Computerized Intertemporal Choice Task in Chimpanzees (*Pan troglodytes*) With/Without Postreward Delay

Yutaro Sato¹, Yutaka Sakai², and Satoshi Hirata¹ ¹ Wildlife Research Center, Kyoto University ² Brain Science Institute, Tamagawa University

In intertemporal choice (ITC) tasks, animals are presented with alternative choices between a smaller reward that becomes available sooner and a larger reward that becomes available later. To equate the duration of a trial across the 2 options, postreward delays (PRDs) are inserted after the delivery of the reward. Animals need to incorporate this to increase the long-term reward rate. However, recent studies suggest that they have difficulty understanding the contingency associated with PRDs. Previous research indicates that chimpanzees exhibit particularly great self-control in ITC tasks, but it remains unclear whether chimpanzees do so when considering PRDs. Therefore, we used touchscreen experiments to explore chimpanzee intertemporal preferences when trial duration was equated by a PRD as well as when the PRD was eliminated. The computerized setting was used to try to control delay length flexibly and precisely while reducing the impact of the interaction with human experimenters. Moreover, choice options were presented on touchscreens using symbolic cues. This may reduce the impact of seeing food rewards on making a choice (i.e., the animals' robust tendency to reach for the larger amount of food). In an ITC task in which the trial duration was equated, 4 chimpanzees preferred larger rewards but chose smaller rewards more often when the ratio of the reward amount was smaller. In an ITC task with no PRDs, 2 of 4 chimpanzees did switch their preference to smaller rewards and enhanced the reward rate although this result should be interpreted in light of some methodological limitations.

Keywords: choice behavior, self-control, impulsivity, intertemporal choice, chimpanzee

Humans (*Homo sapiens*) can deliberately consider the consequences of decisions, yet frequently make impulsive decisions, for instance, when influenced by affective or appetitive drives (Loewenstein, 1996, 2000). Intertemporal choice (ITC) entails situations in which the individual is faced with the choice between two alternatives: for example, a less preferred reward available sooner and a more preferred reward that becomes available later (Loewenstein, 1996; Santos & Rosati, 2015). For nonhuman animals (hereafter, animals), ITC situations involve various resources such as food patches, prey animals, or mating partners (Stevens, 2011; Stevens & Stephens, 2010). For example, among chimpanzees (*Pan troglodytes*), an individual may engage in cracking a hard nut shell using a stone hammer to obtain a preferable food item, rather than consuming a less preferred, but immediately accessible, item (Paglieri et al., 2013). Chimpanzees may also use a stick to fish termites from a specific mound or move on to a new mound that might be more abundant in termites (Stevens, 2011).

The ITC task has been used to study animal ITCs in laboratory experiments (Hayden, 2016). In this task, a subject is presented with two food reward options: typically, a smaller amount of reward that becomes available earlier (smaller-sooner) and a larger amount of reward that becomes available later (larger-later). Usually, the duration of an experimental trial is equalized across two choice alternatives by adding postreward delays (PRDs) after the reward delivery, which serve to adjust the intertrial intervals (ITIs) depending on the choice. In this task structure, the larger-later reward is optimal in terms of the long-term reward rate (i.e., the amount of reward acquired per unit of time) regardless of the delays to reward delivery. Thus, it appears to broadly be assumed that animals who prefer larger-later rewards to smaller-sooner ones are self-controlled, whereas those who choose smaller-sooner rewards are impulsive (but for a critical review, see Hayden, 2016). To make optimal choices, animals need to exert self-control abilities while understanding the contingencies associated with each option, such as reward amount, reward delay, and PRD.

However, several studies have suggested that animals generally have difficulty appropriately integrating temporal components other than reward delay (Goldshmidt et al., 1998; Lea, 1979; Mazur, 1989; Mazur et al., 1985; but see Smethells & Reilly, 2015). In particular, animals may not fully understand that the smaller-sooner reward involves a longer PRD than the larger-later reward when the trial duration is equated across two options (Hayden, 2016). This is in line with observations that several animal species exhibit a level of self-control that is best explained by maximization of the short-term reward rate, which is insensitive to PRD and ITI (i.e., reward amount divided by reward delay; starlings [Sturnus vulgaris]: Bateson & Kacelnik, 1996; blue jays [Cyanocitta cristata]: Stephens & Anderson, 2001; tamarins [Saguinus oedipus]: Stevens et al., 2005). Indeed, some studies have shown that animals are sensitive to PRD to some extent, but the sensitivity to PRD is much smaller than the sensitivity to the reward amount and delay (e.g., pigeons [Columba livia]: Hata & Saeki, 2018; Logue et al., 1985; rats [Rattus norvegicus]: Yamaguchi et al., 2015). If the difference in PRD between two options is ignored, the longterm reward rate obtained by choosing either option would be misestimated, which may be consistent with the hyperbolically discounted value derived from ITC behavior in many species (Hwang et al., 2009; Kirby & Marakovic', 1995; Mazur & Biondi, 2009). Previous studies have shown that rhesus monkeys (Macaca mulatta) increase self-control choices when the PRD is indicated by an explicit cue, suggesting that their impulsive choices may be partly driven by a failure to understand the PRD in the absence of any cues (Blanchard et al., 2013; Pearson et al., 2010). Moreover, Blanchard et al. (2013) reported that monkeys underestimate PRD length without explicit cues, suggesting that seemingly impulsive choices of animals in ITC tasks may partly be based on a rate maximization strategy with underestimation of the PRD. These findings illustrate the capacity of animals to learn PRD, especially when these elements are relatively salient, but in general, PRD may be much more challenging for animals to learn than the reward amount and delay (Stephens, 2002).

Great apes such as chimpanzees exhibit much more self-control in ITC tasks than other animal species (Stevens & Stephens, 2010). In Study 1 of Rosati et al. (2007), on average, chimpanzees and bonobos (Pan paniscus) waited for larger rewards (six slices of grape) with delays of 120 s and 70 s, respectively, pitted against smaller rewards (two slices of grape) delivered immediately. Surprisingly, a post hoc analysis indicated that chimpanzees showed even greater self-control than predicted by a long-term reward maximization model (Rosati et al., 2007). Moreover, chimpanzees outperformed human participants, which challenges the common view that humans have higher levels of self-control than nonhumans (Rosati et al., 2007; Study 2). In a follow-up study, Genty et al. (2012) examined the effect of PRD on ITC behavior of human participants under an experimental protocol similar to Study 2 of Rosati et al. (2007). Participants increased self-control choices when trial duration was equated by PRDs, compared with when the ITIs were fixed as in Study 2 of Rosati et al. (2007) (Genty et al., 2012; Experiment 2). This suggests that human choice behavior may shift toward the optimal strategy depending on the PRDs. This result is in accord with previous studies showing that human participants make seemingly impulsive choices without PRDs (Flora & Pavlik, 1992; Ito & Nakamura, 1998; Paglieri et al., 2015). Therefore, although chimpanzees seem able to show great self-control (Rosati et al., 2007), it remains unclear whether their self-control choices depend on PRD, as observed in human participants (Genty et al., 2012).

