ANIMAL BEHAVIOUR, 2006, **71**, 1379–1387
doi:10.1016/j.anbehav.2005.11.012

The effect of handling time on temporal discounting in two New World primates

ALEXANDRA G. ROSATI, JEFFREY R. STEVENS & MARC D. HAUSER
Cognitive Evolution Laboratory, Department of Psychology, Harvard University

*(Received 21 July 2005; initial acceptance 8 September 2005;
final acceptance 21 November 2005; published online 11 May 2006; MS. number: A10212R)*

Foraging decisions in nonhuman animals often require choosing between small, immediate food rewards and larger, more delayed rewards. Faced with such choices, animals typically discount or devalue the future quite strongly. Although discounting studies often focus on delays to reward access, other temporal intervals contribute to foraging rate, and thus may potentially influence discounting levels. Here, we examine the effect of handling time, the time required to process and consume food, on discounting in cottontop tamarins, *Saguinus oedipus*, and common marmosets, *Callithrix jacchus*, two species that differ in levels of temporal discounting. We presented subjects with a discounting task under two conditions. In the first condition, we made the entire reward available after the delay expired. In the second condition, we experimentally increased the minimum length of time required to consume the reward to simulate a longer handling time. We found that tamarins and marmosets showed sensitivity to increases in the time necessary to process food rewards. Both species adjusted their preferences to account for different handling times at long delays to accessing food. Consequently, models of discounting behaviour that include handling times may better describe animal choices than models that focus exclusively on delays prior to access.

In an ultimate, evolutionary sense, the significance of any decision rule is measured in lifetime reproductive success. Although this implies that animals should attempt to maximize the consequences of their actions over the long term, overwhelming experimental evidence from laboratory studies of temporal discounting indicate that animals rarely make far-sighted decisions (Green et al. 1981; Logue 1988; Bateson & Kacelnik 1996; Rachlin 2000; Roberts 2002; Kacelnik 2003). Rather, they appear to discount or devalue the future and maximize intake in the short term, one decision at a time. Specifically, animals do not treat all temporal components of the decision-making process as equally relevant. Stephens & Anderson (2001) emphasized that in experimental situations, foragers often ignore the time between trials (Mazur 1989; Bateson & Kacelnik 1996), postfeeding delays (Lea 1979; Logue et al. 1985) and the latency from when the choice period begins to when a decision is made (Bateson & Kacelnik 1996). The delay-to-food access, or the time between making a choice and receiving the reward, has the strongest influence over choice behaviour: animals subjectively devalue rewards even when the delay is no more than a few seconds (Ainslie 1974; Mazur 1987; Kacelnik 1997). Taken together, these findings suggest that animals pay more attention to the time between a decision and its consequences than to intervals that occur outside of this range.

Another key temporal component that falls inside this critical range is handling time, or the period necessary for a forager to actually process and consume food (Stephens & Krebs 1986). Studies of optimal foraging theory have demonstrated the importance of handling time in prey selection (Lea 1979; Snyderman 1983; Shettleworth 1985). For example, in various species, the ease of cracking open nuts (i.e. handling time) influences an individual's decision to either consume or cache those nuts (Woodrey 1990; Jacobs 1992; Cristol 2001).

Handling time is integral to studies of temporal discounting because it occurs after the food is initially accessed, but before another decision can be executed. Many studies of discounting, however, ignore handling time. In fact, most psychologists studying animal discounting confound reward amount and handling time by using time of access to the food as the reinforcer (Rachlin

Correspondence: J. R. Stevens, Cognitive Evolution Laboratory, Department of Psychology, Harvard University, 33 Kirkland Street, Cambridge, MA 02138, U.S.A. (email: jstevens@wjh.harvard.edu).

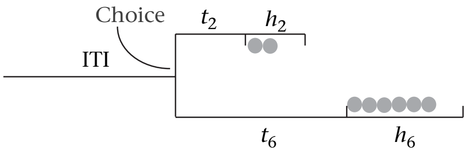
0003–3472/06/$30.00/0

& Green 1972; Ainslie 1974; Mazur 1987; Tobin & Logue 1994; Mazur 2000). There are, however, two notable exceptions. Bateson & Kacelnik (1996) used food pellet number as the reward amount and measured European starlings', *Sturnus vulgaris*, handling time in a foraging task. They found that a rate maximization model that included both delay to access and handling time best described the subjects' decisions. Further evidence that handling time may be important in discounting comes from research examining animal preferences between sequences of rewards (Brunner & Gibbon 1995). Brunner & Gibbon allowed rats, *Rattus norvegicus*, to choose between two delayed sequences of rewards in which individual pieces of food become available successively. By varying the time between rewards, they could assess the role of the temporal spacing of food accrual in the overall discounting decision. Subjects preferred a more delayed clumped option to a less delayed spaced-out reward sequence that took longer to eat, implying that they may have avoided options with longer handling times.

Here, we examine how lengthening handling time affects discounting preferences in two New World monkeys: cottontop tamarins, *Saguinus oedipus*, and common marmosets, *Callithrix jacchus*. Specifically, we presented subjects with a choice between smaller, immediate food rewards and larger, delayed rewards under two conditions. In the first condition, the chosen food reward dispensed immediately after the delay expired. In the second condition, we increased the minimum amount of time necessary to consume both reward options by adding an interpellet interval (IPI) between each successive piece of food (Fig. 1). If handling time is a component of the discounting calculation in these animals, then they should have a stronger preference for immediate rewards under the second condition, because the total amount of time necessary to acquire and process rewards is longer.

