

Are capuchin monkeys (*Sapajus* spp.) sensitive to lost opportunities? The role of opportunity costs in intertemporal choice

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Abstract

Principles of economics predict that the costs associated with obtaining rewards can influence choice. When individuals face choices between a smaller, immediate option and a larger, later option, they often experience opportunity costs associated with waiting for delayed rewards because they must forego the opportunity to make other choices. We evaluated how reducing opportunity costs affects delay tolerance in capuchin monkeys. After choosing the larger option, in the *High cost* condition subjects had to wait for the delay to expire, whereas in the *Low cost different* and *Low cost same* conditions they could perform a new choice during the delay. To control for the effect of intake rate on choices, the *Low cost same* condition had the same intake rate ratio as the *High cost* condition. We found that capuchins attended both to intake rates and to opportunity costs. They chose the larger option more often in the *Low cost different* and *Low cost same* conditions than in the *High cost* condition, and more often in the *Low cost different* condition than in the *Low cost same* condition. Understanding how non-human primates represent and use costs in making decisions not only helps to develop theoretical frameworks to explain their choices but also addresses similarities with and differences from human decision making. These outcomes provide insights into the origins of human economic behaviour.

Keywords: delay tolerance; intake rates; intertemporal choice; opportunity costs; non-human primates

* EA, FP and JRS conceived the study and designed the experimental protocol; VT, VF, FR, SG and FDP tested the subjects; EA and JRS analyzed the data; EA, FP and JRS wrote the paper; EA, FP and JRS contributed equally to this study.

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In press at *Philosophical Transactions of the Royal Society B: Biological Sciences*.

INTRODUCTION

Intertemporal choices, i.e. economic decisions whose consequences occur at different times¹, are pervasive in everyday life, with potentially critical implications for health and well-being as humans devalue future options relatively to more immediate ones². Intertemporal choices have played a key role in the debate around economic rationality and the deviations from normative models observed in decision making over time³. Non-human animals also face intertemporal choices, most commonly during foraging activities⁴, which have been investigated within the framework of Darwinian fitness maximization⁵.

In the laboratory, researchers commonly test the ability to tolerate delay with the delay choice task, in which subjects encounter a series of choices between a smaller option available sooner and a larger option available later. Some researchers consider the high degree of delay tolerance observed in humans on this task to be one of the key features distinguishing our species from non-human animals³. However, a fair comparison is highly problematic since, whereas humans usually answer questionnaires about hypothetical choices, non-human animals are generally tested in operant tasks with choices between food rewards. Questionnaires employed with humans and operant tasks employed with non-human animals usually differ on several dimensions: reward delivery (always present in operant tasks, often hypothetical in questionnaires), reward magnitude (small in operant tasks, large in questionnaires), reward type (usually consumable rewards in operant tasks, usually money in questionnaires), and length of delay (shorter in operant tasks, longer in questionnaires)⁶. In the few studies in which human subjects experienced operant tasks, they waited for delayed rewards much less than when tested with questionnaires⁷ and rarely for more than two minutes⁸⁻¹¹. Interestingly, when tested with the same methodology, humans waited less than chimpanzees¹¹ and exhibited a preference for the larger, later option comparable to capuchin monkeys¹².

A further, critical difference between operant tasks and questionnaires is in their *opportunity costs*, defined as the loss of the potential opportunities of engaging in other activities after choosing an option available after a certain amount of time. In operant tasks, opting for the delayed option forces non-human animals to sustain the delay associated with their choice¹¹. In contrast, humans presented with questionnaires do not suffer any restrictions on their activities during the delay. Thus, non-human animals experience higher opportunity costs of waiting than humans, and this factor may devalue the larger, later option in comparison to the smaller, sooner one (as waiting may prevent non-human animals to engage in other activities and thus, possibly, collect other rewards).

A few previous studies investigated how alternative actions during the delay may allow distraction and thus increase waiting time across different tasks. In delay maintenance tasks, in which individuals had to wait to obtain a larger or more preferred reward rather than an immediately available, less appealing reward, the opportunity to engage in alternative activities (e.g., manipulating toys or key pecking) during the delay similarly improved delay tolerance in children¹³⁻¹⁵ and non-human animals (pigeons¹⁶ and chimpanzees¹⁷). Similarly, rats preferred receiving sunflower seeds with a husk, that they had to remove before consumption, to waiting for an equivalent amount of time without doing anything and then receiving sunflower seeds without a husk¹⁸.