Furthermore, in the Rosati et al. (2007) study, a human experimenter offered a participant two arrays of visible food items and the participant indicated their choice by pointing to either option. Such a procedure may affect participants' behavior independent of their intertemporal preferences. First, it can be difficult for non- human animals to inhibit reaching for the larger array when faced with two arrays of visible foods (the "go for more" behavior or reversed-contingency effect: Beran et al., 2016; Boysen & Berntson, 1995; Boysen et al., 1996; Paglieri et al., 2013; Vlamings et al., 2006). As some researchers (Paglieri et al., 2015) have pointed out, this natural and strong tendency may increase spurious self- control choices in ITC tasks. For example, Experiment 1 of Genty et al. (2012) suggested that long-tailed macaques (*Macaca fascicularis*) choose the larger-later rewards more often when the

food rewards are visible than when they are masked. Addessi et al. (2014) examined ITC task performances of capuchin monkeys (Sapajus spp.), 3- and 4-year-old human children, and human adults using not only visible food items but also two types of symbolic cues: one consisting of a number of elements corresponding to the number of food rewards (i.e., low symbolic) and the other with no such quantitative correspondence with the food rewards (i.e., high symbolic) such as different kind of objects, illustrations, or numerals for monkeys, human children, and adults, respectively. Capuchin monkeys chose larger-later rewards more often when food rewards were presented than when low- or high- symbolic cues were presented. Human children also chose larger- later rewards more often when food rewards were presented than when high-symbolic cues were presented, although this difference was no longer observed when some of the same children were tested again ~ 2 years later (Pecora et al., 2020). Similarly, Labuschagne et al. (2017) suggested that 4-year-old human children seemed to choose larger-later rewards more often when rewards (stickers) were indicated by photographs of stickers than when rewards were indicated by symbolic cues depending on the amount of rewards (but note that Evans et al. [2012] reported a negligible or even an opposite effect of using symbols in accumulation tasks with chimpanzees and capuchin monkeys). Second, participant animals' behaviors may be modulated by their relationships or previous experiences with the human experimenters or with humans in general. A previous study suggested that in delay gratification tasks, bonobos are less willing to wait for delayed rewards when tested with an unreliable human experimenter (Stevens et al., 2011). Similarly, human children who experienced a human experimenter breaking promises exhibited less self-control than those who experienced the human experimenter keeping promises in an ITC task (Mahrer, 1956) and in a marshmallow task (Kidd et al., 2013). In addition, Michaelson et al. (2013) showed that in an ITC task, human adult participants chose the smaller-sooner rewards more often when choice alternatives were presented as if offered by a character perceived as untrustworthy. Those issues should be considered when designing ITC tasks, especially for those species that can develop relationships with humans, such as captive chimpanzees (e.g., Funkhouser et al., 2020). Previously Beran and Evans (2006) implemented a computerized setting and directly examined whether the presence of a human experimenter affects chimpanzee performances in accumulation tasks. Although they reported that the presence of a human experimenter did not affect chimpanzee behaviors, such a computerized experiment seems effective to reduce unexpected effects derived from methodological factors irrelevant for intertemporal preferences.

Here, we aimed to examine chimpanzees' performance in a computerized ITC task using touchscreen experiments. The food reward amounts in two options were indicated by a corresponding number of small red squares presented on the touchscreens. This setting may reduce the effect of the presence of visible real food items and human experimenters. The delays for the two rewards were determined randomly within a certain range rather than fixed at specific values (cf. Schweighofer et al., 2006; Tanaka et al., 2014). This enabled us to explore chimpanzee intertemporal preferences using a diverse combination of reward delays. Note that this setting could occasionally yield trials in which a larger reward was associated with an identical or even shorter delay than a smaller reward; thus, for the current study we described rewards simply as "larger/smaller" rather than "larger-later/smaller- sooner." In the first experiment, we used two patterns of reward amount combination to examine how the effect of reward delay on chimpanzee behaviors varied depending on the reward amount while maintaining chimpanzee motivation to participate in the experiments. Importantly, the trial duration was equated by the PRD across two options (hereafter, standard ITC task). Thus, would switch their choice to smaller rewards, thereby increasing the reward rate.

Method

Participants

Four female chimpanzees housed at Kumamoto Sanctuary, Wildlife Research Center, Kyoto University, participated in the study (13.8 ± 5.68 years old, $M \pm SD$; Table 1). These chimpanzees were well familiarized with cognitive experiments with touchscreens. Two other chimpanzees who had originally participated in experiments were excluded, as they failed to learn to discriminate between options associated with different reward amounts. Two of the participants (Mizuki and Hatsuka) had been reared by human caretakers while interacting with conspecific peers, as their biological mothers failed to raise them.

Chimpanzees usually spent the day in three outdoor enclosures connected to each other (300 m² in total). These enclosures were furnished with climbing structures such as wooden stages, hammocks, and ropes, creating three-dimensional complex environments where the chimpanzees could exercise and rest comfortably. They received a variety of foods, such as fresh fruit, vegetables, nuts, or monkey chow three times per day. Additionally, caretakers provided the chimpanzees with enrichment items to facilitate active foraging activities (e.g., juice feeders, small packages of food items) or for their comfort (e.g., pieces of burlap bags). The indoor enclosures, where they received the daily meal, were also furnished with wooden stages and hammocks. Chimpanzees could access water from taps in the indoor and outdoor enclosures whenever they wanted. They were never deprived of water or food for the experiments, and they participated in the study voluntarily. Animal husbandry and study protocols complied with the Guide for Animal Research Ethics provided by the Wildlife Research Center, Kyoto University (No. WRC-2018-KS006A).

Apparatus

Touchscreens and other devices were installed in an experimental booth, which was attached to an outdoor enclosure (see Figure 1). Chimpanzees could contact the touchscreens through an opening while they were in the outdoor enclosure. Six 17-in. LCD touchscreens (ET1790L/ET1739L, Touch Panel Systems K.K., Kanagawa, Japan) were placed in a row, 49 cm or 105 cm apart. The resolution was set at 1024 px X 768 px. This setting enabled all six chimpanzees in this group to engage in cognitive tasks in parallel. Each touchscreen was enclosed in a box made of polycarbonate panels. These boxes were mounted in metallic frames attached to the wall of the experimental booth. Chimpanzees accessed the boxes at the side of the outdoor enclosure. Each box had an opening of approximately 37 cm X 15 cm (or X 12 cm) at the bottom, which allowed chimpanzees to contact the touchscreen (the touchscreen surface was approximately 16 cm away from the opening) but prevented them from banging it aggressively. This box had small holes on the lateral side from which food rewards were delivered. We used 190 mg banana flavor precision pellets (Dustless Precision Pellets Primate Purified F0035, Bio-Serv, Flemington, NJ, United States) as food rewards. Food rewards were delivered using automated food dispensers (ENV-203-190IR/ ENV-203-190, Med Associates Inc., Fairfax, VT, United States). The dispensers were connected to a laptop computer via an I/O unit (DIO-8/8 [USB] GY, Contec, Osaka, Japan) and a switching power supply (S82J-0124D, Omron, Kyoto, Japan). Task presentation, detection of touch on the screens, and activation of the food dispensers were controlled by laptop computers (ProBook 4540s and Compag 6720s, HP Inc., Palo Alto, CA, United States; dynabook R732/F, Toshiba, Tokyo, Japan). The task was controlled by the programming software Microsoft Visual Basic 6.0 (Microsoft Corp., Redmond, WA, United States).

