniscus*) was reported to travel for 50 min before arriving at a sought location (Menzel, Savage-Rumbaugh, & Menzel, 2002). In these studies, it was suggested that the transport of tools might be bound to the present defined by their current motivational state (Suddendorf & Corballis, 1997). Silverberg, Widholm, Bresler, Fujita, and Anderson (1998) noted that chimpanzees exhibited *temporal myopia*—the inability to anticipate a future need—because they were unable to stock fruits in advance. However, in both common chimpanzees and bonobos species, animals trained to use symbols were able to announce intended action and travel destination plans (Menzel et al., 2002). More recently, orangutans and bonobos were shown to anticipate a night ahead a coming task and to select and transport the adequate tool so as to fulfill their future need (Mulcahy & Call, 2006). Such cases, however, do not prove that animals are aware of the time needed to reach their goals. Indeed, there was no need for them to keep a mental record of the time elapsed between the moment they anticipate some reward and the receipt of this reward, because there was no immediate and durable cost for the animals. In our study, chimpanzees could be said to incur an immediate cost, in that they had to refrain from eating the initial reward at increasing delays in anticipation of a larger, preferred reward.

Two different but nonexclusive types of processes may limit the duration of the maximum waiting periods in chimpanzees: the relative value of delay versus reward, and action inhibition during the test. On the one hand, relative valuation of the expected reward can help in deciding whether to wait or not. On the other hand, if the reward is considered worth the wait, the chimpanzee must still inhibit its consumption for as long as requested by the task.

Concerning the first process, future reward evaluation, at least two mechanisms are known to influence choice in animals: shortsighted rules and temporal discounting. First, many animals appear to favor immediate action (Stephens, 2002; Stevens, Rosati, Ross, & Hauser, 2005), dismissing any solution that requires an estimation of future benefits. The use of such shortsighted rules may explain why many animals prefer immediate small rewards over delayed large rewards. Because we found that chimpanzees matched their waiting time to the expected food amount, we may rule out the occurrence of shortsighted rules as an explanation for their limited waiting time. The second mechanism, temporal discounting, involves the subjective value of benefits reducing with delay (Mazur, 1987; Stevens, Hallinan, & Hauser, 2005). In the present study, chimpanzees sustained longer waiting times for larger returns, supporting a temporal discounting explanation. In choice tasks, pigeons, rats, tamarins, and marmosets also seemed to discount the value of delayed rewards (Baker & Rachlin, 2002; Mazur, 1987; Richards et al., 1997; Stevens, Hallinan, & Hauser, 2005), yet the length of the delay was measured in seconds, not minutes. Therefore, although the mechanism may be similar, the capacity to delay appears to be much more developed in chimpanzees than in the other tested species.

Differences between chimpanzees and other species may be linked to the second process, action inhibition during the test. Our results show that chimpanzees could suppress food consumption for 4 to 8 min. The current test, however, differed in one important aspect from other temporal discounting tests. The chimpanzees were not only requested to suppress their urges at the start of the task but also to inhibit their impulses during the whole trial in order to bridge the time interval between decision to wait and the receipt of the reward (Ramseyer et al., 2005). If they failed late in the trial, they received no more reward than if they failed at the start of the trial. This suggests that the current task was more difficult than choice tasks such as reverse-delayed reward contingency tasks (Mazur, 1987). In the reverse-delayed reward contingency task, the decision to wait for a larger reward or to eat the smallest available reward is made at the beginning of the trial. An animal cannot opt for the alternative option during the delay. In addition, there is no need to keep track of the elapsed time because a decision, once made, is always rewarded accordingly. Chimpanzees tested in a reverse-delayed reward contingency task may therefore tolerate longer delay than in our task.