Previous experiments with these species have characterized both their temporal discounting (Stevens et al. 2005a) and spatial discounting (Stevens et al. 2005b) levels. In the temporal discounting task, marmosets waited a significantly longer time for the larger reward than did tamarins, whereas in the distance discounting task, tamarins travelled much further for the large reward than did the marmosets. These results are consistent with differences in their species-typical ecology. Both species feed on fruit, insects and tree exudates such as sap and gum (Snowdon & Soini 1988; Stevenson & Rylands 1988; Garber 1993; Rylands & de Faria 1993). Cottontop tamarins, however, spend 0–5% of their foraging time feeding on exudates, whereas common marmosets spend 20–70% (Stevenson & Rylands 1988; Power 1996). Therefore, marmosets rely much more heavily on exudates (Coimbra-Filho & Mittermeier 1976; Stevenson & Rylands 1988; Rylands & de Faria 1993; Harrison & Tardif 1994), a relatively stable food source that requires considerable investment: individuals must chew at the surface of the tree and wait for sap to exude, so marmosets often spend 3–75 s actively gouging holes in the trees before they begin feeding (Lacher et al. 1981; Stevenson & Rylands 1988). Owing to this dietary niche, exudate-feeding species of marmosets have a number of specializations in dental, muscle and gut morphology and physiology that tamarin species lack (Coimbra-Filho & Mittermeier 1976; Sussman & Kinzey 1984; Ferrari et al. 1993; Harrison & Tardif 1994; Power & Oftedal 1996; Dumont 1997; Vinyard et al. 2003; Taylor & Vinyard 2004). Some suggest that selection for exudate feeding is strong enough to influence marmoset social systems, home range size and even spatial memory (Ferrari & Lopes Ferrari 1989; Ferrari 1993; Harrison & Tardif 1994; Platt et al. 1996). In contrast, tamarins feed more on insects and fruit. When they do feed on exudates, they primarily consume gums and saps that have been previously exposed, thereby obtaining an immediate reward in the absence of significant investment in extraction (Neyman 1977; Garber 1980; Sussman & Kinzey 1984; Garber 1992, 1993). The marmosets' specialization on exudate feeding may have also shaped their temporal discounting functions (Stevens et al. 2005a).

(a) Normal distribution of food



(b) Incremental distribution of food

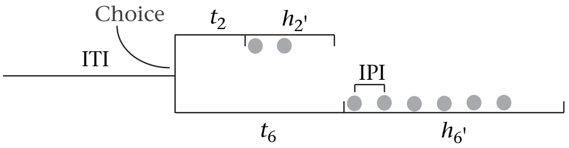


Figure 1. Experimental conditions. Following a 30-s intertrial interval (ITI), subjects chose between receiving two food pellets immediately ($t_2 = 0.5$ s) or six food pellets after a delay ($t_6 = 5$, 10 or 15 s). (a) In the normal condition, the entire food reward was available following the chosen delay, so the subjects could consume or 'handle' the pellets at their leisure (h_2 and h_6). (b) In the incremental condition, an additional interpellet interval (IPI) spaced out the distribution of the pellets and experimentally lengthened handling times $h_{2'}$ and $h_{6'}$.

What is not yet clear, however, is whether tamarins and marmosets demonstrate sensitivity to changes in handling time, or if they can adjust their choice behaviour to accommodate such changes. The temporal discounting experiment (Stevens et al. 2005a) showed that tamarins, but not marmosets, rate-maximized over a time interval that included the delay-to-food (tamarins: 5.6–9.8 s, marmosets: 10.0–19.0 s) and handling time (tamarins: 4.8–46 s, marmosets: 6.2–21.8 s). Notably, this research suggests that tamarins and marmosets may actually make decisions over different temporal horizons, with marmosets rate maximizing over a longer interval. We contend that differences in optimal time horizons may be especially relevant when considering handling time, because handling time varies in its contribution to total foraging time across species. That is, although handling time may be a significant temporal component of foraging for some animals, for others, handling time may be negligible. For instance, the size and type of food item greatly influence handling time. Large items or items with coverings and inedible parts require longer handling times than small items that lack protective coatings. Consequently, differences in handling time may be less salient to some species than others, simply because it makes a trivial contribution to foraging rate under some conditions. Moreover, handling or processing different food resources may impose different opportunity costs. Some food types are durable and transportable, whereas others must be utilized on the spot. We hypothesize that these considerations may be especially relevant when considering tamarins and marmosets because of their specialized feeding ecologies: insects, fruits and exudates differ in the temporal properties associated with processing. Since the insects upon which tamarins and marmoset feed are primarily mobile insects such as grasshoppers, crickets, cicadas and cockroaches (Stevenson & Rylands 1988), they can escape quickly once predators are detected. In addition, both fruits and insects can be consumed soon after capture. Foraging for exudates as marmosets do, however, requires gouging holes and waiting for gum or sap to seep out over a longer time span. Therefore, when monkeys make a foraging choice by gouging holes in trees, they cannot reap the rewards until after some delay. Because marmosets are specialized exudate feeders, they may tolerate longer handling times than tamarins. In contrast, tamarins might be more sensitive to variation in search time, given their primary consumption of fruits and insects.

METHODS

Subjects

Four adult cottontop tamarins (two females and two males) and four adult common marmosets (three males and one female) participated in this experiment. All four marmosets had prior experience in a temporal discounting experiment (Stevens et al. 2005a), and the tamarins were naïve to the discounting task but had experience with a wide diversity of experiments on tool use, cooperation, call perception, language processing and number representation (Hauser et al. 2001, 2003; Uller et al. 2001; Miller et al. 2002; Santos et al. 2003). In addition to food received in experiments, we fed subjects a nightly meal and maintained both species at approximately 90% free-feeding weight. This weight range is similar to that observed for both species in the wild (Snowdon & Soini 1988; Stevenson & Rylands 1988). Before beginning the experiment, the marmosets weighed 310–365 g, and the tamarins weighed 400–465 g (Table 1).