Procedure

We conducted experiments between 9 a.m. and 11 a.m., after chimpanzees had received morning meals consisting of fruits and vegetables roughly at 8:30 a.m. Data were collected from October 2018 to May 2019. When a chimpanzee settled in front of a touchscreen, an experimenter started the session by

activating the touchscreen. The basic trial design is illustrated in Figure 2. Chimpanzees started a trial by touching the start key (a green rectangle, 150 px X 150 px). Two option tables were then presented side by side (except for forced-choice trials). Each option table consisted of a white rectangle (400 px X 550 px) on which an array of red squares (40 px X 40 px) appeared. The number of red squares indicated the number of food pellets this option delivered. This array of red squares appeared at different heights to indicate the length of delay to reward delivery. The height was determined such that the reward with the longest delay in a given session was presented at the top of the white rectangle, and rewards with medium delays were presented at a height proportional to the longest delay in the session. The delays to reward delivery for the two options were determined to three decimal places independently of each other and randomly within certain ranges (see below) based on the Rnd function and the Randomize statement in Visual Basic 6.0. Chimpanzees selected either option by touching the white rectangle (or a red square on it; this function was added during prelearning phases). If chimpanzees failed to make a choice within 10 s from the start key press, the trial was over and an ITI of 1.5 s began. The selected rectangle remained on the screen and the unselected one disappeared; then, the delay to reward delivery started. Responses that were made in under 200 ms were excluded because they were considered too rapid for the chimpanzees to have fixated on both options and assessed them (Kano et al., 2011). During the delay to reward delivery, an animation of red squares falling to the bottom was displayed on the remaining rectangle. The duration of the animation corresponded to the length of the delay to reward delivery. The speed of the motion was identical throughout the study. When the delay had elapsed, the rectangle and red squares disappeared, a sound ("ding- dong," played once for the smaller reward and three times for the larger reward) was played, and the food dispenser was activated to deliver pellets. In the standard ITC task and prelearning phases, the PRD started only after delivery of the sooner reward. The length of the PRD was determined by subtracting the delay to sooner reward from the delay to later reward. Thus, the length of a trial was equal whichever option chimpanzees chose. A blank screen was presented during the PRD. An ITI of 1.5 s then followed the delivery of the later reward or the end of the PRD for the sooner reward. In the no PRD ITC task, the ITI followed the delivery of both sooner and later rewards. The blank screen was presented during the ITI.

We conducted one session consisting of 20 trials (or 28 trials for the no PRD ITC task) per testing day. If a session was interrupted (because the chimpanzee had left the touchscreen, another chimpanzee had interfered, or a problem occurred with the dispenser etc.), the session was cancelled and another session was started; otherwise, the session was administered on another day. In several trials, the dispensers failed to deliver the intended number of pellets due to, for instance, getting stuck (slightly fewer pellets were released) or a sensor problem (slightly more pellets were released), but we continued the session if the problem was rapidly resolved. After chimpanzees completed a given session, they could engage in other cognitive tasks (e.g., visual search task) that were irrelevant to the current study. This prevented chimpanzees from interfering with other participants who were completing the tasks. The following subsections describe each testing phase, and Table 2 shows a brief overview of these testing phases.

Discrimination of Delay to Reward Delivery

First, chimpanzees learned to discriminate two options based on the delay to reward delivery. They were presented with two options: five pellets available sooner (1 s to 5 s) versus five pellets available later (5 s to 30 s; Table 2). One session consisted of 20 trials. We randomized the side of presentation. Participants had to complete at least four sessions, and the number of sessions for each participant was determined as follows. For each session, we calculated the proportion of choice of either option (sooner or later) to the number of trials including no choice trials (i.e., 20). Then, for the last four completed sessions, we calculated the difference between the maximum and minimum of the proportion of choice. We decided that each participant continued this phase until the difference became ≤ 0.1 (by that time, one individual [Mizuki] had already completed five sessions, the first four of which met the criteria). Note that we did not make an a priori prediction about which option chimpanzees would prefer

or whether they would exhibit clear preferences for either option, because the two alternatives were equivalent in terms of reward rate. Thus, chimpanzees could prefer the option with a longer delay because it had a shorter PRD, if chimpanzees found the PRD with a blank screen more boring and aversive than the reward delays with an animation indicating upcoming rewards. After this phase, one individual (Mizuki) participated in a pilot experiment for the standard ITC task (see the following text) over 5 days to ensure that the procedure worked for the chimpanzees.

Discrimination of Reward Amount

Next, chimpanzees learned the relationship between the number of red squares and the number of pellets delivered under the condition of the fixed delay to reward delivery (5 s). The combination of reward amount was 3 versus 5 (i.e., the smaller reward was associated with three pellets and the larger one with five pellets) or 4 versus 5 (i.e., the smaller reward was associated with four pellets and the larger one with five pellets). We randomized the side of presentation. One session consisted of 20 trials. The amount combination was fixed within a session. We conducted alternate sessions for each amount combination, starting with the 3 versus 5 condition. For each session, we calculated the proportion of larger-reward choices to the number of trials including no choice trials (i.e., 20). We continued this phase for each participant until this proportion was ≥ 0.75 ($p \leq .05$, binominal test) in the last four completed sessions (i.e., two sessions for each amount combination).

Preference in Standard ITC Task

The combination of the reward amount was either 3 versus 5 or 4 versus 5, and the combination was fixed within a session. The delay was randomly assigned within 1 s to 10 s for the smaller reward and 1 s to 30 s for the larger reward, independently of each other. This yielded some trials in which a larger reward was associated with an identical or even shorter delay than a smaller reward ($M \pm SD = 17.0\% \pm 1.20\%$ of trials analyzed: Figures S1–S4 in the online supplemental materials). We randomized the side of presentation. We blocked two sessions of the 3 versus 5 condition and two sessions of the 4 versus 5 condition. The order of these conditions (i.e., 3 vs. 5 or 4 vs. 5) was pseudorandomized within a block so that chimpanzees did not receive a specific condition in four consecutive sessions across two blocks. Participants completed four blocks, in total 160 trials for the 3 versus 5 condition and 160 trials for the 4 versus 5 condition (20 trials/ session X 2 sessions/block X 4 blocks). The first block served as a practice block and data from the last three blocks were analyzed (120 trials for the 3 vs. 5 condition and 120 trials for the 4 vs. 5 condition). One individual (Natsuki) failed to complete the first session in the 4 versus 5 condition, but we regarded the session as valid, as she completed 80% of trials (i.e., 16 out of 20 trials) and this was part of a practice session.