Action inhibition has been suggested to provide “free” time to discriminate between options and improve decision making (Stephens, 2002). We further investigated the mechanisms behind decision making by examining chimpanzees’ giving up times. If chimpanzees assessed the cost of the combined effect of delay and exchange reward size, they might make the decision to consume the initial reward early in the trial. We showed that chimpanzees’ failure time occurred earlier than would be expected if chimpanzees exhibited a constant rate of giving up. This suggests that chimpanzees anticipated the duration of the delay in combination with the size of the exchange reward and reversed their preference to the smaller immediate reward. The alternative, lower level explanation only implies associative learning. The delay would have caused a reduction in the association between the initial choice and the exchange reward, resulting in an extinction of the exchange behavior. This interpretation could be supported by the behavior of Tho in Phase 2 because Tho gradually stopped waiting for longer delays. The behavior of the other 4 chimpanzees, however, was not consistent with this interpretation. Although these subjects consumed the small immediate reward in a number of consecutive trials, seemingly indicating the extinction of the waiting behavior, they subsequently waited again for a long delay to obtain the exchange reward (see the Appendix). Therefore, our data suggest that chimpanzees anticipate the duration of the delay to a reward and may be able to decide at the beginning of a trial whether to opt for the small immediate reward or wait for the larger one.

Despite the small number of subjects, the present findings have important implications for the occurrence of delayed reciprocity in animals. Our study indicates that chimpanzees are not exclusively bound to the present because they appeared to anticipate the duration of the delay before exchange. Although our results do not directly support the hypothesis of mental time travel in animals (Suddendorf & Corballis, 1997) because chimpanzees were working for a current goal from the start of the trials, the capacity to accept some cost in the present (waiting and controlling the impulse to eat food) according to future consequences opens the possibility for chimpanzees to make use of calculated reciprocity. Our results are also consistent with the recent conclusions of Mulcahy and Call (2006), who reported planning capacities in bonobos and orangutans.

Despite the fact that a delay of more than 8 min in our experimental setting is quite long in terms of abilities demonstrated by other animals, it still constitutes a rather limited time window. Our results conflict with expectations that chimpanzees exchange food for mating or support in coalitions on a long-term basis by using calculated reciprocity (de Waal, 1989; Mitani & Watts, 2001; Stanford, Wallis, Matama, & Goodall, 1994) or that they can plan social strategies and predict their eventual outcome several weeks or months in advance (de Waal, 1982; Nishida, 1983). It might be that food-related tasks are not an optimal choice for assessing mechanisms of reciprocal altruism. Recent studies on chimpanzees have failed to show altruistic or other-regarding behavior toward conspecifics in food-acquisition situations (Jensen, Hare, Call, & Tomasello, 2006; Silk et al., 2005) but revealed other-regarding behavior in nonfood situations (Warneken & Tomasello, 2006). Similar effects might reduce the delay to reward in food-related tasks. The current results suggest that chimpanzee anticipation of a loss is restricted to a time scale counted in minutes, which would preclude the occurrence of long-term, calculated reciprocal altruism. Future studies should test whether delayed exchanges using variable associated costs or non-food-related items may provide different time windows into the future.

References

Abeyesinghe, S. M., Nicol, C. J., Hartnell, S. J., & Wathes, C. M. (2005). Can domestic fowl, *Gallus gallus domesticus,* show self-control? *Animal Behaviour, 70,* 1–11.

Baker, F., & Rachlin, H. (2002). Self-control by pigeons in the prisoner’s dilemma. *Psychonomic Bulletin & Review, 9,* 482–488.

Beran, M. J. (2002). Maintenance of self-imposed delay of gratification by four chimpanzees (*Pan troglodytes*) and an orangutan (*Pongo pygmaeus*). *Journal of General Psychology, 129,* 49–66.

Beran, M. J. (2004). Long-term retention of differential values of Arabic numerals by chimpanzees (*Pan troglodytes*). *Animal Cognition, 7,* 86–92.

Beran, M. J., & Beran, M. M. (2004). Chimpanzees remember the results of one-by-one addition of food items to sets over extended time periods. *Psychological Science, 15,* 94–99.

Beran, M. J., Savage-Rumbaugh, E. S., Pate, J. L., & Rumbaugh, D. M. (1999). Delay of gratification in chimpanzees (*Pan troglodytes*). *Developmental Psychobiology, 34,* 119–127.

Boesch, C., & Boesch, H. (1984). Mental map in wild chimpanzees: An analysis of hammer transports for nut cracking. *Primates, 25,* 160–170.

Brosnan, S. F., & de Waal, F. B. M. (2002). A proximate perspective on reciprocal altruism. *Human Nature, 13,* 129–152.

Brosnan, S. F., & de Waal, F. B. M. (2004). A concept of value during experimental exchange in brown capuchin monkeys, *Cebus apella. Folia Primatologica, 75,* 317–330.