The present study aims to evaluate, for the first time, how reducing opportunity costs affects preferences in a delay choice task in tufted capuchin monkeys (*Sapajus* spp.), a South-American primate species whose choice behaviour in delay choice tasks has been extensively investigated^{12,19-21}. To explore the role of opportunity costs on intertemporal choice, we manipulated whether capuchins could make additional choices during the delay. The ability to make choices during the delay reduces opportunity costs by allowing animals to gain further rewards while waiting. Subjects experienced three experimental conditions. In the *High cost* condition, if the subject chooses the larger option, s/he must wait for the delay to expire to receive the reward and then the intertrial interval starts (i.e., the standard way that most operant studies are conducted). In the *Low cost different* condition, if the

subject chooses the larger option, the intertrial interval starts immediately after choice and, while the delay is still expiring, the subject can proceed to a new choice. However, allowing another choice during the delay increases the overall intake rate for the subject (defined as the amount of food acquired per unit of time⁵) in the *Low cost different condition* compared to the *High cost* condition, which could alter choice²². To assess the possible effect of changing the intake rate on subjects' choices, we carried out the *Low cost same* condition, in which the intake rate ratio (larger option intake rate/smaller option intake rate) was the same as in the *High cost* condition. In each condition, we measured the proportion of choices of the larger, later option. We expected that: (1) if subjects ignore both intake rates and opportunity costs, no difference will emerge across conditions; (2) if subjects attend to intake rates in general but not to the opportunity costs *per se*: *Low cost different* > *Low cost same* ~ *High cost*; (3) if subjects attend to opportunity costs regardless of intake rates: *Low cost different* ~ *Low cost same* > *High cost*; (4) if subjects attend to both opportunity costs and intake rates: *Low cost different* > *Low cost same* > *High cost*.

METHODS

Subjects

We tested 10 adult capuchin monkeys, belonging to four social groups, housed at the Primate Center of the Consiglio Nazionale delle Ricerche, Rome. All subjects had extensive experience in cognitive tasks and most of them had previously participated in studies in which the delay choice task was employed (Table 1). Only one subject did not have any previous experience with the delay choice task. Seven subjects had also previously participated in a pilot experiment in which a similar methodology to the one used in the current study was employed (Supplementary Materials, Table S1).

Table 1. Subjects' sex, age (years), and presentation order

Subject	Sex	Age	Order of condition presentation	Previous experience in delay choice tasks	Previous participation in opportunity cost pilot experiment
Gal	M	28	<i>Low Same, High, Low Different</i>	12,19,20,21	Yes
Paprica	F	29	<i>High, Low same, Low Different</i>	19, 20, 21	Yes
Roberta	F	32	<i>High, Low Different, Low Same</i>	12, 19,37, 20	No
Robin Hood	M	21	<i>High, Low Different, Low Same</i>	12, 19, 37, 20, 21	Yes
Robinia	F	24	<i>Low Same, Low Different, High</i>	19, 20, 21	Yes
Robiola	F	20	<i>Low Same, High, Low Different</i>	None	No
Robot	M	23	<i>High, Low same, Low Different</i>	12, 19, 20, 21	Yes
Rucola	F	18	<i>Low Different, Low Same, High</i>	19	No
Sandokan	M	18	<i>Low Different, Low Same, High</i>	12, 19, 37, 20, 21	Yes
Saroma	F	17	<i>Low Different, High, Low Same</i>	11,31,40,41	Yes

Each capuchin group was housed in indoor–outdoor compartments. The outdoor compartments measured 53.2-374.0 m³, depending on group size, and the two indoor compartments measured 25.4 m³ in total for each group. All compartments were furnished with wooden perches, tree trunks and branches. We tested subjects individually in one of the two indoor compartments. We separated subjects for individual testing by first splitting the group into smaller units using sliding doors and then

allowing the subject to enter the indoor compartment. Testing occurred between 09:30 and 13:30 h, at least two hours after capuchins were released from the indoor compartments (where food is available overnight) and before their main meal, which takes place in the afternoon, when fresh fruits, vegetables and monkey chow are provided. Water was available *ad libitum*.