Reconfirmation of Amount Discrimination

It may be difficult for chimpanzees to discriminate between two numerosities with a small difference (Tomonaga, 2008). We thus ensured that chimpanzees could discriminate the reward amount again. Chimpanzees completed two sessions of the 3 versus 5 condi- tion and two sessions of the 4 versus 5 condition with the same procedure as used in the *Discrimination of reward amount* phase.

Preference in No PRD ITC Task

We then administered the no PRD ITC task. The reward amount combination was 3 versus 5, and the delay was assigned randomly from 1 s to 10 s and 20 s to 30 s for the smaller and the larger rewards, respectively. In this setting, choosing the smaller reward maximizes the long-term reward rate (see online supplemental materials). We decided to administer the 3 versus 5 condition rather than the 4 versus 5 condition, because chimpanzees clearly discriminated between the two alternatives and had a strong preference for the larger reward in the standard ITC task (Figures S1–S4 in the online supplemental materials). This also indicated that chimpanzees were tolerant enough to wait for the larger rewards with

that range of reward delays, and it was unlikely that they would increase smaller-reward choices in the no PRD ITC task simply because they became impulsive.

To ensure that participants experienced the contingencies of both options, we included forced-choice trials, in which only one option was presented at a time. Each smaller and larger-reward option was presented four times, producing a total of eight trials. The order and the side of presentation were randomized. These trials were included at the start of a session. Then, 20 free-choice trials followed, in which options of smaller and larger rewards were presented side by side. We randomized the side of presentation. Participants completed eight sessions.

Analysis

Preference in Standard ITC Task

Statistical analyses were performed using R (v.3.5.3; R Core Team, 2019). We analyzed the choice data for the last three blocks, but excluded 17 trials in which participants did not make any choice. We fitted a generalized linear mixed model (GLMM) with Bernoulli distribution and logit link function, using an R package, brms (v.2.9.0; Bürkner, 2017, 2018), which was based on a programing language, Stan (v.2.19.1; Carpenter et al., 2017). We attempted Bayesian modeling using the brms package, which enabled model convergence without dropping subject-level (random) effects (see the following text), with the aid of weakly informative priors (for details, see online supplemental materials). As this approach did not produce p values, we assessed the effect of each predictor variable based on the extent to which the sampling from the posterior distribution for the coefficient deviated from zero, summarized here with its mean and 95% credible interval (CI; based on percentile: equal-tailed interval). For population-level (fixed) effects, we included intercept, delay to the smaller reward, delay to the larger reward, reward amount combination (3) vs. 5/4 vs. 5, coded as -0.5/0.5), session (1–6 coded as 0–5), and all interactions. The delays to reward delivery were standardized to avoid high collinearity between interactions and main effects in-volving them, and to improve model convergence (Harrison et al., 2018; Schielzeth, 2010; Young, 2018). The model also included subject-level effects for all predictors (Barr et al., 2013; Brauer & Curtin, 2018); yet, to simplify the model, we did not assume correlations between these effects. Note that although we chose priors reasonably, the degree of uncertainty in parameter estimation some- what depended on our choice of priors for the subject-level effects (see online supplemental materials), possibly due to the small sample size (Baldwin, & Fellingham, 2013; Stegmueller, 2013; van de Schoot et al., 2017), and hence the GLMM results must be interpreted carefully in light of this. Further details about statistical models are described in online supplemental materials.

Effect of PRD on Preference

We analyzed the choice data of free-choice trials (20 trials/session) in all eight sessions but excluded three trials in which participants did not make any choice. We used a GLMM with the same setting as the one for the standard ITC task. The model included population-level effects of intercept, delay to the smaller reward, delay to the larger reward (both standardized), session (1–8 coded as 0–7), and all interactions. The model also included the subject-level effects for all predictors.

We then compared chimpanzee behaviors in the standard ITC and the no PRD ITC tasks. We used a subset of the standard ITC task data; specifically, to control for task factors other than PRD, we used data from the 3 versus 5 condition in three blocks (i.e., six sessions), in which the delay to the larger reward was 20 s to 30 s. We omitted three trials in which participants did not choose either option. This resulted in 38.3 \pm 5.12 trials per participant ($M \pm SD$). We then fitted a GLMM with the same setting as the ones described earlier. The model included the population-level effects of intercept, experiment (standard/no PRD ITC task coded as -0.5/0.5), session (1–6 for the standard and 1–8 for the no PRD ITC task, coded as 0–5 and 0–7, respectively), and the interaction. The model also included the subject-level effects for all predictors.

Results

Discrimination of Delay to Reward Delivery

Chimpanzees completed 12.8 \pm 7.63 sessions ($M \pm SD$) until they exhibited stable preferences. Finally, all four chimpanzees preferred sooner rewards to later ones. The range of proportion of the sooner-reward choice in the last four sessions was as follows: Hatsuka: 0.80–0.95; Iroha: 0.95–1.0; Mizuki: 0.85–0.90; Natsuki: 0.90–1.0 (for one individual [Hatsuka], the difference between the maximum and the minimum proportion of the sooner-reward choice was 0.15 due to experimenter error).

Discrimination of Reward Amount

Chimpanzees completed 5.50 ± 1.91 sessions ($M \pm SD$) until they exhibited stable preferences to the larger rewards ($p \le .05$, binomial tests). The range of proportion of the larger-reward choice in the last four sessions was as follows: Hatsuka: 0.75-1.0; Iroha: 0.75-1.0; Mizuki: 0.80-1.0; Natsuki: 0.80-1.0. The chimpanzees had experienced similar tasks using this setting in preceding experiments not reported here, which may have helped them to learn the discrimination of reward amount and delay with a relatively small number of sessions this time.

Preference in Standard ITC Task

In the 3 versus 5 condition, chimpanzees chose mostly the larger rewards (94.1% \pm 2.67%; $M \pm$ SD, six sessions were pooled). They also did so in the 4 versus 5 condition, but chose the smaller rewards more often (76.0% \pm 17.5%; $M \pm$ SD, six sessions were pooled; Figure 3), as shown by a negative coefficient for the population-level effect of amount combination ($\beta \pm$ SD = -2.04 \pm 0.70, 95% CI [-3.46, -0.68]). The other predictors did not affect chimpanzee behaviors substantially (Table S1 in the online supplemental materials).

In a few cases, at the start of a session, chimpanzees touched the touchscreen immediately after it was activated, even before any keys were presented (it took a few seconds after activation for keys to appear). The touchscreen might have accidentally detected a touch to a rectangle before showing the rectangles. This might have occurred only rarely but to be conservative, we analyzed the data using the same model but excluding the first trial of each session. The overall findings were the same, so we did not consider this factor further. Data plots for each participant are shown in Figures S1–S4 in the online supplemental materials.