Experimental Design

We presented subjects with a choice between two immediate and six delayed banana-flavoured food pellets (Research Associates, 45 mg of purified primate diet pellets). We used these food pellets to both gain direct control over the quantity and size of food delivered and to directly contrast with prior experiments using the same food rewards. Each subject experienced two food distribution conditions (normal and incremental) at three delays to the large reward (5 s, 10 s and 15 s). We pseudorandomized the order of presentation such that each subject started with a different condition/delay combination. In the normal distribution, all the food dispensed approximately at once following the chosen delay (constraints on the dispensing machine resulted in a short 0.4-s IPI between each successive piece of food being dispensed). In the incremental condition, an additional IPI was added between each individual piece of food being dispensed (Fig. 1). We calculated this IPI for each subject to manipulate an individual's overall handling time (Table 1). For each condition–delay combination, subjects completed three consecutive session replicates.

Table 1. Incremental condition interpellet interval (IPI) for each subject, based on average handling time for six pellets

Subject	Species	Weight (g)	Handling time (s)	IPI (s)
ANT	M	310	9.99	3.3
OTH	M	315	15.3	5.1
JUL	M	365	11.1	3.7
ROM	M	330	15.3	5.1
RB	T	440	14.4	4.8
SH	T	465	14.1	4.7
JM	T	450	11.4	3.8
PJ	T	400	23.7	7.9

To determine the IPI for each subject, we first measured each individual's average handling time for consuming the larger reward of six pellets (h_6) over three training sessions in which all the food dispensed at once (as in the normal condition). Handling time consisted of the period from when food was first available to when the subject placed the last piece in his/her mouth. We divided this measurement by the total number of pellets (six) to determine the per-pellet handling time, and finally doubled it to lengthen each subject's individual IPI. That is,

$$\text{Incremental IPI} = 2\left(\frac{h_6}{6}\right)$$

Apparatus and Set-up

We placed subjects in a small transport cage (30 × 30 × 30 cm) inside a Plexiglas test enclosure (46 cm tall, 35.5 cm wide and 40 cm deep; Fig. 2a). The back and side walls of the test apparatus were opaque black; the front was white and had three openings into which subjects could reach (Fig. 2b). Transparent Plexiglas doors prevented access to the two side openings. When subjects were allowed to make a choice, solenoids raised the doors, giving access to the openings, which contained small plastic bars mounted by a spring to a back wall. Subjects touched these tools to make their choice: by reaching through either of the openings to touch the tool inside, subjects broke an infrared beam (MED Associates ENV-253SD) positioned slightly above the tool. Breaking either beam signalled a choice and started the corresponding delay. Food dropped into a bin in the centre opening via a small tube attached to a pellet dispenser (MED Associates ENV-203IR). A small camera (Videolabs FlexCam) mounted directly outside the food bin allowed the experimenter

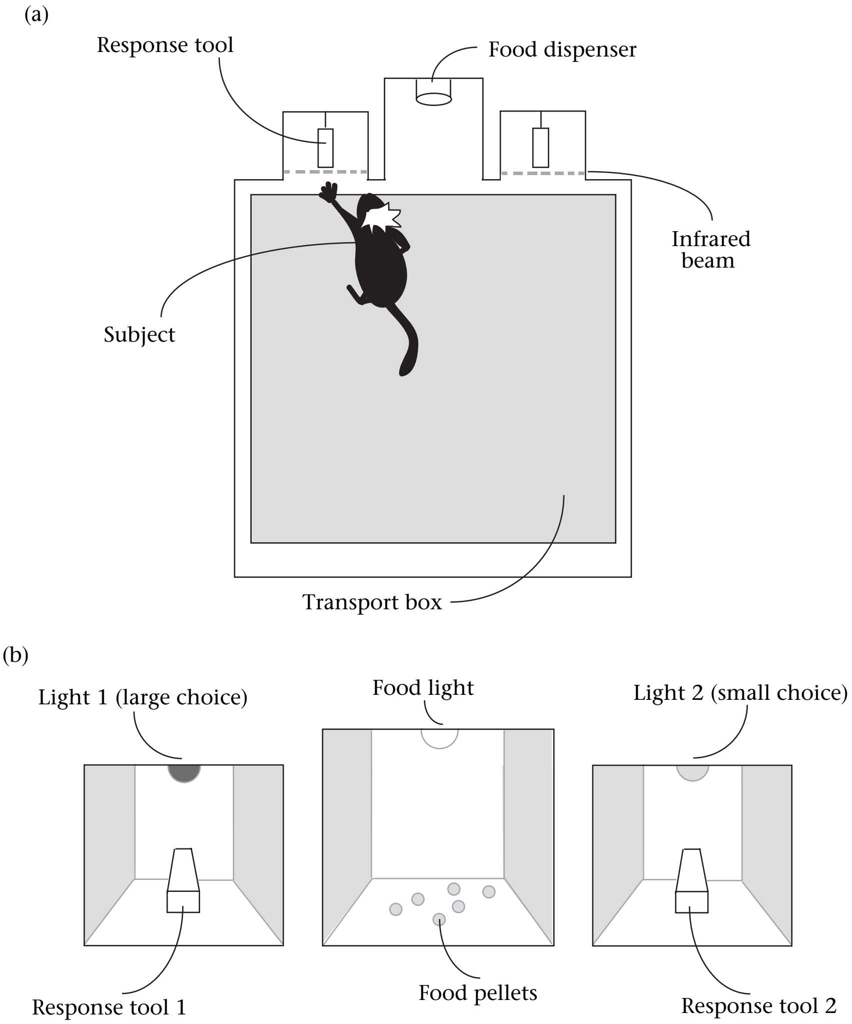


Figure 2. Experimental apparatus. The transport cages containing the subjects were placed in the operant chamber. (a) Top view of chamber: subjects made a choice by reaching into one of the two side boxes and touching the response tool inside, thereby breaking an infrared beam. (b) Subjects' view of front panel: once the chosen delay ended, food rewards dispensed into the centre food bin.

to observe when the subject finished eating all the food in a given trial. A computer running MED-PC control and data acquisition software controlled all outputs (stimulus lights, pellet dispenser, tone generator and solenoids) and recorded inputs (infrared beams, user-input button) via a program written in Medstate Notation.