Apparatus

Two food options (see below) were presented to capuchins on a platform (65 x 40 x 16 cm) with two transparent boxes (9.5 x 20 x 15 cm each), 28 cm apart (Figure 1). We used small pieces of peanuts (each food item corresponding to 1/8 of peanut, weighing on average \pm standard error 0.11 ± 0.004 g). Food options were placed under the transparent boxes, each covered by a coloured upside-down cup. For each condition (see below), a unique pair of differently coloured cups covered the two options and the assignment of the cups to each option was counterbalanced across subjects. We covered the food options by coloured cups to avoid the possibility that, if food items were fully visible, tolerance to delay could be at least partially confounded with impulsivity towards food quantity at the time of choice^{12,23-25}. Subjects could choose one of the two options by inserting a finger in the hole (diameter: 2 cm) of one of the two boxes, through one of two openings in the wire mesh (8.5 cm x 3.8 cm each), aligned with the boxes. Beside the choice apparatus, we set up a wooden table (65 x 13 x 26 cm) on which we positioned three dark ceramic plates (diameter 12 cm), clearly visible from the capuchins' testing compartment. In all conditions, following the choice of the larger option, the experimenter placed the food in one of the three plates for the whole duration of the delay associated to this option (see below). Following the choice of the smaller option, the experimenter directly handed the food to the subject.



Fig. 1 Experimental set-up in the Low cost same condition. Robin hood (an adult male) has just chosen the larger, later option and the experimenter has placed it on the central plate, out of his reach. Another reward associated with the choice of the larger, later option in a previous trial is on the left plate. The experimenter will provide Robin Hood with the rewards when their respective delays expire.

Procedure

We used an adaptation of the delay choice task with a fixed-delay procedure^{11,12}. Each subject experienced three experimental conditions: *High cost*, *Low cost same*, and *Low cost different*. The order in which the three conditions were presented was counterbalanced across subjects (Table 1).

In all conditions, subjects chose between a smaller food amount available sooner and a larger food amount available later. In the *High cost* and *Low cost different* conditions, the smaller, sooner option was one food item available after 2 s (Figure 2a and b). In the *Low cost same* condition, the smaller, sooner option consisted of three food items available after 2 s (Figure 2c). In all conditions, the larger, later option was six food items available after an 80-s delay. This delay was chosen because it corresponds to the average delay tolerated at indifference point by the same capuchins previously tested in a delay choice task with an adjusting delay procedure¹⁹.