Reconfirmation of Amount Discrimination

All but one individual clearly discriminated between the two options. Three chimpanzees (Iroha, Mizuki, and Natsuki) chose the larger rewards (five pellets) over the smaller ones (three or four pellets) in \geq 15 out of 20 trials ($p \leq .05$, binomial tests) in four sessions. One individual (Hatsuka) chose the larger reward in 13 trials in the last session of the 4 versus 5 condition.

Preference in No PRD ITC Task and Effect of PRD on ITC

On average, chimpanzees chose the larger reward in 67.5% \pm 39.8% of trials ($M \pm SD$, eight sessions were pooled). Chimpanzees reduced the larger-reward choices in later sessions (see Figure 4), as shown by a negative coefficient for the population-level effect of session ($\beta \pm SD = -1.09 \pm 0.47$, 95% CI [-2.07, -0.18], although care is needed for a potential effect of autocorrelation). The other predictors did not affect chimpanzee behaviors substantially (Table S2 in the online supplemental materials). When we compared the performances across the two ITC tasks, the model revealed that none of the predictors substantially affected chimpanzee behaviors (Table S3 in the online supplemental materials).

However, we observed a large individual difference in behavioral changes across tasks; in particular, two chimpanzees shifted their preference to smaller rewards, whereas the other two chimpanzees consistently chose larger rewards (see Figure 4). Notably, Natsuki's choice of larger rewards decreased in the no

PRD ITC task (pooled across sessions: 11.3%) compared with the standard ITC task (83.9%; odds ratio = 0.02, p < .001: Fisher's exact probability test, two-tailed; Figure 4). Another individual, Mizuki, also decreased the choice of larger rewards (no PRD ITC task: 67.7%; standard ITC task: 90.0%, odds ratio = 0.23, p = .005). This shift was more evident when we focused on the last three sessions (see Figure 4). Hatsuka persisted in choosing larger rewards (no PRD ITC task: 95.6%; standard ITC task: 95.3%, odds ratio = 1.06, p = 1), and the other individual, Iroha, slightly increased larger-reward choices (no PRD ITC task: 95.6%; standard ITC task: 95.6%; standard ITC task: 95.6%; standard ITC task: 95.6%; standard ITC task: 84.6%, odds ratio = 3.97, p = .023). Data plots for each participant are shown in Figures S5–S8 in the online supple- mental materials.

Discussion

In the standard ITC task, in which the trial duration was kept identical across the two options, four chimpanzees preferred larger rewards to smaller ones, although they also chose smaller rewards, especially when the smaller rewards comprised four rather than three pellets. In the no PRD ITC task, in which the PRDs were eliminated, two chimpanzees (Mizuki and Natsuki) shifted their preference to smaller rewards, whereas the other two individuals (Hatsuka and Iroha) continued to choose larger rewards, although this reduced the reward rate. This suggests that some individuals could incorporate the PRD and improve the reward rate, although this finding was based on individual-level analyses, rather than the group-level analysis. The other individuals may have attempted to increase the amount for the individual trial, which may produce a greater overall reward amount. Alternatively, it may be that they could not learn the contingency of the length of the PRD within eight sessions. Importantly, in the current study, we used touch- screens to present two choice alternatives as well as (low-) symbolic cues (i.e., red squares) to indicate the reward amount. By reducing the saliency of food rewards, this setting may have helped chimpanzees to choose the smaller rewards and hence improve their reward rate. Future studies could reduce the saliency of the reward amount even more by using high-symbolic cues whose perceptual features do not directly correspond to the reward amount (Addessi et al., 2014).

One of the limitations of the current study was that the order of the two experiments (i.e., the standard and the no PRD ITC tasks) was not counterbalanced. This factor, as well as the small sample size, should be taken into account when interpreting the findings. Nonetheless, although we could not completely rule out experiment order effects, it seems unlikely that these alone explain the results. In the standard ITC task, we did not observe a substantial change in chimpanzee intertemporal preferences across sessions (Table S1 in the online supplemental materials). Additionally, for the standard ITC task, visual inspection of the data indicated that chimpanzees still preferred the larger rewards even in later sessions, especially for the reward amount combination identical to that used in the no PRD task (i.e., 3 vs. 5; Figures S1–S4 in the online supplemental materials). However, more direct evidence is needed from experiments testing larger numbers of chimpanzees and counterbalancing the experiment order.

Future studies with larger samples would also be useful in investigating potential individual differences in ITC tasks. Al- though tentative, we made the observation that the two chimpanzees who shifted to the smaller-reward choices in the no PRD ITC task (Mizuki and Natsuki) chose smaller rewards more often in the standard ITC task than the other two chimpanzees did (Hatsuka and Iroha). Such individual differences may be mediated not only by different levels of self-control, but also by different levels of learning abilities or cognitive flexibilities. For example, these occasional "impulsive" choices may have helped Mizuki and Nat- suki to learn the PRD contingency associated with smaller re-wards. These two

individuals were older than the other two chimpanzees (see Table 1), and thus had relatively more experience of cognitive experiments, which may have helped them learn more quickly (Beran, 2019). Moreover, a recent study by Beran and Hopkins (2018) showed that chimpanzees' g scores (a proxy for general intelligence, based on the primate cognitive test battery) were positively correlated with performance in another self-control task (i.e., hybrid delay task). This may indicate that relatively "intelligent" chimpanzees learn the contingencies of the hybrid delay task better, and hence show more optimal behaviors (Beran & Hopkins, 2018). Furthermore, g scores were more strongly correlated with the overall efficiency of performance, rather than with the proportion of larger-reward choices or the number of food items accumulated when larger rewards were chosen. This suggests that choosing smaller rewards flexibly depending on situations (e.g., when the delayed rewards seem difficult to obtain) is by no means "irrational," but rather may demonstrate "intelligent" behavior (Beran & Hopkins, 2018).

To conclude, our results at least suggest that the use of touch- screens and symbolic cues could be an alternative and promising tool to reduce the saliency of food rewards and/or human experimenters when measuring chimpanzee intertemporal preferences. Additionally, we also made a tentative observation that two chimpanzees switched their preference from larger to smaller rewards when the PRD was eliminated, thereby increasing the reward rate, whereas the other two chimpanzees preferred larger rewards regardless of whether PRD was added or not. Although the latter finding should be interpreted in light of limitations such as the small sample size and the experiment order, these findings illustrate the potential importance of the experimental setting in chimpanzee decision-making, and thus call for careful consideration when designing ITC tasks or interpreting the results.

