Will Travel for Food: Spatial Discounting in Two New World Monkeys

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Abstract

Nonhuman animals steeply discount the future, showing a preference for small, immediate over large, delayed rewards [1–5]. Currently unclear is whether discounting functions depend on context. Here, we examine the effects of spatial context on discounting in cotton-top tamarins (*Saguinus oedipus*) and common marmosets (*Callithrix jacchus*), species known to differ in temporal discounting [5]. We presented subjects with a choice between small, nearby rewards and large, distant rewards. Tamarins traveled farther for the large reward than marmosets, attending to the ratio of reward differences rather than their absolute values. This species difference contrasts with performance on a temporal task in which marmosets waited longer than tamarins for the large reward. These comparative data indicate that context influences choice behavior, with the strongest effect seen in marmosets who discounted more steeply over space than over time. These findings parallel details of each species' feeding ecology. Tamarins range over large distances and feed primarily on insects, which requires using quick, impulsive action. Marmosets range over shorter distances than tamarins and feed primarily on tree exudates, a clumped resource that requires patience to wait for sap to exude [6–9]. These results show that discounting functions are context specific, shaped by a history of ecological pressures.

Results and Discussion

Tradeoffs between smaller, immediate gains and larger, delayed rewards are ubiquitous for both humans and nonhuman animals (hereafter, animals) [10, 11]. Many animal species highly discount the future, devaluing rewards by 50% in the first few seconds of delay [1–3, 5, 12, 13].

Animal discounting stands in stark contrast to human discounting, where subjects wait for weeks, months, and years [10, 14]. In these experiments, however, subjects often chose between hypothetical monetary rewards over hypothetical timeframes (e.g., "Would you prefer to receive $50 now or $2000 in three years?"). Experiments that more closely mimic the animal foraging tasks by offering real monetary rewards and making subjects wait for real time delays show much more impulsive choices in humans [15]. This implies that the experimental context in which discounting choices are framed can directly influence decision making.

Few studies have examined the effect of context on discounting behavior in animals (but see [4, 16–19]). Here, we examine the role of context by comparing choice preferences in different types of discounting tasks: temporal and spatial.

In previous research on temporal discounting, we offered cotton-top tamarins and common marmosets choices between a small food reward available immediately and a larger reward available after a time delay [5]. Results showed that marmosets waited significantly longer for the larger reward, suggesting that they discounted the temporal delay less steeply than tamarins. In the current task, we assessed these species' spatial discounting levels by presenting subjects with a choice between a smaller, closer reward and a larger, more distant reward. This choice maps onto natural foraging decisions frequently faced by animals: consume the few remaining food items nearby or travel to locate an untapped patch replete with food [20, 21]. We placed the close reward 35 cm from the starting position and placed the distant reward at one of seven distances, ranging from 35 to 245 cm away (Figure 1). With this design, we characterized how both species devalue food rewards as a function of travel distance. If context does not affect discounting, then we should find the same pattern observed in the temporal discounting experiment. Because the time to receiving the reward is proportional to the distance traveled, the more patient marmosets should also prefer to travel farther. If, however, context does influence discounting in these primates (as it can in humans [15, 22–24]), spatial discounting preferences may differ from temporal discounting preferences.

The magnitude of the reward also influences discounting decisions. Models predict that the ratio between reward values, and not the absolute magnitude of those rewards, should determine discounting patterns [1, 25, 26]. Discounting studies in pigeons and rats support these predictions: varying the magnitude of rewards does not influence discounting levels [3, 27, 28] (but see [29, 30] for possible exceptions). In contrast, humans seem to discount small rewards more highly than large rewards [14, 31, 32]. We tested for magnitude effects by offering our subjects two sets of numerical contrasts. Subjects chose between either one close and three far food pellets in one condition or two close and six far pellets in another condition. Therefore, we maintained the 1:3 ratio of the reward amounts but varied their absolute magnitudes, allowing us to assess whether these monkeys ignore magnitude, as demonstrated by other animals, or discount differently over different magnitudes like humans.