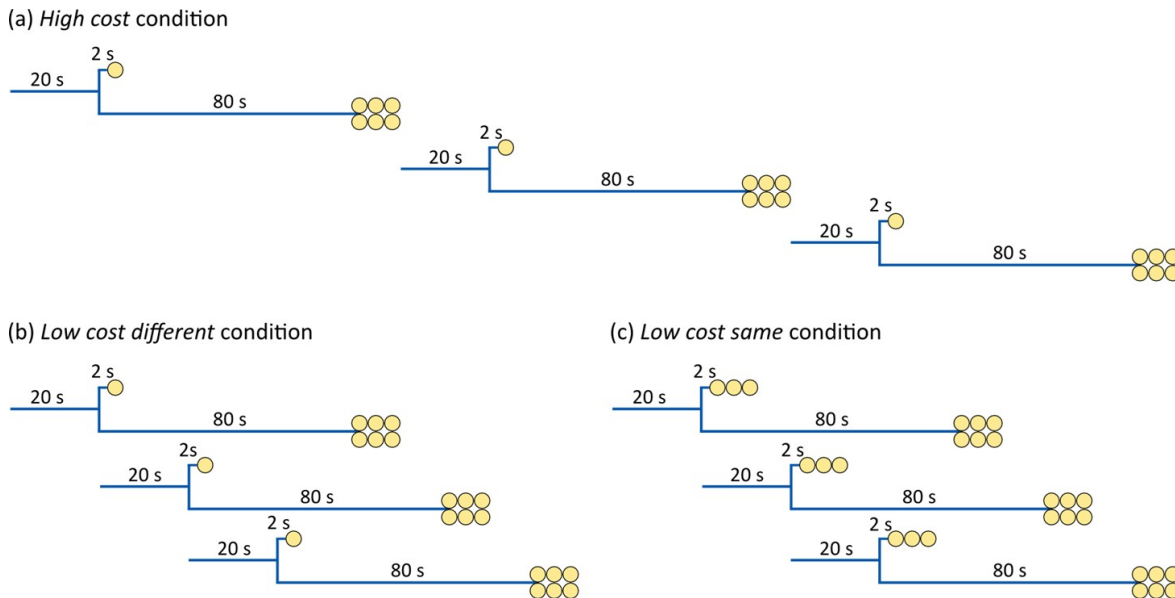


Fig. 2 Graphical representation of experimental conditions. Each subfigure represents three example trials in which the subject chooses the larger, later option. The yellow dots represent the number of food items. In all conditions, the ITI was 20 s, the delay to the smaller option was 2 s, and the delay to the larger option was 80 s. (a) In the *High cost* condition, ITIs and the next trial did not start until the subject consumed all of the food from the previous trial. (b and c) In the *Low cost different* and *Low cost same* conditions, if the subject chose the larger, later option, the ITI for the next trial started immediately after the choice.

Intake rates

The critical difference between the *High cost* and the *Low cost different* conditions is that in the latter the subject can proceed to the next choice trial while the delay(s) associated with choices made on previous trials are still expiring (Figure 2b). However, in this way, the total waiting time decreases and consequently the intake rate¹ associated with the choice of choosing the larger option is three times higher in the *Low cost different condition* than in the *High cost* condition. In fact, if in the *Low cost different condition* the subject always chooses the larger option, the intake rate is 0.18 (intake rate = (# trials × # food items) / ((# trials × ITI) + delay)) for the larger option but remains 0.05 for the smaller option. In the *High cost* condition, if the subject always chooses the smaller option, the intake rate is

¹ The (long-term) intake rate is the amount of food acquired per unit time⁵. In a delay choice task, it depends on the number of trials, number of food items obtained after choice, intertrial interval (ITI), handling times for processing rewards, and delay. Since handling times for capuchins with this type of food are negligible, we ignored them for ease of calculation.

0.05 (intake rate = # food items / ITI), whereas if the subject always chooses the larger option, the intake rate is 0.06 (intake rate = # food items / (ITI + delay)).

To rule out the possibility that a stronger preference for the larger option in the *Low cost different* condition is due to its higher intake rate (compared to the *High cost* condition), we ran also the *Low cost same* condition, in which the subject chooses between three food items available after 2 s and six food items available after 80 s. In this way, the intake rate ratio (larger option intake rate/smaller option intake rate) is the same as in the *High cost* condition. If in the *Low cost same* condition the subject always chooses the smaller option, the intake rate is 0.15, whereas if s/he always chooses the larger option the intake rate is 0.18, as in the *Low cost different* condition. Thus, the intake rate ratio is 1.2 in both the *High cost* and *Low cost same* conditions, whereas it is 3.6 in the *Low cost different* condition.

Experimental sessions

Sessions consisted of two forced-choice trials with only one option available for familiarization (one with the smaller option and one with the larger option), and six free-choice trials, in which capuchins could choose between the smaller option and the larger option. The forced-choice trials were presented at the beginning of each session, alternating their order and position (left or right) between sessions. The order and the position of the six free-choice trials were pseudo-randomized throughout the session. The intertrial interval was 20 s. Each subject received one session per day and, in each condition, subjects were tested up until a criterion of five consecutive sessions in which the number of choices for the larger, later option diverged by no more than one unit. This resulted in subjects experiencing 5-34 sessions (Figure S1).

The apparatus was placed in front of the indoor compartment. Two experimenters tested the subjects: experimenter 1 sat in front of the subject's indoor compartment, behind the apparatus, and experimenter 2 sat next to experimenter 1. In each trial, experimenter 1 baited the apparatus while experimenter 2 blocked the subject's visual access to the apparatus by means of an opaque screen so that the subject could neither observe the baiting process nor reach the boxes during baiting. After baiting, experimenter 2 lifted the opaque screen and experimenter 1 pushed the apparatus towards the wire mesh, so that the subject could make his/her choice. Both experimenters refrained from looking at the boxes to avoid providing visual cues to the subject.