Trial and Session Procedures

Every trial consisted of an initial intertrial interval (ITI) of 30 s, a 15-s period during which subjects could make a choice, the delay following the subject's choice, and a handling period during which subjects consumed the food reward. At the beginning of a choice period, a short (0.5 s) tone sounded, both doors opened, and lights above the tools illuminated to denote each available option. We counterbalanced across subjects whether purple or yellow lights were associated with receiving two pellets immediately or six pellets after a time delay. For all trials, we randomly assigned the side of the enclosure for larger and smaller rewards. Subjects then had 15 s to make a response. Once subjects responded, the light associated with the chosen option flashed, a tone sounded, the alternate option's light extinguished, and its door closed. The chosen delay then began, and during the delay, the experimenter closed the chosen door (via a user-input button) after the subject removed his/her hand.

Once the delay finished, the tone stopped and the white light in the centre food bin illuminated. This light flashed every time a piece of food dispensed; once all the food was dispensed, the light remained illuminated during the handling period. The light associated with the subject's choice also remained illuminated during the handling time. When the subject finished eating (marked when the subject placed the last piece of food in his/her mouth), the experimenter pressed the user response button to extinguish all lights and begin the next ITI.

Each daily session consisted of 14 completed trials. For each condition/delay combination, subjects first completed a forced-choice session in which they received only one option per trial (either two pellets immediately or six pellets after a delay); this session allowed them to gain familiarity with the reward contingencies. To pass the forced-choice session, subjects could fail to make a choice within 15 s no more than twice in a session. If a subject failed to choose more than two times, then we aborted the session and started afresh the next day. After passing the forced-choice session, subjects completed three free-choice sessions at that same condition and delay, in which we allowed them to freely choose between the two options. In a free-choice session, the first four trials were forced-choice, and the last 10 were free-choice. Subjects had to successfully complete all forced trials but could fail to make a choice in no more than two nonconsecutive free trials.

Statistical Analysis

We analysed the data using repeated measures analysis of variance (ANOVA). For the choice data, we performed two ANOVAs. In the first, we used condition and delay period as within-subjects factors (a 2 × 3 design) and species as a between-subjects factor. In the second, we reanalysed these data to examine whether subjects' choices changed over the course of a session by using trial number as a within-subjects factor (10 trials) and species as a between-subjects factor. Choice data consisted of the proportion of total picks for the large reward in a free-choice session. We arcsine, square-root transformed the proportions to normalize the data. Two separate ANOVAs were conducted on the timing data: one for choice latencies (time between stimulus onset and choice) and one for per-pellet handling time (time between first pellet dispensed and last pellet consumed divided by number of pellets). Both of these ANOVAs had condition and delay period as within-subjects factors and species as a between-subjects factor. We used the Huynh–Feldt correction when assumptions of sphericity or homogeneity of variance were violated (Myers & Well 1995). We used Bonferroni test statistics on all comparisons of means in the within-subject design, and we report the pairwise comparisons with $P \leq 0.05$ (Maxwell & Delaney 2004).

RESULTS

IPI Determination

Based on observational measurements of individual-specific handling times for six pellets (range 9.99–23.7 s), each subject was assigned an experimental IPI that doubled their handling time (range 3.3–7.9 s; Table 1).

Handling Time and Choice Data

Subjects required a mean ± SE of 2.3 ± 0.2 s to consume one piece of food in the normal condition and a mean ± SE of 4.3 ± 0.5 s to consume one piece in the incremental condition. As factors, neither delay (ANOVA: $F_{2,\ 10} = 2.32$, $P = 0.15$) nor species (ANOVA: $F_{1,\ 6} = 0.85$, $P = 0.39$) influenced handling times: marmosets and tamarins took equivalent amounts of time to consume food rewards across all three delays.

Subjects (pooled across species) chose the large reward 74 ± 5% of the time at a 5-s delay-to-large, 70 ± 4% of the time at a 10-s delay, and 63 ± 5% of the time at a 15-s delay. These differences were not statistically significant (ANOVA: $F_{2,\ 12} = 1.51$, $P = 0.26$). Subjects chose the large reward 71 ± 4% of the time in the normal condition and 67 ± 4% of the time in the incremental condition, but this difference also was not significant (ANOVA: $F_{1,6} = 1.19$, $P = 0.32$). There was, however, a significant interaction between delay and condition (ANOVA: $F_{2,12} = 11.57$, $P < 0.01$). At the 15-s delay, subjects chose the large reward less on the incremental condition relative to the normal condition: subjects chose the large reward 71 ± 5% of the time in the normal condition, but only 56 ± 6% of the time when in the incremental condition (Bonferroni post hoc comparison: $P = 0.02$; Fig. 3). Moreover, subjects chose the large reward less in the incremental condition at the 15-s delay than in the incremental condition at a 10-s delay, as well as in the 5-s delay for both conditions (Bonferroni post hoc comparisons: $P < 0.05$). This indicates that subjects in both species devalued rewards with increased handling times when the delay to the large reward was long (Fig. 4).

The two species also differed with respect to the proportion of trials in which individuals chose the larger reward (ANOVA: $F_{1,\ 6} = 8.97$, $P = 0.02$). Across all delays and conditions, marmosets selected the large reward an average of 80 ± 5% of the time, whereas tamarins selected the large reward an average of 59 ± 5% of the time (Fig. 5).