When we presented both rewards at the shortest distance (increment one), subjects (pooled over species) chose the large reward in 96.1% ± 1.5% (mean ± SEM) of the trials but only chose it in 68.8% ± 8.0% of the trials when we placed the large reward at the farthest distance (increment seven). The
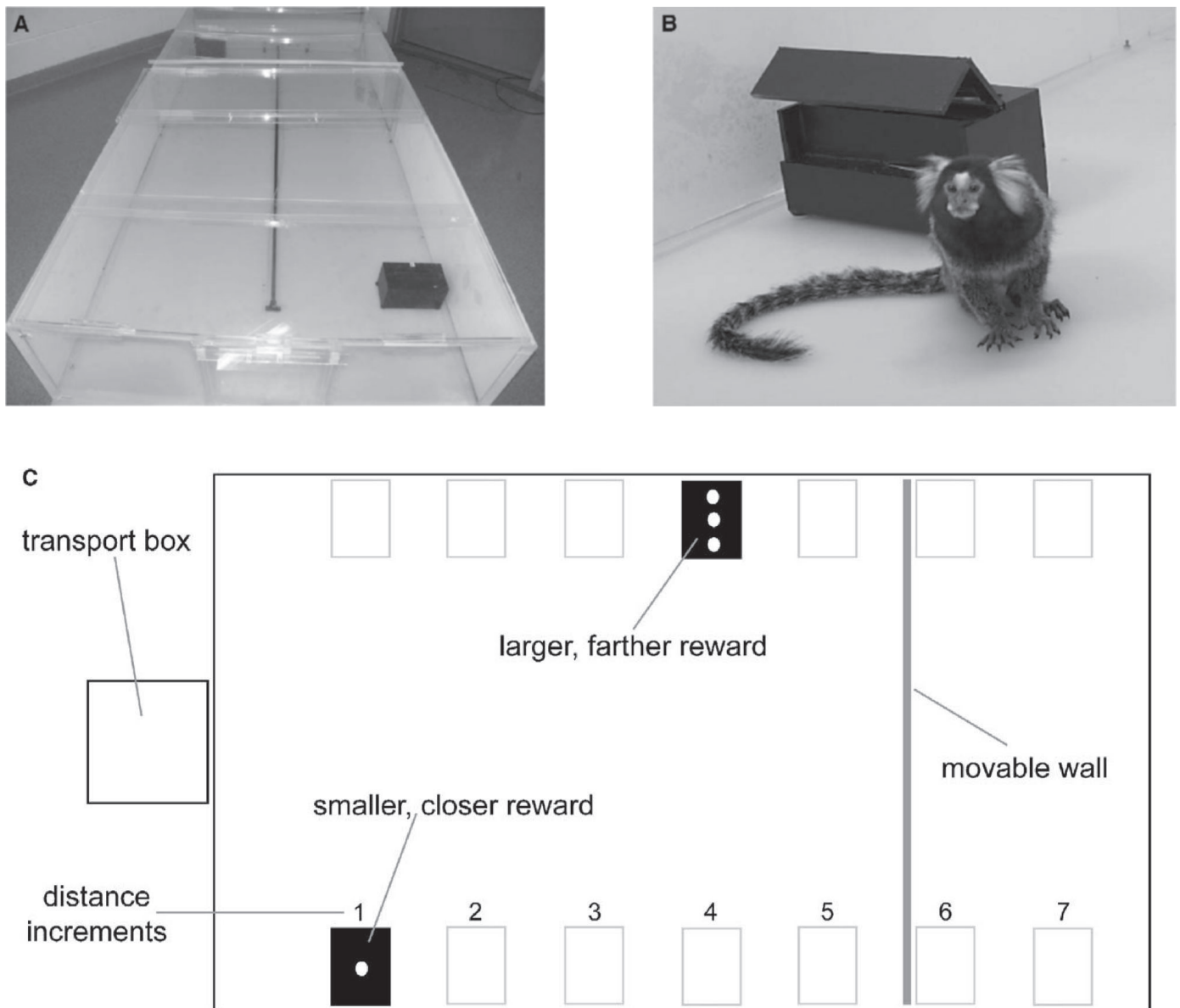
Figure 1. Experimental Apparatus
(A) Both tamarins and marmosets traveled to receive their rewards in a plexiglas enclosure.
(B) The food rewards were lined up in an array on a ledge in the box, each piece ~1 cm apart.
(C) Food boxes were placed at one of seven distances (35–245 cm) from the front of the enclosure. A wall was placed behind the far box.

distance to the large reward significantly affected the subject's probability of choosing the large reward (repeated-measures ANOVA: $F_{5,32}$ = 5.35, $p < 0.01$). Subjects reduced their preferences for the large reward when placed farther away from them. However, a species difference appears to drive this distance effect. The two species tended to differ in their overall preference for the large reward, although this difference did not reach statistical significance ($F_{1,6}$ = 4.42, p = 0.08). There was, however, a significant interaction between species and distance ($F_{5,33}$ = 3.43, p = 0.01). Marmosets selected the larger reward less at the farthest distances (increments six and seven) relative to the closest distance (increment one), but tamarins were equally likely to choose the larger reward at all

distances (Bonferroni posthoc tests, $p < 0.05$). Thus, marmosets selected the larger reward less frequently as a function of increasing distance, whereas tamarins maintained their preferences for the large reward independently of distance (Figure 2). Further analyses and a follow-up experiment suggest that neither satiation nor visual discrimination differences can account for this pattern (see the Supplemental Data available at the end of this article).