In all experimental conditions, if the subject chose the smaller option, experimenter 1 directly handed the food to the subject after a 2-s delay. As soon as the subject put the last piece of food in his/her mouth, experimenter 2 replaced the opaque screen and, after the intertrial interval, the next trial began. If the subject chose the larger option, the smaller option was removed, the experimenter placed the food items in one of the plates placed on the wooden table positioned beside the apparatus (Figure 1) and, depending on the condition, a different procedure was employed. In the *High cost* condition, the subject had to wait for the 80-s delay to expire before performing the subsequent choice. Then, the subject received the food and, after the intertrial interval, the next trial began (Figure 2a). In contrast, in both the *Low cost same* and the *Low cost different* conditions, when the subject chose the larger option, the intertrial interval started immediately after his/her choice, while the 80-s delay was running. At the end of the intertrial interval, the subject received the next choice trial. Only when the 80-s delay expired, the subject received the food amount associated to the previous choice trial. The same procedure was repeated until the last trial (Figures 2b and c). The only difference between the two *Low cost* conditions was the use of one food item in the *Low cost different* condition (as in the *High cost* condition) compared to three food items in the *Low cost same* condition (Table 2).

Before the onset of each experimental condition, subjects experienced three familiarization sessions consisting of 16 forced-choice trials with only one option available (either the smaller one or the larger one). We pseudo-randomized their order and position (left or right) within each session. After each choice, we presented the food to the subject following the same procedure described above.

Table 2. Intake rate comparison across conditions

Condition	Small amount (2-s delay)	Large amount (80 s delay)	Smaller, sooner long-term rate	Larger, later long-term rate	Ratio of long-term rates (LL:SS)*	Smaller, sooner short-term rate	Larger, later short-term rate	Ratio of short-term rates (LL:SS)*
High cost	1	6	0.05	0.06	1.2	0.5	0.08	0.15
Low cost different	1	6	0.05	0.18	3.6	0.5	0.08	0.15
Low cost same	3	6	0.15	0.18	1.2	1.5	0.08	0.05

*Ratios > 1 predict choice for LL, ratios < 1 predict choice for SS.

Experimenter 2 collected data on a laptop running a software (developed by Uwe Czienskowski at Max Planck Institute for Human Development, Berlin, Germany) that automatically tracked delays and intertrial intervals; experimenter 2 also signalled to experimenter 1 when to deliver each food amount and when to present a new choice. Data collection was carried out between July and November 2018.

Data analysis

We conducted both frequentist and Bayesian analyses. For Bayesian analyses, we used the *brms* package in R to fit models using a generic, weakly informative prior: normal (0, 1). We report Bayes factors (BF) to provide evidence for the alternative hypothesis relative to the null hypothesis²⁶. Data were analysed using R statistical software version 4.0.2²⁷. Data and R scripts are available as Supplementary Materials and on Dryad Data Repository (<https://doi.org/10.5061/dryad.mcvdncjxd>).