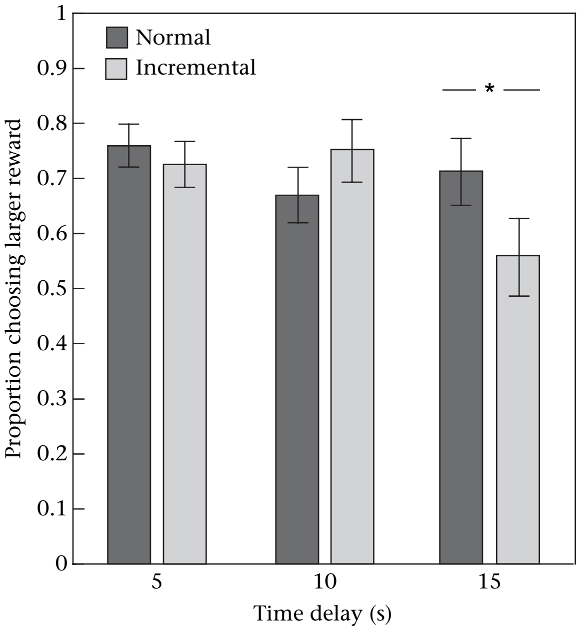


Figure 3. Mean ± SE proportion of trials during which subjects (collapsed across species) chose the larger reward when the entire food reward was dispensed at once (normal condition) and when an additional interpellet interval was added before each additional food pellet was dispensed (incremental condition) following a delay-to-reward of 5, 10 or 15 s. *$P < 0.05$.

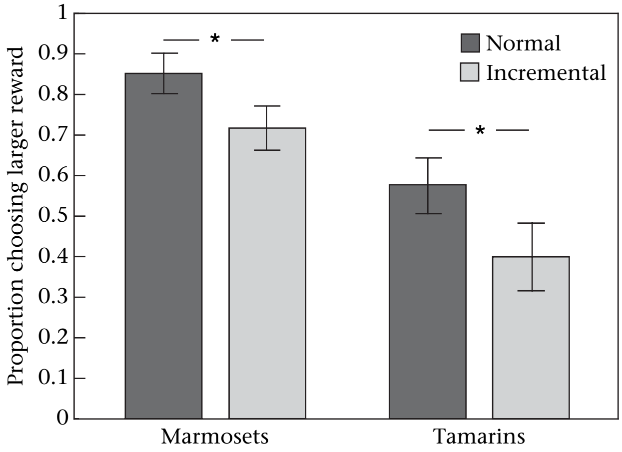


Figure 4. Mean ± SE proportion of trials during which marmosets and tamarins chose the larger reward in each condition (normal, incremental) following a 15-s delay-to-reward. $*P < 0.05$.

A second ANOVA on the choice data for each subject's performance across a session indicated that there was no effect of trial (ANOVA: $F_{9,\ 54} = 0.60$, $P = 0.79$) on discounting preferences. Subjects of both species chose consistently throughout an experimental session, suggesting that the species difference in discounting level did not result from different levels of satiation.

DISCUSSION

Handling Time and Rate Maximization

When faced with a decision between receiving two pieces of food immediately and six pieces of food after 15 s, handling time affected discounting preferences in tamarins and marmosets. This implies that both species showed sensitivity to differences in handling time and adjusted their preferences to account for these differences. As predicted by a rate maximization model in which animals maximize over the entire delay and handling time interval (Bateson & Kacelnik 1996), a longer handling time caused marmosets and tamarins to be less likely to choose the larger reward.

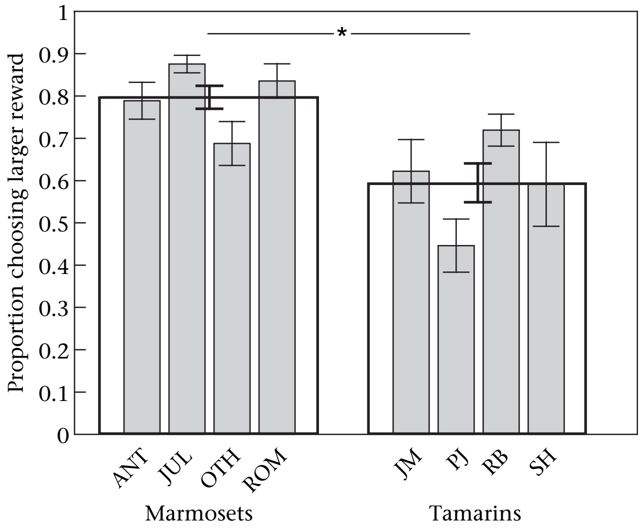


Figure 5. Mean ± SE proportion of trials during which individuals of both species chose the larger reward (collapsed across all delays and conditions). $*P < 0.05$.

Although many aspects of long-term rate do not affect animal choices, tamarins and marmosets adjust their behaviour to account for the handling times associated with food rewards. Why do animals include handling time within their time horizon but ignore other temporal intervals in a discounting task (such as ITI and postfeeding delays)? One possibility is that animals have evolved to attend only to those intervals that occur between a decision and its outcome (see Bateson & Kacelnik 1996). Animals have control over the time they spend processing food because different options are associated with different handling times. In contrast, intervals that do not occur between a decision and its outcome are not under the direct control of a forager: animals have no choice but to wait their entire duration. Animals may therefore pay more attention to those temporal intervals that they can directly affect with their behaviour but ignore those that are obligatory and out of their control, even if they influence the optimal long-term intake rate. Gallistel & Gibbon (2000, page 322) make the analogy between ignoring certain time intervals and the 'sunk cost' effect described by economists, which is 'a cost that appears to be relevant to the computation of the utility of an alternative but in fact is not and ought to be ignored in rational (normative) economic decision making'.

Handling time did not significantly affect discounting choices across all delays, however, suggesting that the increases in handling time are more relevant to tamarins and marmosets when the delay to accessing food rewards is already long. This contradicts the predictions of rate maximization, because handling time should affect discounting levels more when it comprises a greater proportion of the total time interval. Since handling times are a larger proportion of total time at short delays-to-food access, according to rate maximization, handling time should influence decisions more at the 5-s delay-to-large than the 15-s delay-to-large. One possible explanation for our finding is that, despite increased handling times, subjects were still below their indifference points at the shorter delays. That is, even including the additional handling time does not push the subject to the point at which it should switch preferences. Alternatively, delays to food and handling times may not be weighted linearly in discounting decisions; for example, handling times may be more heavily weighted depending on the length of the initial delay to accessing the food. Therefore, if we had included longer delays-to-large, we might have seen a larger effect of handling time at those delays. One way to address these possibilities is to perform a discounting titration that simultaneously manipulates both delay-to-access and handling time. Such an experiment could assess the differential contributions of delays and handling time to the monkeys' discounting preferences.