The marmosets' relative preference for near contrasts with their ability to wait longer than tamarins for the large reward in the temporal discounting task [5]. This reversal could occur because tamarins travel faster than marmosets, therefore requiring less time to receive the large reward. To inves-
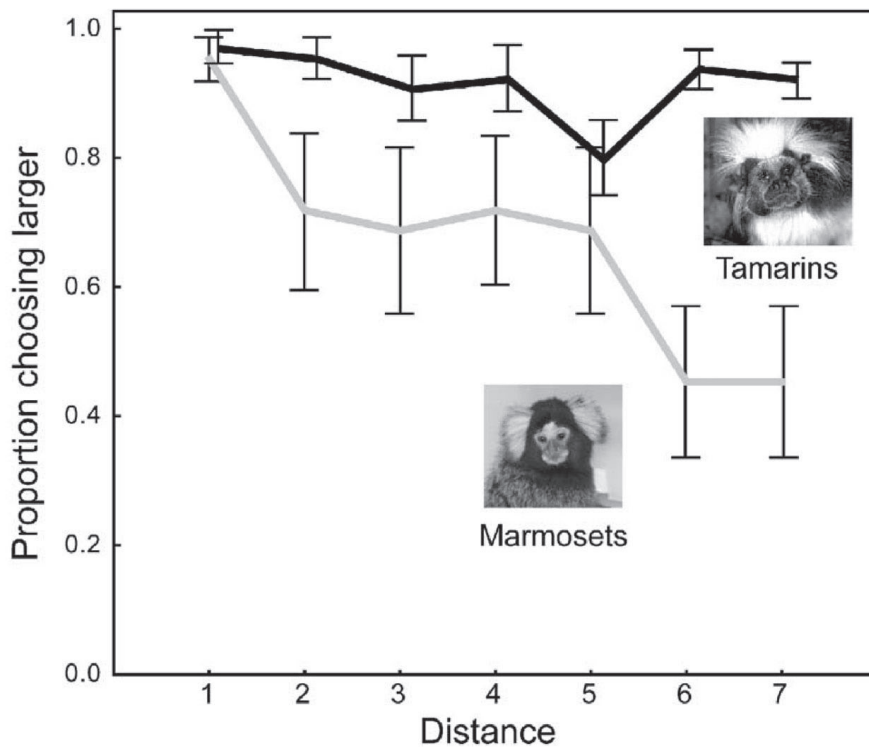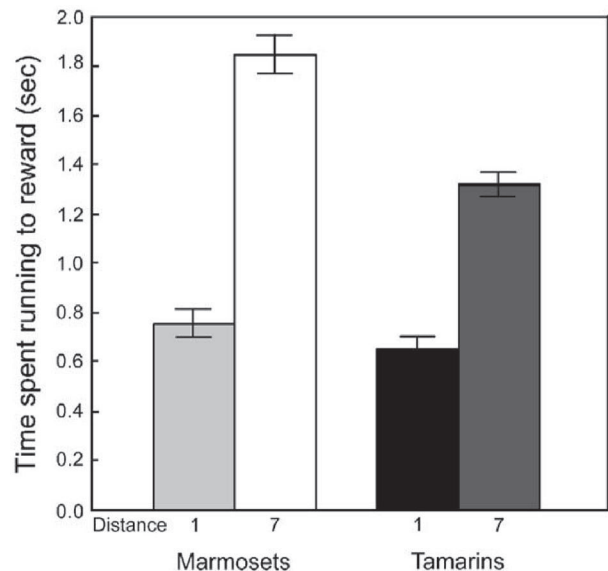
Figure 2. Effect of Species and Distance on Choice.
Tamarins maintained their preference for the large reward across all distances, whereas marmosets reduced their preference for the large reward as the distance to large increased. Error bars represent standard error of the mean.