RESULTS

We analysed data pertaining only to the last five sessions (i.e., upon reaching choice stability). First, since data were not normally distributed (Shapiro Wilk test: *High cost*: $W = 0.688$, $df = 10$, $p = 0.001$, *Low-cost different*: $W = 0.828$, $df = 10$, $p = 0.032$, *Low-cost same*: $W = 0.533$, $df = 10$, $p < 0.001$), we performed one-sample Wilcoxon tests to determine if preferences differed from chance (0.5). Capuchins preferred the smaller, sooner option over the larger, later option in all conditions (*High cost*: $V = 0$, $p = 0.005$, $BF > 100$; *Low-cost different*: $V = 4$, $p = 0.019$, $BF = 10.5$; *Low-cost same*: $V = 7$, $p = 0.039$, $BF = 10.9$). Then, we conducted logistic Generalized Linear Mixed Models and used forwards and backwards model selection, likelihood ratio tests, and comparisons of Bayes factors of models to find the best model. A likelihood ratio test shows that the model including the random effects of subject performed better than the model without random effects ($X^2 = 57.61$, $p < 0.001$, $BF > 100$). We then tested models with condition and trial number as fixed effects. We found that the model with condition fit better than the model with no fixed effects ($X^2 = 60.19$, $p < 0.001$) and adding trial number did not improve model fit over condition only ($X^2 = 0.07$, $p = 0.78$; Table S2). Similarly, the Bayesian analysis found extreme evidence for the condition model over the model with no fixed effects ($BF > 100$) and strong evidence for the condition only model over the model with condition and trial number ($BF = 16.0$). From the contrasts, it emerged that each condition is different from the other (*High cost - Low cost different*: estimate = -2.21, SE = 0.33, $df = \text{Inf}$, z ratio = -6.63, $p < 0.001$, $BF > 100$; *High cost - Low cost same*: estimate = -1.61, SE = 0.34, $df = \text{Inf}$, z ratio = -4.69, $p < 0.001$, $BF > 100$; *Low cost same - Low cost different*: estimate = 0.61, SE = 0.22, $df = \text{Inf}$, z ratio = 2.74, $p = 0.017$, $BF = 5.0$; p value adjustment: Tukey method for comparing a family of three estimates, Figure 3a). Nonetheless, the subject Robot appears to be a clear outlier in those data, with a mean choice over the three conditions which was 7.0 standard deviations larger than the overall mean (Figure 3a).

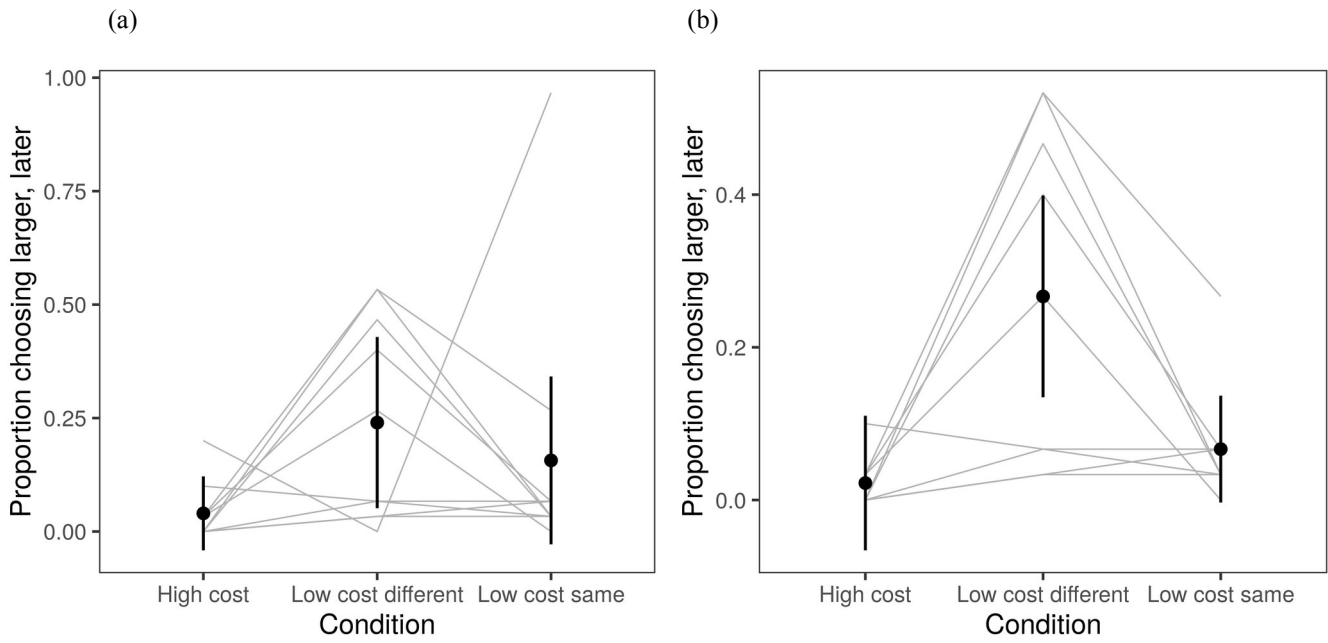


Fig. 3 Proportion of choices of the larger, later option in the three experimental conditions for (a) all subjects and (b) without the outlier Robot. Grey lines represent the mean proportion of choices of the larger, later option for each individual. Black circles and error bars represent means and within-subjects 95% confidence intervals.