Acknowledgements

We are grateful to N. Morimura, F. Kano, and R. Song for their kind help in conducting the study. We thank all the staffs at Kumamoto Sanctuary, Wildlife Research Center, Kyoto University, especially Mr. H. Ogi, Mr. M. Teramoto, and Ms. E. Nogami. Special thanks are given to T. Matsuzawa for financial support. We thank Diane Williams, from Edanz Group (www.edanzediting.com/ac) for editing a draft of this article. This study was supported financially by the Ministry of Education, Culture, Sports, Sci- ence and Technology through a Japan Society for the Promotion of Science Grant-in-Aid for Japan Society for the Promotion of Science Grant-in-Aid for Scientific Research on Innovative Areas to Yutaka Sakai [Grants 26119526, 16H01516, and 18H05524]; a Grant-in-Aid for Scientific Research (A) and a Grant-in-Aid for Scientific Research on Innovative Areas to Satoshi Hirata [Grants 26245069 and 18H05524]; a Grant-in-Aid for Specially Promoted Research to Tetsuro Matsuzawa [Grant 16H06283]; a Program for Leading Graduate Schools to Tetsuro Matsuzawa [LDG-U04]; and the Great Ape Information Network.

References

Addessi, E., Bellagamba, F., Delfino, A., De Petrillo, F., Focaroli, V., Macchitella, L., Maggiorelli, V., Pace, B., Pecora, G., Rossi, S., Sbaffi, A., Tasselli, M. I., & Paglieri, F. (2014). Waiting by mistake: Symbolic representation of rewards modulates intertemporal choice in capuchin monkeys, preschool children and adult humans. *Cognition*, 130(3), 428 – 441. https://doi.org/10.1016/j.cognition.2013.11.019

Baldwin, S. A., & Fellingham, G. W. (2013). Bayesian methods for the analysis of small sample multilevel data with a complex variance structure. *Psychological Methods*, *18*(2), 151–164. https://doi.org/10.1037/ a0030642

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, 68(3), 255–278. https://doi.org/10.1016/j.jml .2012.11.001

Bateson, M., & Kacelnik, A. (1996). Rate currencies and the foraging starling: The fallacy of the average revisited. *Behavioral Ecology*, 7(3), 341–352. https://doi.org/10.1093/beheco/7.3.341

Beran, M. J. (2019). All hail suboptimal choice! Now, can we "fix" it? Comparative Cognition and Behavior Reviews, 14, 19–23. https://doi .org/10.3819/CCBR.2019.140002

- Beran, M. J., & Evans, T. A. (2006). Maintenance of delay of gratification by four chimpanzees (*Pan troglodytes*): The effects of delayed reward visibility, experimenter presence, and extended delay intervals. *Behav- ioural Processes*, 73(3), 315–324. https://doi.org/10.1016/j.beproc.2006 .07.005
- Beran, M. J., & Hopkins, W. D. (2018). Self-control in chimpanzees relates to general intelligence. *Current Biology*, 28(4), 574–579. https://doi.org/ 10.1016/j.cub.2017.12.043
- Beran, M. J., James, B. T., Whitham, W., & Parrish, A. E. (2016). Chimpanzees can point to smaller amounts of food to accumulate larger amounts but they still fail the reverse-reward contingency task. *Journal of Experimental Psychology: Animal Learning and Cognition*, *42*(4), 347–358. https://doi.org/10.1037/xan0000115
- Blanchard, T. C., Pearson, J. M., & Hayden, B. Y. (2013). Postreward delays and systematic biases in measures of animal temporal discount- ing. *Proceedings of the National Academy of Sciences of the United States of America*, 110(38), 15491–15496. https://doi.org/10.1073/pnas .1310446110
- Boysen, S. T., & Berntson, G. G. (1995). Responses to quantity: Perceptual versus cognitive mechanisms in chimpanzees (*Pan troglodytes*). Journal of Experimental Psychology: Animal Behavior Processes, 21(1), 82–86. https://doi.org/10.1037/0097-7403.21.1.82
- Boysen, S. T., Berntson, G. G., Hannan, M. B., & Cacioppo, J. T. (1996). Quantity-based interference and symbolic representations in chimpan- zees (*Pan troglodytes*). Journal of Experimental Psychology: Animal Behavior Processes, 22(1), 76–86. https://doi.org/10.1037/0097-7403 .22.1.76
- Brauer, M., & Curtin, J. J. (2018). Linear mixed-effects models and the analysis of nonindependent data: A unified framework to analyze cate- gorical and continuous independent variables that vary within-subjects and/or within-items. *Psychological Methods*, 23(3), 389-411. https://doi.org/10.1037/met0000159
- Bürkner, P. C. (2017). brms: An R package for Bayesian multilevel models using stan. Journal of Statistical Software, 80(1), 1–28. https://doi.org/ 10.18637/jss.v080.i01
- Bürkner, P. C. (2018). Advanced Bayesian multilevel modeling with the R package brms. *The R Journal*, *10*(1), 395–411. https://doi.org/10.32614/ RJ-2018-017
- Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., & Riddell, A. (2017). Stan: A probabilistic programming language. *Journal of Statistical Software*, *76*(1), 1–32. https://doi.org/10.18637/jss.v076.i01
- Depaoli, S., & van de Schoot, R. (2017). Improving transparency and replication in Bayesian statistics: The WAMBS-checklist. *Psychological Methods*, 22(2), 240–261. https://doi.org/10.1037/met0000065
- Evans, T. A., Beran, M. J., Paglieri, F., & Addessi, E. (2012). Delaying gratification for food and tokens in capuchin monkeys (*Cebus apella*) and chimpanzees (*Pan troglodytes*): when quantity is salient, symbolic stimuli do not improve performance. *Animal Cognition*, *15*(4), 539–548. https://doi.org/10.1007/s10071-012-0482-1
- Flora, S. R., & Pavlik, W. B. (1992). Human self-control and the density of reinforcement. *Journal of the Experimental Analysis of Behavior*, 57(2), 201–208. https://doi.org/10.1901/jeab.1992.57-201
- Funkhouser, J. A., Mayhew, J. A., Mulcahy, J., & Sheeran, L. K. (2020). Human caregivers are integrated social partners for captive chimpan- zees. *Primates*. https://doi.org/10.1007/s10329-020-00867-6
- Genty, E., Karpel, H., & Silberberg, A. (2012). Time preferences in long-tailed macaques (*Macaca fascicularis*) and humans (*Homo sapi- ens*). *Animal Cognition*, 15(6), 1161–1172. https://doi.org/10.1007/ s10071-012-0540-8
- Goldshmidt, J. N., Lattal, K. M., & Fantino, E. (1998). Context effects on choice. *Journal of the Experimental Analysis of Behavior*, 70(3), 301–320. https://doi.org/10.1901/jeab.1998.70-301
- Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher,

D. N., Goodwin, C. E. D., Robinson, B. S., Hodgson, D. J., & Inger, R. (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*, 6, Article e4794. https://doi.org/10.7717/ peerj.4794