tigate this possibility, we measured the time required to travel to the closest and farthest rewards in follow-up sessions (see Supplemental Data). Overall, tamarins ran to the boxes in less time than the marmosets ($F_{1,6}$ = 10.38, p = 0.02), and this difference depended on distance ($F_{1,6}$ = 15.93, p < 0.01): tamarins traveled to the farthest rewards faster than the marmosets (planned comparison, $F_{1,6}$ = 15.15, p < 0.01; Figure 3). Although marmosets did take longer than tamarins to reach the farthest reward, their travel times were nonetheless much shorter than the intervals that marmosets waited in the temporal discounting task. For temporal discounting, tamarins waited an average of 7.9 s for six food pellets whereas marmosets waited an average of 14.4 s [5]. To more quantitatively assess whether temporal discounting can account for the species difference in preferences, we used the hyperbolic discounting equation

$$V = \frac{A}{1 + kt}$$

(where V = subjective value of a reward, A = reward amount, k = discount factor, and t = time delay to receiving the reward [33]) to estimate a discounting factor for each species with the data from the temporal discounting experiment (see Supplemental Data). When we analyzed these discounting factors along with the travel times in the spatial discounting experiment, we found that these temporal discounting factors predicted complete preference for the more distant reward. Thus, we conclude that factors beyond those imposed by temporal discounting influenced the spatial discounting of marmosets. Though the marmoset results are inconsistent with temporal discounting alone, we cannot rule out an exclusive effect of temporal discounting on tamarins' preferences. Further data are needed to clarify the role of time in tamarin spatial preferences.

Figure 3. Effect of Species and Distance on Running Time
Tamarins and marmosets took the same amount of time to travel to the short distance (increment one, 35 cm). Tamarins, however, traveled to the farthest distance (increment seven, 245 cm) significantly faster than marmosets. Error bars represent standard error of the mean.

To determine whether reward magnitude influences tamarin and marmoset discounting, we compared sessions in which subjects chose between one and three pellets to those in which they chose between two and six pellets. Subjects showed no significant difference in preference for the larger
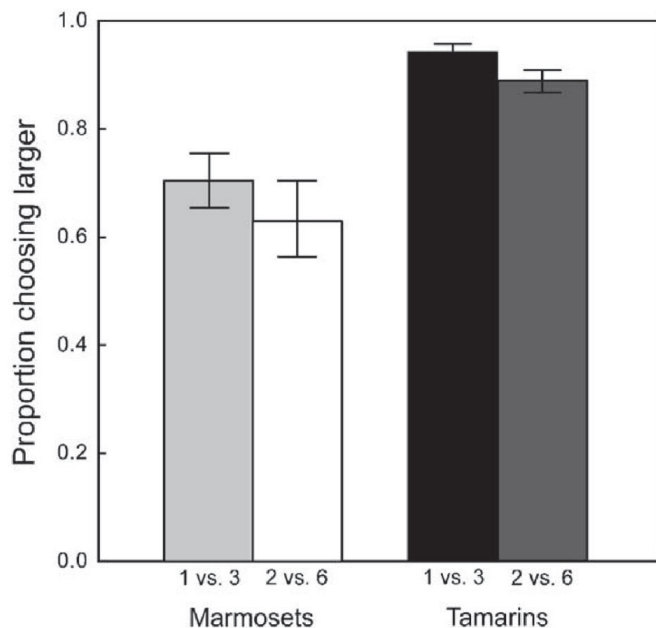
Figure 4. Effect of Species and Reward Magnitude on Choice
Neither tamarins nor marmosets altered their preferences for the larger reward when choosing between one and three pellets or between two and six pellets. Therefore, they maintained their preferences for the same ratio of rewards but ignored absolute magnitude. Error bars represent standard error of the mean.

reward across the two magnitude conditions ($F_{1,6}$ = 1.55, p = 0.26). There was also no significant interaction between magnitude and distance ($F_{5,29}$ = 1.50, p = 0.22) or between magnitude and species (Figure 4—$F_{1,6}$ = 0.03, p = 0.88). Therefore, changes in absolute magnitude did not influence discounting in these monkeys when the ratio between rewards remained constant.

Space and Time

Faced with the same sets of decisions between smaller, closer rewards and larger, more distant rewards, tamarins traveled farther for rewards than marmosets. Whereas marmosets reduced their preference for the large reward at the farthest distances (210–245 cm), tamarins did not discount at these distances. This demonstrates a reversal from the previous findings in which marmosets waited longer in a temporal discounting task [5]. Because the tamarins did not discount over these distances, we cannot determine whether spatial context in particular and context more generally affect their discounting. However, both the disparity between the marmosets' preferences in these two tasks and a quantitative analysis of their temporal discounting levels imply that context influenced their decision making—spatial discounting was not equivalent to temporal discounting. As a result, something in addition to time must have played a role in their spatial discounting decisions.

