Supplemental Data

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

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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 ($k_{\text{marmoset}} = 0.149$, $k_{\text{tamarin}} = 0.279$) 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. Research on the anatomy of tamarin and marmoset eyes suggests that they have similar visual acuity. Specifically, common marmosets (*Callithrix jacchus*) have very similar peak cone densities and eye diameters as 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

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

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.

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 to 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].

Supplemental References

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