Brosnan, S. F., & de Waal, F. B. M. (2005). Responses to a simple barter task in chimpanzees, *Pan troglodytes. Primates, 46,* 173–182.

Chauvin, C., & Thierry, B. (2005). Tonkean macaques orient their food search from olfactory cues conveyed by group mates. *Ethology, 111,* 1–10.

de Waal, F. B. M. (1982). *Chimpanzee politics.* London: Jonathan Cape.

de Waal, F. B. M. (1989). *Peacemaking among primates.* Cambridge, MA: Harvard University Press.

de Waal, F. B. M. (2000). Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behaviour, 60,* 253–261.

de Waal, F. B. M., & Luttrell, L. M. (1988). Mechanism of social reciprocity in three primates species: Symmetrical relationship characteristics or cognition? *Ethology and Sociobiology, 9,* 101–118.

Drapier, M., Chauvin, C., Dufour, V., Uhlrich, P., & Thierry, B. (2005). Food exchange with humans in brown capuchin monkeys. *Primates, 46,* 241–248.

Dufour, V., & Sterck, E. H. M. (2007). *Planning for an exchange task in chimpanzees (Pan troglodytes).* Unpublished manuscript.

Evans, T. A., & Westergaard, G. C. (2006). Self-control and tool use in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology, 2,* 163–166.

Haccou, P., & Meelis, E. (1992). *Statistical analysis of behavioural data.* Oxford, England: Oxford University Press.

Hemelrijk, C. K. (1996). Reciprocation in apes: From complex cognition to self-structuring. In W. C. McGrew, L. F. Marchand, & T. Nishida (Eds.), *Great ape societies* (pp. 185–195). Cambridge, England: Cambridge University Press.

Hyatt, C. W., & Hopkins, W. D. (1998). Interspecies object exchange: Bartering in apes? *Behavioural Processes, 42,* 177–187.

Janson, C. H. (1998). Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella. Animal Behaviour, 55,* 1229–1243.

Jensen, K., Hare, B., Call, J., & Tomasello, M. (2006). What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proceedings of the Royal Society of London, B, 273,* 1013–1021.

Lefebvre, L. (1982). Food exchange strategies in an infant chimpanzee. *Journal of Human Evolution, 11,* 195–204.

Mazur, J. E. (1987). An adjusting procedure for studying delayed reinforcement: The effects of delay and intervening events on reinforcement value. In M. L. Commons, J. E. Mazur, J. A. Nevin, & H. Rachlin (Eds.), *Quantitative analyses of behavior* (Vol. 5, pp. 55–73). Hillsdale, NJ: Erlbaum.

Melis, A. P., Hare, B., & Tomasello, M. (2006, March 3). Chimpanzees recruit the best collaborators. *Science, 311,* 1297–1300.

Menzel, C. R. (1999). Unprompted recall and reporting of hidden objects by a chimpanzee (*Pan troglodytes*) after extended delays. *Journal of Comparative Psychology, 113,* 426–434.

Menzel, C. R., Savage-Rumbaugh, S. E., & Menzel, E. W. (2002). Bonobo (*Pan paniscus*) spatial memory and communication in a 20-hectare forest. *International Journal of Primatology, 3,* 601–619.

Milinski, M. (1987, January 29). Tit for tat and the evolution of cooperation in sticklebacks. *Nature, 325,* 433–435.

Mischel, W., Shoda, Y., & Rodriguez, M. L. (1989, May 26). Delay of gratification in children. *Science, 244,* 933–938.

Mitani, J. C., & Watts, D. P. (2001). Why do chimpanzees hunt and share meat? *Animal Behaviour, 61,* 915–924.

Mulcahy, N. J., & Call, J. (2006, May 19). Apes save tools for future use. *Science, 312,* 1038–1040.

Nishida, T. (1983). Alpha status and agonistic alliance in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Primates, 24,* 318–336.

Packer, C. (1977). *Reciprocal altruism in Papio anubis. Nature, 265,* 441–443.

Padoa-Schioppa, C., Jandolo, L., & Visalberghi, E. (2006). Multi-stage mental process for economic choice in capuchins. *Cognition, 99,* B1–B13.

Rachlin, H., Raineri, A., & Cross, D. (1991). Subjective probability and delay. *Journal of Experimental Analysis of Behavior, 55,* 233–244.