Two other factors may account for the observed differences: energetic costs of traveling and predation risk. Models of temporal discounting behavior that take only reward quantity and time delays into account may make good approximations of animal choice, because the metabolic cost of waiting for a food reward to appear may be negligible. However, when animals must actively work to obtain food, the associated energetic costs are no longer trivial. For example, European starlings (*Sturnus vulgaris*) adjusted their preference to account for both the gain associated with rewards and the travel cost of obtaining those rewards by means of walking as opposed to flying [16]. Additionally, brown capuchin monkeys (*Cebus apella*) demonstrated a rapid decrease in preferences for distant rewards, perhaps due to energetic costs of movement as well as temporal aspects of intake rate [20, 21]. It is likely that tamarins and marmosets also include the energetic costs of traveling in their spatial discounting decisions.

Concerning predation risk, Waite [17] found that gray jays (*Perisoreus canadensis*) were more reluctant to retrieve a large food reward deep inside a tube when they previously had to travel only halfway into the tube for the same reward amount. Waite interpreted this result as a reflection of the increased predation risk associated with traveling farther into the tube. Although the tamarins and marmosets in our study were all born in captivity, they have observed free-flying raptors outside of their colony room and have experienced direct exposure to approaches by a trained Northern goshawk (*Accipiter gentiles*) (A. Palleroni, C. Sproul, and M.D.H., unpublished data). Consequently, they might have perceived a potential predation risk when entering our apparatus.

Our results suggest that, at least in marmosets, discounting behavior is context specific: they will wait for food longer than tamarins but will not travel as far. A major selective force that underlies foraging decisions is ecological context. Previously, we ascribed the differences in tamarin and marmoset temporal discounting to ecological pressures and, in particular, aspects of their feeding behavior [5] (see [34] for a similar argument for memory differences in other tamarin and marmoset species). A key difference between the two species is the primary food items in their diet: tamarins specialize on insects, whereas marmosets specialize on gum and sap exuding from trees [6–9]. This difference in foraging ecology aligns with the temporal discounting results: tamarins primarily consume an ephemeral food source that requires impulsive action, whereas marmosets prefer to feed on a food source that requires scratching tree bark and then patiently waiting for sap to exude. These foraging differences may also account for ranging differences between species [9]. Because tamarins feed on an ephemeral, dispersed food source, they travel through large territories to find insects. Marmosets, however, feed on a localized, immobile food source and, consequently, face little pressure to travel long distances for food [9]. As a result, the territory sizes of these species are nonoverlapping, with tamarins averaging 7.8–10 ha and marmosets 0.5–5 ha [7, 8]; moreover, tamarins travel farther on a daily basis (1700 m) than marmosets (700 m) [35, 36]. As such, these two discounting tasks may actually trigger different discounting strategies in the two species and reflect the innate preferences each species has for one foraging mode over the other.

Although our data are consistent with the foraging ecology hypothesis, we cannot completely exclude other hypotheses. It is possible that foraging ecology has shaped the cost/benefit functions of the species, such that these species differ in their

travel costs or predation risk and, therefore, have different optimal strategies. Alternatively, other differences between these species may account for our results, such as general activity level, muscle mass, limb length, or basal metabolic rate. However, gummivory is a very powerful selective force that has led to adaptive specializations in tooth morphology and digestive physiology in marmosets [6, 37]. The far-reaching effects of gummivory on other aspects of physiology and behavior are difficult to disentangle from other selective forces.

Reward Magnitudes

Reward magnitude does not appear to influence tamarin or marmoset preferences: both species discounted at the same rate regardless of whether they chose between one and three pieces of food or between two and six pieces of food. This corroborates previous studies of animal discounting levels in which there is no effect of magnitude on choice behavior [3, 27, 28]. As of yet, only humans reliably demonstrate a magnitude effect in discounting tasks, discounting smaller rewards more highly than large rewards [14, 31, 32].

This divergence between the human and animal data may result from different methodologies used to study discounting. Studies of human discounting use monetary rewards that are often hypothetical. As such, these rewards can be much larger than any feasible food reward. For example, in two studies that found a magnitude effect, one [14] titrated large money amounts ranging from $100 to $100,000 and the other [31] used reward amounts ranging up to $1,000,000. Thus, animals may not demonstrate a magnitude effect simply because the phenomenon in humans is an artifact of presenting extremely large reward quantities—quantities that are both impossible to offer animals in the laboratory, and unlikely to occur in the wild, including our own species' early history.