- Hata, Y., & Saeki, D. (2018). Effects of pre- and post-reinforcer delays on choice in pigeons. *Japanese Journal of Animal Psychology*, 68(1), 17–23. https://doi.org/10.2502/janip.68.1.6
- Hayden, B. Y. (2016). Time discounting and time preference in animals: A critical review. *Psychonomic Bulletin and Review*, 23(1), 39-53. https://doi.org/10.3758/s13423-015-0879-3
- Hwang, J., Kim, S., & Lee, D. (2009). Temporal discounting and inter- temporal choice in rhesus monkeys. *Frontiers in Behavioral Neurosci- ence*, *3*, 9. https://doi.org/10.3389/neuro.08.009.2009
- Ito, M., & Nakamura, K. (1998). Humans' choice in a self-control choice situation: Sensitivity to reinforcer amount, reinforcer delay, and overall reinforcer density. *Journal of the Experimental Analysis of Behavior*, 69(1), 87–102. https://doi.org/10.1901/jeab.1998.69-87
- Kano, F., Hirata, S., Call, J., & Tomonaga, M. (2011). The visual strategy specific to humans among hominids: A study using the gap–overlap paradigm. Vision Research, 51(23–24), 2348–2355. https://doi.org/10 .1016/j.visres.2011.09.006
- Kidd, C., Palmeri, H., & Aslin, R. N. (2013). Rational snacking: Young children's decision-making on the marshmallow task is moderated by beliefs about environmental reliability. *Cognition*, 126(1), 109-114. https://doi.org/10.1016/j.cognition.2012.08.004
- Kirby, K. N., & Marakovic', N. N. (1995). Modeling myopic decisions: Evidence for hyperbolic delay-discounting within subjects and amounts. Organizational Behavior and Human Decision Processes, 64(1), 22–30. https://doi.org/10.1006/obhd.1995.1086
- Labuschagne, L. G., Cox, T. J., Brown, K., & Scarf, D. (2017). Too cool? Symbolic but not iconic stimuli impair 4-year-old children's performance on the delay-of-gratification choice paradigm. *Behavioural Pro- cesses*, *135*, 36–39. https://doi.org/10.1016/j.beproc.2016.11.014
- Lea, S. E. G. (1979). Foraging and reinforcement schedules in the pigeon: Optimal and non-optimal aspects of choice. *Animal Behaviour*, 27(3), 875-886. https://doi.org/10.1016/0003-3472(79)90025-3
- Loewenstein, G. (1996). Out of control: Visceral influences on behavior. Organizational Behavior and Human Decision Processes, 65(3), 272-292. https://doi.org/10.1006/obhd.1996.0028
- Loewenstein, G. (2000). Emotions in economic theory and economic behavior. *The American Economic Review*, 90(2), 426–432. https://doi .org/10.1257/aer.90.2.426
- Logue, A. W., Smith, M. E., & Rachlin, H. (1985). Sensitivity of pigeons to prereinforcer and postreinforcer delay. *Animal Learning and Behav- ior*, 13(2), 181–186. https://doi.org/10.3758/BF03199271

Mahrer, A. R. (1956). The role of expectancy in delayed reinforcement. *Journal of Experimental Psychology*, 52(2), 101–106. https://doi.org/10.1037/h0040837

- Matsuura, K. (2016). Shuusoku shinai baai no taisyohou [Solutions for convergence problems]. In D. Ichikawa, K. Takahashi, S. Takayanagi, S. Fukushima, & K. Matsuura (Eds.), *Stan to R de beizu toukei moderingu [Bayesian statistical modeling using stan and R]* (Wonderful R Series, Vol. 2, pp. 177–201). Kyoritsu Shuppan.
- Mazur, J. E. (1989). Theories of probabilistic reinforcement. Journal of the Experimental Analysis of Behavior, 51(1), 87–99. https://doi.org/10 .1901/jeab.1989.51-87
- Mazur, J. E., & Biondi, D. R. (2009). Delay-amount tradeoffs in choices by pigeons and rats: Hyperbolic versus exponential discounting. *Journal of the Experimental Analysis of Behavior*, 91(2), 197–211. https://doi.org/ 10.1901/jeab.2009.91-197
- Mazur, J. E., Snyderman, M., & Coe, D. (1985). Influences of delay and rate of reinforcement on discrete-trial choice. *Journal of Experimental Psychology: Animal Behavior Processes*, 11(4), 565–575. https://doi .org/10.1037/0097-7403.11.4.565
- Michaelson, L., de la Vega, A., Chatham, C. H., & Munakata, Y. (2013). Delaying gratification depends on social trust. *Frontiers in Psychology*, *4*, 355. https://doi.org/10.3389/fpsyg.2013.00355
- Paglieri, F., Addessi, E., Sbaffi, A., Tasselli, M. I., & Delfino, A. (2015). Is it patience or motivation? On motivational confounds in intertemporal choice tasks. *Journal of the Experimental Analysis of Behavior*, 103(1), 196–217. https://doi.org/10.1002/jeab.118
- Paglieri, F., Focaroli, V., Bramlett, J., Tierno, V., McIntyre, J. M., Addessi, E., Evans, T. A., & Beran, M. J. (2013). The hybrid delay task: Can capuchin monkeys (*Cebus apella*) sustain a delay after an initial choice to do so? *Behavioural Processes*, 94, 45–54. https://doi.org/10.1016/j .beproc.2012.12.002
- Pearson, J. M., Hayden, B. Y., & Platt, M. L. (2010). Explicit information reduces discounting behavior in monkeys. *Frontiers in Psychology*, *1*, 237. https://doi.org/10.3389/fpsyg.2010.00237
- Pecora, G., Bellagamba, F., Chiarotti, F., Paoletti, M., Castano, M. L., & Addessi, E. (2020). The effect of symbolic distancing on delay tolerance across the preschool period. *Journal of Cognition and Development*, 21(1), 92–103. https://doi.org/10.1080/15248372.2019.1693374
- R Core Team. (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R- project.org/ Rosati, A. G., Stevens, J. R., Hare, B., & Hauser, M. D. (2007). The evolutionary origins of human patience: Temporal preferences in chim- panzees,

bonobos, and human adults. Current Biology, 17(19), 1663-1668. https://doi.org/10.1016/J.CUB.2007.08.033