Ramseyer, A., Pelé, M., Dufour, V., Chauvin, C., & Thierry, B. (2005). The temporal limits of reciprocity in brown capuchin monkeys. *Proceedings of the Royal Society of London, B, 273,* 179–184.

Richards, J. B., Mitchell, S. H., de Wit, H., & Seiden, L. S. (1997). Determination of discount functions in rats with an adjusting-amount procedure. *Journal of Experimental Analysis of Behavior, 67,* 353–366.

Roberts, W. A. (2002). Are animals stuck in time? *Psychological Bulletin, 128,* 473–489.

Savage-Rumbaugh, E. S., Rumbaugh, D., & Boysen, S. (1978). Linguistically mediated tool use and exchange by chimpanzees (*Pan troglodytes*). *Behavioral and Brain Sciences, 4,* 539–554.

Seyfarth, R. M., & Cheney, D. L. (1984, April 5). Grooming, alliances, and reciprocal altruism in vervet monkeys. *Nature, 308,* 541–543.

Siegel, S., & Castellan, J. N. (1988). *Non parametric statistics for the behavioral sciences.* New York: McGraw-Hill.

Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. F., et al. (2005). Chimpanzees are indifferent to the welfare of other group members. *Nature, 435,* 1357–1359.

Silverberg, A., Widholm, J. J., Bresler, D., Fujita, K., & Anderson, J. R. (1998). Natural choice in nonhuman primates. *Journal of Experimental Psychology: Animal Behavior Processes, 24,* 215–228.

Sousa, C., & Matsuzawa, T. (2001). The use of tokens as rewards and tools by chimpanzees (*Pan troglodytes*). *Animal Cognition, 4,* 213–221.

Stanford, C. B., Wallis, J., Matama, H., & Goodall, J. (1994). Patterns of predation by chimpanzees on red colobus monkeys in Gombe National Park, 1982–1991. *American Journal of Physical Anthropology, 94,* 213–228.

Stephens, D. W. (2002). Discrimination, discounting and impulsivity: A role for an informational constraint. *Philosophical Transactions of the Royal Society of London, B, 357,* 1527–1537.

Stevens, J. R., Cushman, F. A., & Hauser, M. D. (2005). Evolving the psychological mechanisms for cooperation. *Annual Review of Ecology and Systematics, 36,* 499–518.

Stevens, J. R. Hallinan, E. V., & Hauser, M. D. (2005). The ecology and evolution of patience in two New World monkeys. *Biological Letters, 1,* 223–226.

Stevens, J. R., & Hauser, M. D. (2005). Cooperative brains: Psychological constraints on the evolution of altruism. In S. Dehaene, J. R. Duhamel, G. Rizolatti, & M. D. Hauser (Eds.), *From monkey brain to human brain* (pp. 159–187). Cambridge, MA: MIT Press.

Stevens, J. R., Rosati, A. G., Ross, K. R., & Hauser, M. D. (2005). Will travel for food: Spatial discounting in two New World monkeys. *Current Biology, 15,* 1855–1860.

Suddendorf, T., & Corballis, M. C. (1997). Mental time travel and the evolution of the human mind. *Genetic, Social, and General Psychology Monographs, 123,* 133–167.

Szalda-Petree, A. D., Craft, B. B., Martin, L. M., & Deditius-Island, H. K. (2004). Self-control in rhesus macaques (*Macaca mulatta*): Controlling for differential stimulus exposure. *Perceptual and Motor Skills, 98,* 141–146.

Tobin, H., Logue, A. W., Chelonis, J. J., Ackerman, K. T., & May, J. G. (1996). Self-control in the monkey *Macaca fascicularis. Animal Learning and Behaviour, 24,* 168–174.

Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology, 46,* 35–57.

Warneken, F., & Tomasello, M. (2006, March 3). Altruistic helping in human infants and young chimpanzees. *Science, 311,* 1301–1303.

Westergaard, G. C., Liv, C., Rocca, A. M., Cleveland, A., & Suomi, S. J. (1998). Token-mediated tool-use by a tufted capuchin monkey (*Cebus apella*). *Animal Cognition, 1,* 101–106.

Westergaard, G. C., Liv, C., Rocca, A. M., Cleveland, A., & Suomi, S. J. (2004). Tufted capuchin (*Cebus apella*) attribute value to foods and tools during voluntary exchanges with humans. *Animal Cognition, 7,* 19–24.