Experimental Procedures

Experimental Design

Four cotton-top tamarins (three females and one male) and four common marmosets (two males and two females) of mixed experimental history participated in this experiment. Each subject experienced seven distance comparisons. For all distance comparisons, we placed the small reward one distance increment (35 cm) from the front of the enclosure and we placed the larger reward progressively farther away from the subject on subsequent sessions. Initially, the distance to the larger reward was the same as the distance to the smaller reward (35 cm); in the next session, the larger reward was moved two distance increments (70 cm) away while the smaller reward remained at one distance increment. This process continued until the larger reward was placed seven distance increments (245 cm) away, the total length of the enclosure (Figure 1C).

Subjects completed these seven distances for two reward magnitude comparisons: one versus three banana-flavored food pellets (Research Associates 45 mg purified primate diet pellets) and two versus six food pellets. We counter balanced the order of presenting the two magnitude conditions across subjects.

Apparatus and Setup

We placed subjects in a small transport cage (30 × 30 × 30 cm) abutting the front of the large, plexiglas test enclosure (240 × 120 × 45 cm). A transparent plexiglas door allowed the subjects to see into the enclosure. The enclosure consisted of opaque white walls and a transparent plexiglas ceiling (Figure 1A). In addition, the enclosure had a movable back wall that we adjusted such that it was placed 70 cm behind the far reward for distance increments one to six and 35 cm behind the far reward for increment seven.

Trial and Session Procedures

The experimenter placed two black boxes (20 × 11 × 11 cm) that contained the food rewards in the enclosure (Figure 1B). We lined up the food rewards in an array on a ledge inside the box, each piece ~1 cm apart. After placing food in the boxes at the appropriate distances, the experimenter waited 10 s for the subject to view the choices and then removed the door. After removing the door, the subject had one minute to leave the transport box and enter the apparatus and then had 30 s to make a decision. As soon as the subject made a choice (by touching a pellet) in a free session, the experimenter used a remote control to close the nonchosen reward box, eliminating the possibility of obtaining these food pellets. We trained subjects to return to the starting transport box after consuming their chosen reward.

For each distance, increment subjects first completed a forced-choice session of eight trials. In these sessions, subjects received only one option per trial and thus gained experience with both distances and reward contingencies. We presented four smaller, closer reward trials and four larger, farther reward trials in randomized order. The following day, subjects completed a free-choice session of eight trials at the same distance increment in which we allowed them to choose between the two options. In both session types, we randomly assigned the side of the enclosure for larger and smaller rewards for each trial. Please see the Supplemental Data for further details on experimental methodology.

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Supplemental Data

Supplemental Results

The Role of Time in Spatial Discounting

Because tamarins traveled to the rewards more quickly than marmosets, the species' differences in preferences could result from the differential time delay to accessing the reward. To examine whether temporal discounting could account for the observed difference, we calculated a discounting factor for each individual in the temporal discounting experiment [S1] and tested whether using this discounting factor predicts preferences in the spatial task. We used the hyperbolic equation

$$V = \frac{A}{1 + kt}$$

(where V = subjective value of a reward, A = reward amount, k = individual discount factor, and t = time delay to receiving the reward) as a model of subjective value in this analysis [S2]. By measuring indifference points in the temporal experiment, we found the point at which the subjects valued the small, immediate and large, delayed rewards equally. Therefore, we can substitute our reward amounts and time delays into the hyperbolic equation such that

$$\frac{2}{1 + kt_1} = \frac{6}{1 + kt_2}$$

and solve for k for each individual. Because we used different individuals in the temporal and spatial experiments, we calculated the mean discount factor for each species ($k_{marmoset}$ = 0.149, $k_{tamarin}$ = 0.279) to use in the analysis of the spatial task. We then substituted these species discount factors and the times required to access the food rewards at different distances in the spatial task into the hyperbolic equation to calculate a subjective value for each option. Table S1 illustrates the subjective value placed on the closest and farthest options, assuming that the subjects use only temporal discounting to determine their choices. This analysis predicted that all subjects should value the more distant reward more than the closer reward. Though the tamarins do follow these predictions, the marmosets show reduced preference for the distant reward, suggesting that temporal discounting alone cannot account for their preferences in the spatial task. However, because tamarins did not show indifference at the distances experienced in this apparatus, we cannot quantitatively assess the role of temporal discounting.