When we performed the same analysis without the subject Robot, both frequentist and Bayesian approaches favour the same model with subject as a random effect and condition as a fixed effect (Table S3). From the contrasts, we confirmed that each condition is different from the other (*High cost* - *Low cost different*: estimate = -2.95, SE = 0.44, df = Inf, z ratio = -6.70, $p < 0.001$, BF > 100; *High cost* - *Low cost same*: estimate: -1.18, SE = 0.48, df = Inf, z ratio = -2.45, $p = 0.038$, BF = 6.3; *Low cost same* - *Low cost different*: estimate = 1.77, SE = 0.29, df = Inf, z ratio = 6.11, $p < 0.001$, BF > 100; p value adjustment: Tukey method for comparing a family of three estimates, Figure 3b).

DISCUSSION

Overall, capuchin monkeys chose the larger, later option more in the *Low cost different* and *Low cost same* conditions, in which they moved to the next choice trial while the delay associated to the previous choice trial was still expiring, than in the *High cost* condition, in which they had to wait for the delay to expire before moving to the next choice trial. Our results extend to the delay choice task the findings obtained in children, chimpanzees, pigeons, and rats in other self-control tasks¹³⁻¹⁸ that alternative actions during delays enhance the ability to wait. Whereas previous studies explored the effect of opportunity costs on delay of gratification by providing distractions or alternative activities during the delays, but not additional rewards, our study was, to our knowledge, the first one to allow for additional choices and rewards during the delays. The current paradigm mimics human intertemporal choices in which, after choosing larger, later payoffs (e.g., investing in retirement funds), we continue to make additional choices while waiting for our investments to pay back. Manipulating opportunity costs by changing the intertemporal choice architecture is markedly different from just providing relief from the stress of waiting via distractions. Although we believe that the opportunity of performing any activity (playing with toys, making additional choices, etc.) during a delay may release the discomfort of waiting, we cannot definitively conclude that this was the case in the current study. Future research should quantify behavioural correlates of stress (as scratching and other self-directed behaviours²⁸) when subjects are allowed, or not, to perform additional choices during the delay. The question of opportunity costs raises important implications for different types of scenarios in which

animals must wait for delayed rewards in natural decision-making contexts. Our findings support the view that animals may tolerate delays better when opportunity costs are low and they can engage in other actions and decisions during the delay. Caching, or hiding food for later consumption, is a good example of this²⁹. Many species cache food for consumption days, weeks, or even months later³⁰. Not only can the cachers engage in many other activities while waiting to recover their caches, but they can also continue to cache more. Likewise, gummivores such as common marmosets can chew on tree bark and commence other activities (include more tree gouging) while waiting for the sap to exude. Other forms of waiting, however, do not allow for alternative activities during the delay. Ambush, stalking, and coursing hunters cannot engage in other activities during the hunt. Thus, though this hunting strategy does require waiting, these types of hunters may not tolerate delay as much as species that can pursue other actions during the delay.

Choices of the larger, later option were not only affected by minimizing opportunity costs, but also by the long-term intake rate ratio. Capuchins chose the larger option more in the *Low cost different* condition (i.e., the condition with the highest long-term intake rate ratio) than in the *Low cost same* condition (in which the opportunity costs were comparable to the *Low cost different* condition, but the long-term intake rate ratio was smaller). However, capuchins did not choose in a way to maximize their long-term intake rate. In order to do so, they should have systematically chosen the larger, later options, which offered the highest long-term intake rates. Instead, capuchins consistently preferred the smaller, sooner option in all conditions. This finding suggests that, whereas across conditions capuchins are sensitive to the long-term intake rate ratio, within conditions they maximize short-term intake rates² rather than long-term intake rates (similarly to how European starlings, *Sturnus vulgaris*, and cotton-top tamarins, *Saguinus oedipus*, may do³¹⁻³³).