The Temporal Properties of Food and Ecological Factors

The results of this experiment also replicate the earlier findings by Stevens et al. (2005a) that tamarins devalue rewards more heavily than marmosets in temporal discounting tasks. Although that experiment used a titration adjustment procedure to determine subjects' indifference points between the large and small rewards, and this experiment examined subject's preferences across three different delays to the large reward, tamarins discounted more steeply than marmosets in both paradigms. Additionally, in the previous study, subjects had full visual access to both potential food rewards, whereas in this study, neither reward was visible until after the chosen time delay.

As previously mentioned, differences in ecology and diet composition may explain the observed difference in discounting level between these two species. The variation in the temporal distribution of their primary food sources further suggests that tamarins and marmosets may be differentially sensitive to changes in handling time: marmosets may tolerate relatively long handling times, whereas tamarins might be more sensitive to variation in search time. This experiment, however, indicates that both species respond similarly to increases in handling times, suggesting a more general role of handling time in foraging strategies. Nevertheless, tamarins' and marmosets' respective dietary specializations raise the possibility that more natural ways of altering handling times may trigger different responses. The handling time manipulation presented here was very general and involved altering the handling time of a food item that the monkeys do not naturally consume. Additionally, because banana pellets are neither natural nor available in their daily diets, subjects had to learn and remember the handling times required in different conditions. Moreover, they had reduced control over the times they spent processing the food. This raises the possibility that when feeding on actual gum, fruit or insects, such known physical entities might cue different discounting levels.

Although the experiment presented here did not explicitly address the mechanistic basis of discounting decisions, one possible explanation for the differences in tamarin and marmoset discounting levels is that the two species differ in either their ability to time intervals or in the strength of their timing preferences (for a reviews of cross-species timing experiments, see Gibbon et al. 1984; Richelle & Lejeune 1984). Few studies have explicitly studied timing abilities in primates, and none have compared across two or more species using the same method. One possibility, then, is that tamarins and marmosets differ in their abilities to discriminate temporal intervals. Their similar responses to the incremental condition suggest a lack of large perceptual differences, especially since both species reduced their discounting levels in response to small additional IPIs. However, the two species may differ in their temporal preferences for delays to food: marmosets may actually lack strong time preferences relative to the tamarins. For a marmoset, waiting the shorter delay and waiting the longer delay may be (subjectively) about the same. If they do indeed lack strong time preferences, then the length of delay would influence marmosets less than tamarins when making a discounting decision.

What Is Handling Time and When Is It Relevant?

A possible criticism of our manipulation is its artificiality. We construe the incremental condition as a manipulation of handling time, but the subjects may not have perceived it in this way. Rather than treating the incrementally dispensed food as one reward distributed over a longer interval, they may have interpreted it as many separate, discrete rewards (although Brunner & Gibbon (1995) suggest this is not the case for pigeons). Our experimental design attempted to minimize this possibility by making the additional IPI a function of each individual's handling time. However, in the incremental condition, subjects also did not have visual access to the entire reward throughout the entire handling time period. Since visual attention influences impulsivity in human children (Mischel & Ebbesen 1970), it may influence delay mechanisms in other animals as well.

The potential artificiality of this experiment leads to the further question of how we conceptualize handling time. Handling time is generally treated as a uniform process, but clearly many different activities can compose total handling time (Lea 1979; Snyderman 1983). In this experiment alone, handling time included retrieving the food, eating it, and additional periods of rest during which food was available but the animal had not finished consuming it. Do animals perceive all of these components in the same way, or do they weight them differently in discounting contexts? Do animals perceive our task of waiting between pellets as an increase in handling time? One way to examine whether the composition of handling time matters is to look at discounting across food types that require different sorts of processing. The subjects could easily consume the food rewards utilized in this experiment, but other types of food require more elaborate processing, such as removing seeds from fruit and extracting edible parts of prey items. Manipulating handling time via a more realistic foraging task involving the presentation of fruit or insects will enrich our understanding of how handling time affects discounting in a broader range of foraging contexts.

Similarly, rate maximization models assume that delays-to-food access and time spent handling food are interchangeable: both contribute to the total rate of intake, so increases in one are equivalent to increases in the other. There is evidence, however, that animals may not treat these periods as equivalent. Shettleworth & Jordan (1986) found that rats prefer handling sunflower seeds (that is, spend time removing their husk) over waiting to receive unhusked seeds. The authors point out a potential mechanistic explanation for this result: a husked seed may act as a stronger reinforcer than a delay signal. Since waiting is a passive behaviour, whereas processing is more active, having our subjects simply wait while individual food rewards became available may not be an ideal manipulation of handling time. The level of attention focused on the food item could affect time perception (Brown 1985), thereby influencing rate calculation. To test fully whether waiting and processing are equivalent, one must combine the Shettleworth & Jordan design with our own, having subjects either wait for each reward item or process an equivalent amount for an equivalent time period in a discounting paradigm.

Finally, in natural foraging settings, the delay and handling times may involve different activities and be associated with different risks. For example, a food reward that is being processed is more certain than one that has not yet been obtained. But long handling times may also be risky for a different reason: competitors can steal the food item, which is a risk that obviously does not exist before food has been obtained. As such, long handling times may be more relevant to some foragers than long search times.

Conclusions

Both tamarins and marmosets adjusted their choices to account for handling time at long delays to accessing food rewards. They responded similarly to increases in handling time, despite overall differences in discounting levels: tamarins devalued future rewards more steeply than marmosets, replicating earlier results on temporal discounting in these species (Stevens et al. 2005a). Combined with work by Bateson & Kacelnik (1996), our work implies that models of discounting behaviour that include handling times may better account for the choices that animals make than models that only include delays to food. Further experiments are necessary to determine how animals weight handling time relative to delays to food, as well as whether different types of food-processing activities have equal influence on discounting decisions.