Wilkinson, G. S. (1984). Reciprocal food sharing in the vampire bat. *Nature, 308,* 181–184.

Appendix

Waiting Duration per Chimpanzee in the Longest Time Lag in Phase 2

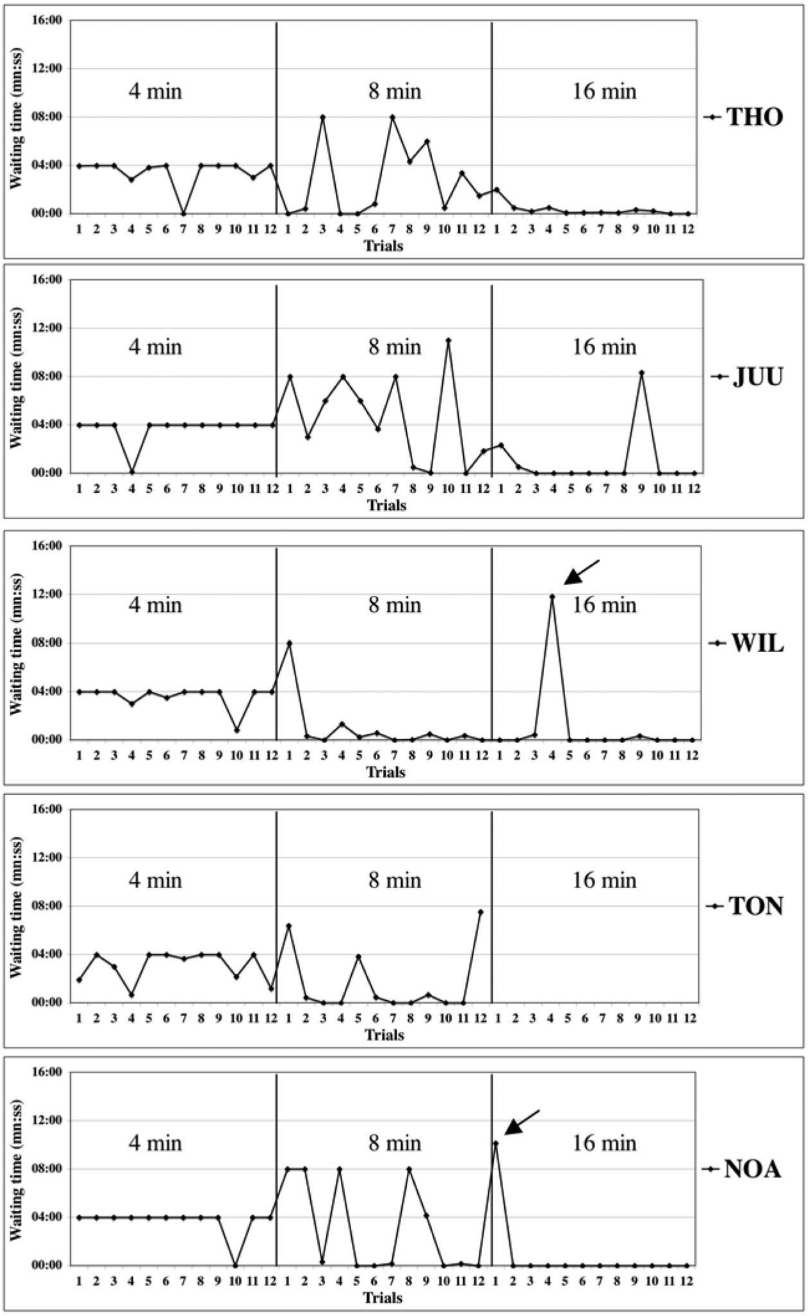

Figure A1. Individual waiting time per trial at 4, 8, and 16 min in chronological order. Of the chimpanzees, 4 of the 5 still attempted to wait for long durations despite previous consecutive failures. Wil (after 14 consecutive failures) and Noa (after 4 consecutive failures) waited for the longest duration observed in the study when tested at the 16-min time lag. They waited, respectively, for 11 min 48 s and 10 min 25 s (see arrows).

Received May 2, 2006
Revision received December 12, 2006
Accepted January 10, 2007 ■