Satiation

Another possible explanation for the species difference in spatial discounting is differing levels of satiation. Although this account is difficult to eliminate without an explicit test (e.g., manipulating levels of satiation), we examined the choice pattern within a session to look for changes in choices over trials. If, for instance, marmosets stopped traveling to the far distances because of increasing satiation during a session, we would expect to see preferences for the larger reward to decline over trials. On the contrary, there was no strong effect of trial number ($F_{7,33}$ = 2.13, p = 0.07), although there was a slight trend to prefer the large reward more often in later trials. Importantly, the lack of a species by trial interaction ($F_{7,33}$ = 1.13, p = 0.37) implies that marmosets did not choose the smaller reward more than tamarins simply because they became satiated more quickly over the course of a session.

Visual Discrimination

If tamarins and marmosets have different abilities to visually discriminate objects, this could account for our spatial discounting effect. That is, if marmosets cannot distinguish the pellets at the far distances, they may prefer the close reward that they can easily distinguish. Re-search on the anatomy of tamarin and marmoset eyes suggests that they have similar visual acuity. Specifically, common marmosets (*Callithrix jacchus*) have peak cone densities and eye diameters very similar to golden-handed tamarins (*Saguinus midas*) [S3, S4], a species of tamarin closely related to our cotton-top tamarins (*Saguinus oedipus*).

To examine species differences behaviorally, we conducted another follow-up study in which we provided subjects with a choice between two versus six pellets at the farthest distance. We began by reacclimating subjects to sessions of the distance increment one comparison. Once subjects reliably chose the six pellets (nine or ten out of ten times for two consecutive sessions), we presented them with a session of both rewards at intermediate distances (135 cm). After passing one session at the intermediate distance, subjects advanced to the test sessions in which they had to choose between two and six pellets both at the farthest distance increment (245 cm). Subjects faced three sessions at the farthest distance. To force subjects to make a choice at the start box, we separated the two options with an opaque plexiglas divider that ran lengthwise in the enclosure from 110 cm to the end of the apparatus. We considered passing the front of the divider on one of the sides as a choice.

We conducted a repeated-measures ANOVA on the arcsine, square-root transformed proportion of choices for the large reward by using replicate as a within-subject factor and species as a between-subject factor (four marmosets and three tamarins). Our analysis showed no effect of species ($F_{1,5}$ = 2.98, p = 0.14) or replicate ($F_{2,10}$ = 2.78, p = 0.11), suggesting that both species could discriminate the rewards equally. Additionally, both marmoset and tamarins preferred the large reward at levels above chance (marmosets: 72.5% ± 6.6%, t = 3.42, p = 0.04; tamarins: 85.6% ± 4.0%, t = 8.86, p = 0.01). This task, combined with the anatomical similarities, suggests that these two species should possess similar visual discrimination abilities. Thus, differences in discrimination cannot account for the species differences in spatial discounting.

Supplemental Experimental Procedures

Subjects

Four cotton-top tamarins (three females and one male) and four common marmosets (two males and two females) of mixed experimental history participated in this experiment. Three tamarins and three marmosets had prior experience in a temporal discounting experiment [1]. Relative to the marmosets, which have only been tested on the temporal discounting experiments and a few studies of auditory perception, the tamarins have been exposed to a wide diversity of experiments on tool use, cooperation, call perception, language processing, and number representation [S5–S9].

Subjects received their daily food allotments after the experiments were completed at the end of the day. Both tamarins and marmosets were maintained at body weights that provided the most reliable performance in food-motivated tasks (about 90% free-feeding weight); these weights approximate those observed in the wild. This experiment was approved by the Institutional Animal Care and Use Committee at Harvard University (Animal Subjects Codes 92-16 and 22-07).

Training

All subjects completed two phases of training prior to beginning this experiment. In the first phase, subjects habituated to the enclosure and reliably walked to the boxes to eat. In the second phase, subjects demonstrated a preference for the larger reward over the smaller reward when the distance to both was equal (one distance unit). Subjects had to complete two consecutive sessions choosing the smaller reward no more than once.