Acknowledgments

We are grateful for funding from the Harvard College Research Program to A.G.R., the National Research Service Award (NIH) to J.R.S., and a National Science Foundation-ROLE grant to M.D.H. We thank Jen Gong, Sarah Heilbronner and Mike Mohammed for assistance in conducting the experiments. We appreciate comments on this manuscript from three anonymous referees. This experiment was approved by the Institutional Animal Care and Use Committee at Harvard University (Animal Subjects Codes 92-16 and 22-07) and conforms to the ABS/ASAB Guidelines for the Use of Animals in Research.

References

Ainslie, G. 1974. Impulse control in pigeons. *Journal of the Experimental Analysis of Behavior*, **21**, 485–489.

Bateson, M. & Kacelnik, A. 1996. Rate currencies and the foraging starling: the fallacy of the averages revisited. *Behavioral Ecology*, **7**, 341–352.

Brown, S. W. 1985. Time perception and attention: the effects of prospective versus retrospective paradigms and task demands on perceived duration. *Perception and Psychophysics*, **38**, 115–124.

Brunner, D. & Gibbon, J. 1995. Value of food aggregates: parallel versus serial discounting. *Animal Behaviour*, **50**, 1627–1634.

Coimbra-Filho, A. F. & Mittermeier, R. A. 1976. Exudate-eating and tree-gouging in marmosets. *Nature*, **262**, 630.

Cristol, D. A. 2001. American crows cache less preferred walnuts. *Animal Behaviour*, **62**, 331–336.

Dumont, E. R. 1997. Cranial shape in fruit, nectar, and exudate feeders: implications for interpreting the fossil record. *American Journal of Physical Anthropology*, **102**, 187–202.

Ferrari, S. F. 1993. Ecological differentiation in the Callitrichidae. In: *Marmosets and Tamarins: Systematics, Ecology, and Behavior* (Ed. by A. B. Rylands), pp. 314–328. Oxford: Oxford University Press.

Ferrari, S. F. & Lopes Ferrari, M. A. 1989. A re-evaluation of the social organization of the Callitrichidae with reference to the ecological differences between genera. *Folia Primatologica*, **52**, 132–147.

Ferrari, S. F., Lopes, M. A. & Krause, E. A. 1993. Gut morphology of *Callithrix nigriceps* and *Saguinus labiatus* from western Brazilian Amazonia. *American Journal of Physical Anthropology*, **90**, 487–493.

Gallistel, C. R. & Gibbon, J. 2000. Time, rate, and conditioning. *Psychological Review*, **107**, 289–344.

Garber, P. A. 1980. Locomotor behavior and feeding ecology of the Panamanian tamarin (*Saguinus oedipus geoffroyi*, Callitrichidae, Primates). *International Journal of Primatology*, **1**, 185–201.

Garber, P. A. 1992. Vertical clinging, small body size, and the evolution of feeding adaptations in the Callitrichinae. *American Journal of Physical Anthropology*, **88**, 469–482.

Garber, P. A. 1993. Feeding ecology and behaviour of the genus *Saguinus*. In: *Marmosets and Tamarins: Systematics, Behaviour, and Ecology* (Ed. by A. B. Rylands), pp. 273–295. Oxford: Oxford University Press.

Gibbon, J., Church, R. M. & Meck, W. H. 1984. Scalar timing in memory. *Annals of the New York Academy of Sciences*, **423**, 52–77.

Green, L., Fisher, E. B., Perlow, S. & Sherman, L. 1981. Preference reversal and self-control: choice as a function of reward amount and delay. *Behaviour Analysis Letters*, **1**, 43–51.

Harrison, M. L. & Tardif, S. D. 1994. Social implications of gummivory in marmosets. *American Journal of Physical Anthropology*, **95**, 399–408.

Hauser, M. D., Newport, E. & Aslin, R. 2001. Segmentation of the speech stream in a non-human primate: statistical learning in cotton-top tamarins. *Cognition*, **78**, B53–B64.

Hauser, M. D., Chen, M. K., Chen, F. & Chuang, E. 2003. Give unto others: genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. *Proceedings of the Royal Society of London, Series B*, **270**, 2363–2370.

Jacobs, L. F. 1992. The effect of handling time on the decision to cache by gray squirrels. *Animal Behaviour*, **43**, 522–524.

Kacelnik, A. 1997. Normative and descriptive models of decision making: time discounting and risk sensitivity. In: *Characterizing Human Psychological Adaptations* (Ed. by G. R. Bock & G. Cardew), pp. 51–70. Chichester: J. Wiley.

Kacelnik, A. 2003. The evolution of patience. In: *Time and Decision: Economic and Psychological Perspectives on Intertemporal Choice* (Ed. by G. Loewenstein, D. Read & R. F. Baumeister), pp. 115–138. New York: Russell Sage Foundation.

Lacher, T. E., Dafonseca, G. A. B., Alves, C. & Magalhaescastro, B. 1981. Exudate-eating, scent-marking, and territoriality in wild populations of marmosets. *Animal Behaviour*, **29**, 306–307.

Lea, S. E. G. 1979. Foraging and reinforcement schedules in the pigeon: optimal and non-optimal aspects of choice. *Animal Behaviour*, **27**, 875–886.

Logue, A. W. 1988. Research on self-control: an integrating framework. *Behavioral and Brain Sciences*, **11**, 665–709.

Logue, A. W., Smith, M. E. & Rachlin, H. 1985. Sensitivity of pigeons to prereinforcer and postreinforcer delay. *Animal Learning & Behavior*, **13**, 181–186.

Maxwell, S. E. & Delaney, H. D. 2004. *Designing Experiments and Analyzing Data: a Model Comparison Approach*. 2nd edn. Mahwah, New Jersey: L. Erlbaum.