- Santos, L. R., & Rosati, A. G. (2015). The evolutionary roots of human decision making. *Annual Review of Psychology*, 66(1), 321–347. https://doi.org/10.1146/annurev-psych-010814-015310
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1(2), 103-113. https://doi.org/10.1111/j.2041-210X.2010.00012.x
- Schweighofer, N., Shishida, K., Han, C. E., Okamoto, Y., Tanaka, S. C., Yamawaki, S., & Doya, K. (2006). Humans can adopt optimal discount- ing strategy under real-time constraints. *PLoS Computational Biology*, 2(11), Article e152. https://doi.org/10.1371/journal.pcbi.0020152
- Smethells, J. R., & Reilly, M. P. (2015). Intertrial interval duration and impulsive choice. *Journal of the Experimental Analysis of Behavior*, 103(1), 153–165. https://doi.org/10.1002/jeab.131
- Stan Development Team. (2019). Prior choice recommendations. https:// github.com/stan-dev/stan/wiki/Prior-Choice-Recommendations
- Stegmueller, D. (2013). How many countries for multilevel modeling? A comparison of frequentist and Bayesian approaches. *American Journal of Political Science*, *57*(3), 748–761. https://doi.org/10.1111/ajps.12001 Stephens, D. W. (2002). Discrimination, discounting and impulsivity: A role for an informational constraint. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, *357*(1427),
- 1527–1537. https://doi.org/10.1098/rstb.2002.1062 Stephens, D. W., & Anderson, D. (2001). The adaptive value of preference for immediacy: When shortsighted rules have farsighted consequences.
- *Behavioral Ecology*, *12*(3), 330–339. https://doi.org/10.1093/beheco/12 .3.330
- Stevens, J. R. (2011). Mechanisms for decisions about the future. In R. Menzel & J. Fischer (Eds.), Animal thinking: Contemporary issues in comparative cognition (pp. 93–104). The MIT Press. https://doi.org/10 .7551/mitpress/9780262016636.003.0007
- Stevens, J. R., Hallinan, E. V., & Hauser, M. D. (2005). The ecology and evolution of patience in two New World monkeys. *Biology Letters*, 1(2), 223–226. https://doi.org/10.1098/rsbl.2004.0285
- Stevens, J. R., Rosati, A. G., Heilbronner, S. R., & Mühlhoff, N. (2011). Waiting for grapes: Expectancy and delayed gratification in bonobos. International Journal of Comparative Psychology, 24(1), 99–111.
- Stevens, J. R., & Stephens, D. W. (2010). The adaptive nature of impul- sivity. In G. J. Madden & W. K.. Bickel (Eds.), Impulsivity: The

behavioral and neurological science of discounting (pp. 361-387). American Psychological Association. https://doi.org/10.1037/12069-013 Tanaka,

S. C., Yamada, K., Yoneda, H., & Ohtake, F. (2014). Neural mechanisms of gain-loss asymmetry in temporal discounting. *The Jour- nal of Neuroscience*, 34(16), 5595–5602. https://doi.org/10.1523/ JNEUROSCI.5169-12.2014

Tomonaga, M. (2008). Relative numerosity discrimination by chimpanzees (*Pan troglodytes*): Evidence for approximate numerical representations. *Animal Cognition*, 11(1), 43–57. https://doi.org/10.1007/s10071-007-0089-0

- van de Schoot, R., Winter, S. D., Ryan, O., Zondervan-Zwijnenburg, M., & Depaoli, S. (2017). A systematic review of Bayesian articles in psychology: The last 25 years. *Psychological Methods*, 22(2), 217–239. https://doi.org/10.1037/met0000100
- Vlamings, P. H. J. M., Uher, J., & Call, J. (2006). How the great apes (*Pan troglodytes, Pongo pygmaeus, Pan paniscus, and Gorilla gorilla*) per- form on the reversed contingency task: The effects of food quantity and food visibility. *Journal of Experimental Psychology: Animal Behavior Processes*, 32(1), 60–70. https://doi.org/10.1037/0097-7403.32.1.60
- Yamaguchi, T., Saeki, D., & Ito, M. (2015). Sensitivity to pre- and post-reinforcer delays in self-control choice. *Behavioural Processes*, 121, 8-12. https://doi.org/10.1016/j.beproc.2015.09.012
- Young, M. E. (2018). Discounting: A practical guide to multilevel analysis of choice data. *Journal of the Experimental Analysis of Behavior*, 109(2), 293–312. https://doi.org/10.1002/jeab.316

Table 1Demographic Characteristics of Chimpanzee Participants

Name	Sex	Age	Rearing history	GAIN ID ^a	
Hatsuka	F	10	Nursery/peer	0704	
Iroha	F	10	Mother	0708	
Mizuki	F	22	Nursery/peer	0559	
Natsuki	F	13	Mother	0677	

Note. In the "Sex" column, "F" means females. The "Age" column shows the participant age in October 2018. In the "Rearing history" column, "Mother" means reared by the biological mother and "Nursery/peer" means reared by human caretakers while allowing interactions with conspecific peers. ^a Great Ape Information Network (GAIN; https://shigen.nig.ac.jp/gain/index.jsp).

Figure 1

Experimental Setups



 $\it Note.$ (a) Six chimpanzees perform cognitive tasks simultaneously. (b) Devices were installed in an experimental booth, which was attached to the outdoor enclosure.

Figure 2

A Diagram Depicting the Task Design



Note. (a) Task flows of the intertemporal choice (ITC) tasks. Yellow (lighter gray) circles represent the reward delivery. In the standard ITC task, the postreward delay (PRD) followed the delivery of the sooner reward (upper). In the no PRD ITC task, the PRD was eliminated and the fixed intertrial interval (ITI) followed immediately after the reward delivery regardless of the choice (lower). Note that the different length of the horizontal lines do not reflect the differences in the length of each temporal component exactly. (b) Examples of screens in each phase of the task. During the reward delay, an animation of red (darker gray) squares falling to the bottom was played.

Table 2

	Reward (a)		Reward (b)			
Task	Amount	Delay (s)	Amount	Delay (s)	Trial duration	
1. Delay discrimination	5	1–5	5	5–30	(a) = (b)	
2. Amount discrimination	5	5	3 or 4	5	(a) = (b)	
3. Standard ITC	5	1-30	3 or 4	1-10	(a) = (b)	
4. Reconfirmation of amount discrimination	5	5	3 or 4	5	(a) = (b)	
5. No PRD ITC	5	20-30	3	1 - 10	(a) > (b)	

The Parameters of Each Task

Note. ITC = intertemporal choice; PRD = postreward delay.

Figure 3

The Proportion of Larger-Reward Choices to the Number of Trials Including No Choice Trials in the Standard ITC Task as a Function of the Delay to Larger Reward



Note. For ease of interpretation, data were grouped according to the delay to reward: delay to smaller reward $(D_s):0s \le D_s \le 5s$ (left panels), $5s \le D_s \le 10s$ (right panels); delay to larger reward $(D_L):0s \le D_L \le 10s$, $10s \le D_L \le 20s$, $20s \le s D_L \le 30s$. For comparison, the data of the no PRD ITC task (pooled across sessions) were shown by open markers at the right side of the top panels. Data of each individual are shown in different colors. ITC = intertemporal choice; PRD = postreward delay.

Figure 4

The Proportion of Each Choice in the Subset of the Standard ITC Task (the Left-Hand Bar; 38.3 ± 5.12 Trials, $M \pm SD$) and in Eight Sessions of the No PRD ITC Task (the Eight Right-Hand Bars; 20 Trials for Each)



Note. The thinnest horizontal lines on the bars indicate the zero values. The blue (dark gray), pink (intermediately dark gray), and yellow (light gray) parts of each bar indicate the larger reward choice, the smaller reward choice, and no choice trials, respectively. ITC = intertemporal choice; PRD = postreward delay.