Table S1. Subjective Value for Both Options When Large Reward Is at the Farthest Distance

Subject	Value for Two Close Pellets	Value for Six Distant Pellets
Marmosets		
DES	1.78	4.66
JUL	1.72	4.52
LYS	1.81	4.82
OTH	1.78	4.87
Mean	1.78	4.72
Tamarins		
DW	1.74	4.43
JK	1.71	4.43
KW	1.71	4.40
UB	1.63	4.18
Mean	1.69	4.36

Trial Setup

Before starting each individual trial, the experimenter placed the food in the reward boxes (in random order for each trial) and moved the boxes to the appropriate distances. Both food rewards were loaded at the front of the apparatus (at one distance increment from the front of the enclosure), and the larger reward was then moved the farther distance. This ensured that subjects had visual access to both food rewards at an equal distance. In addition, food rewards remained visible to subjects throughout the trial even at the farthest distance. In forced trials only one option was available; the second box remained closed and placed at the appropriate distance.

Session Order

All subjects experienced seven distance increments for two magnitude comparisons for a total of 14 experimental sessions in which they could freely choose between the two options (free-choice sessions of eight trials each). In addition, subjects experienced a forced-choice session on the day preceding each free-choice session (also with eight trials each). So, for example, some subjects started off with a forced-choice session of one pellet at distance-1 versus three pellets at distance-1, followed the next day by a free-choice session of the same. The following day, they faced a forced-choice session of one pellet at distance-1 versus three pellets at distance-2, then a free-choice session at the same distances the next day. This pattern continued until they completed all seven distances. After a break of usually 5–14 days (one subject experienced a break of 30 days and another experienced a break of about 80 days), subjects started over at distance one with the other reward magnitude. Half of the subjects started with one versus three pellets and half started with two versus six pellets.

Aborts and Session Passing Criteria

Subjects had to meet a number of criteria for a session's data to be considered acceptable. If subjects aborted on a given trial, then an additional trial was added to the end of the session to bring the completed trial number to eight. If a subject aborted more than two times, then we stopped the session, starting afresh on another day. Three behaviors resulted in an aborted trial in all session types: (1) failing to make a decision in the allotted time constraints (see procedure), (2) failing to eat the chosen food reward (subjects could leave no more

than one piece of food for all rewards quantities greater than one), or (3) running past the farthest reward without choosing either option. All experimenters were trained on these coding methods before running a subject.

In addition, subjects had to meet passing criteria in forced sessions in order to progress to the free-choice session. In forced trials, subjects were required to travel in a direct path to the one available food reward; if subjects moved toward the closed, unavailable reward box before attempting to eat the available option, then the trial was considered incorrect. In forced sessions, subjects had to correctly complete at least seven out of eight trials for the session to count. If they failed to do so, they repeated the forced session. In free-choice sessions, all decisions were considered correct, assuming subjects did not abort. However, in order to ensure that subjects' choices were not driven by a side bias toward one half of the apparatus, all free sessions in which subjects chose the food reward on one particular side seven or more times were discarded, and the condition was repeated.

Time Duration Coding

In order to assess whether subjects' decisions in this discounting task were driven by simple rate maximization, subjects completed four follow-up sessions after they had completed the main experiment. Specifically, subjects completed a forced session at the longest distance (that is, one versus seven distance increments) for both magnitude comparisons. We used these sessions to estimate how long it took subjects to travel the longest and shortest distances they were tested on over the course of the experiment. Two independent coders scored the forced trials for two temporal measurements: (1) travel time—total time spent moving toward the box from when the subject left the transport box to when they reached the chosen reward box and stopped moving (time during which the subject paused while traveling was not included in this measurement)— and (2) handling time—time spent eating the reward (from when the subject reached the reward box and no longer moved forward toward the box to when they put the last piece of food in their mouth). The two coders were 96.1% and 99.7% correlated on these measures, respectively.

One outlier trial was excluded from this analysis, because a marmoset took an exceptionally long time to run to the small reward; her running time was more than seven standard deviations from the mean. This trial was removed from all time analyses.

Statistical Analysis

We analyzed the data with a series of repeated-measures analyses of variance. In the first analysis, we used reward magnitude (one versus three and two versus six) and distance-to-large (seven distances) as within-subjects factors and species as a between-subjects factor. A second analysis looked for changes over the course of a session, using trial number as a within-subjects factor (eight trials) and species as a between-subjects factor. We arcsine, square-root transformed the proportion choosing the larger reward in each free-choice session (eight trials per session) for each subject to normalize the data. We completed two more analyses for timing data on the follow-up experiment. One assessed the effect of distance (35 versus 245 cm) and species on travel time; the second examined the effect of total pellet number (one, two, three, or six) and species on travel time. In all analyses, we used the Huynh-Feldt correction when assumptions of homogeneity of variance were violated [S10]. We used Bonferroni procedures to test multiple comparisons of means in the within-subjects design, and we report the pairwise comparisons with $p \leq 0.05$ [S11].

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