Mazur, J. E. 1987. An adjusting procedure for studying delayed reinforcement. In: *Quantitative Analyses of Behavior: the Effect of Delay and of Intervening Events on Reinforcement Value* (Ed. by M. L. Commons, J. E. Mazur, J. A. Nevin & H. Rachlin), pp. 55–73. Hillsdale, New Jersey: L. Erlbaum.

Mazur, J. E. 1989. Theories of probabilistic reinforcement. *Journal of the Experimental Analysis of Behavior*, **51**, 87–99.

Mazur, J. E. 2000. Tradeoffs among delay, rate, and amount of reinforcement. *Behavioural Processes*, **49**, 1–10.

Miller, C. T., Weiss, D. J. & Hauser, M. D. 2002. Mechanisms of acoustic perception in cotton-top tamarins. In: *Primate Audition: Behavior and Neurobiology* (Ed. by A. A. Ghazanfar), pp. 43–60. Boca Raton, Florida: CRC Press.

Mischel, W. & Ebbesen, E. B. 1970. Attention in delay of gratification. *Journal of Personality and Social Psychology*, **16**, 329–337.

Myers, J. L. & Well, A. D. 1995. *Research Design and Statistical Analysis*. Hillsdale, New Jersey: L. Erlbaum.

Neyman, P. F. 1977. Aspects of the ecology and social organization of free-ranging cotton-top tamarins (*Saguinus oedipus*) and the conservation status of the species. In: *The Biology and Conservation of the Callitrichidae* (Ed. by D. G. Kleiman), pp. 39–71. Washington, D.C.: Smithsonian Institution Press.

Platt, M. L., Brannon, E. M., Briese, T. L. & French, J. A. 1996. Differences in feeding ecology predict differences in performance between golden lion tamarins (*Leontopithecus rosalia*) and Wied's marmosets (*Callithrix kuhli*) on spatial and visual memory tasks. *Animal Learning & Behavior*, **24**, 384–393.

Power, M. L. 1996. The other side of callitrichine gummivory: digestibility and nutritional value. In: *Adaptive Radiations of Neotropical Primates* (Ed. by M. A. Norconk, A. L. Rosenberger & P. A. Garber), pp. 97–110. New York: Plenum.

Power, M. L. & Oftedal, O. T. 1996. Differences among captive callitrichids in the digestive responses to dietary gum. *American Journal of Primatology*, **40**, 131–144.

Rachlin, H. 2000. *The Science of Self-Control*. Cambridge, Massachusetts: Harvard University Press.

Rachlin, H. & Green, L. 1972. Commitment, choice and self-control. *Journal of the Experimental Analysis of Behavior*, **17**, 15–22.

Richelle, M. & Lejeune, H. 1984. Timing competence and timing performance: a cross-species approach. *Annals of the New York Academy of Sciences*, **423**, 254–268.

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

Rylands, A. B. & de Faria, D. S. 1993. Habitats, feeding ecology and range size in the genus *Callithrix*. In: *Marmosets and Tamarins: Systematics, Behaviour, and Ecology* (Ed. by A. B. Rylands), pp. 262–272. Oxford: Oxford University Press.

Santos, L. R., Miller, C. T. & Hauser, M. D. 2003. Representing tools: how two non-human primate species distinguish between the functionally relevant and irrelevant features of a tool. *Animal Cognition*, **6**, 269–281.

Shettleworth, S. J. 1985. Handling time and choice in pigeons. *Journal of the Experimental Analysis of Behavior*, **44**, 139–155.

Shettleworth, S. J. & Jordan, V. 1986. Rats prefer handling food to waiting for it. *Animal Behaviour*, **34**, 925–927.

Snowdon, C. T. & Soini, P. 1988. The tamarins, genus *Saguinus*. In: *Ecology and Behavior of Neotropical Primates* (Ed. by R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho & G. A. B. Fonseca), pp. 223–298. Washington, D.C.: World Wildlife Fund.

Snyderman, M. 1983. Optimal prey selection: partial selection, delay of reinforcement and self-control. *Behaviour Analysis Letters*, **3**, 131–147.

Stephens, D. W. & Krebs, J. R. 1986. *Foraging Theory*. Princeton, New Jersey: Princeton University Press.

Stephens, D. W. & Anderson, D. 2001. The adaptive value of preference for immediacy: when shortsighted rules have farsighted consequences. *Behavioral Ecology*, **12**, 330–339.

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

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

Stevenson, M. F. & Rylands, A. B. 1988. The marmosets, genus *Callithrix*. In: *Ecology and Behavior of Neotropical Primates* (Ed. by R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho & G. A. B. Fonseca), pp. 131–222. Washington, D.C.: World Wildlife Fund.

Sussman, R. W. & Kinzey, W. G. 1984. The ecological role of the Callitrichidae: a review. *American Journal of Physical Anthropology*, **64**, 419–449.

Taylor, A. B. & Vinyard, C. J. 2004. Comparative analysis of masseter fiber architecture in tree-gouging (*Callithrix jacchus*) and nongouging (*Saguinus oedipus*) callitrichids. *Journal of Morphology*, **261**, 276–285.

Tobin, H. & Logue, A. W. 1994. Self-control across species (*Columba livia*, *Homo sapiens*, and *Rattus norvegicus*). *Journal of Comparative Psychology*, **108**, 126–133.

Uller, C., Hauser, M. D. & Carey, S. 2001. Spontaneous representation of number in cotton-top tamarins (*Saguinus oedipus*). *Journal of Comparative Psychology*, **115**, 248–257.

Vinyard, C. J., Wall, C. E., Williams, S. H. & Hylander, W. L. 2003. Comparative functional analysis of skull morphology of tree-gouging primates. *American Journal of Physical Anthropology*, **120**, 153–170.

Woodrey, M. S. 1990. Economics of caching versus immediate consumption by white-breasted nuthatches: the effect of handling time. *Condor*, **92**, 621–624.