In an optimal foraging framework, impulsivity represents an irrational behaviour, since it does not lead to maximizing energetic gain. It has been proposed that a consistent preference for smaller, sooner options in the delay choice task is motivated by economic discounting, according to which a delayed option is devalued over time because of collection risks and lost opportunity costs³⁴. Nonetheless, in an ecological rationality framework³⁵, apparent impulsive choices may be preferred as they lead to long-term gains in other choice contexts, as in patch exploitation, which are more common than intertemporal choices in wild settings³⁶. The computational efficiency of capuchins in maximizing their short-term intake rate likely stems from their extensive experience in delay choice tasks^{12,19-21,37}. Overall, our findings support the view that a decision maker preferring the smaller, sooner option over the larger, later option in a delay choice task may be an efficient, rational rate maximizer in other choice contexts, rather than an impulsive, irrational individual^{2,5,22,38}.

In sum, our data suggest that, in a delay choice task administered in a captive setting, capuchins' choices for the larger, later option were affected by a reduction of the opportunity costs. Nonetheless, even when opportunity costs were minimized, by allowing capuchins to perform other choices while waiting for the delayed reward, they pursued short-term intake rate maximization. These findings contribute to the growing interest for the role of costs in intertemporal choice behaviour^{6,11,39,40} and suggest the need for further experimental studies aimed at measuring their impacts across various species both with the same methodology and when different delays and reward magnitudes are involved. Future studies should also systematically explore whether mere food consumption during the delay, rather than performing additional choices and being rewarded, would affect preference for the larger, later reward. A better understanding of how opportunity costs affect decision-making over time in non-human primates may provide insights into human economic behaviour by constraining models and explaining the origins of how we make decisions. Though we know of no direct test of the role of

² Whereas long-term intake rates include all time components in the calculations (e.g., delay, intertrial interval), short-term rates focus on the amount of food accumulated as a function of the time between choice and receipt of food (# food items/delay), ignoring the intertrial interval.

opportunity costs on human intertemporal choice, their behaviour in operant tasks, in which they choose smaller, sooner options frequently^{7,8,10,11}, suggests sensitivity to opportunity costs as well. Hopefully, this will be a matter for future research.

ACKNOWLEDGMENTS

We are grateful to Uwe Czienskowski for designing and programming the timing software used during the experiment. We thank Silvio Cianciullo, Eva Gabrielli and Luigi Macchitella for help with data collection. We also thank Roma Capitale-Museo Civico di Zoologia and the Fondazione Bioparco for hosting the ISTC-CNR Unit of Cognitive Primatology and Primate Centre, and Arianna Manciooco, Massimiliano Bianchi and Simone Catarinacci for assistance with capuchins. This study was funded by an ISTC-CNR intramural grant to Elsa Addessi and Fabio Paglieri and by the PNR-CNR Aging Program 2012-2014.

Ethical statement

Our study complied with protocols approved by the Italian Health Ministry (DM 12/2011 C to E. Addessi). All procedures were performed in full accordance with the European law on humane care and use of laboratory animals and conformed to the “Guidelines for the treatment of animals in behavioural research and teaching”⁴¹.

Conflict of interest

The authors declare that they have no conflict of interest.

REFERENCES

1. Berkman ET, Hutcherson CA, Livingston JL, Kahn LE, Inzlicht M. 2017 Self-control as value-based choice. *Curr. Dir. Psychol. Sci.* **26**,422-428. (doi: 10.31234/osf.io/n4yy2)
2. Hayden BY. 2019 Why has evolution not selected for perfect self-control? *Philos. Trans. R. Soc. B* **374**, 20180139. (doi: 10.31234/osf.io/3v5ps)
3. Frederick S, Loewenstein G, O'Donoghue T. 2002. Time discounting and time preference: A critical review. *J. Econ. Lit.* **40**, 351-401. (doi: 10.2307/j.ctvc4j8j.11)
4. Kalenscher T, Van Wingerden M. 2011 Why we should use animals to study economic decision making—a perspective. *Front Neurosci* **5**, 82. (doi: 10.3389/fnins.2011.00082)
5. Stephens DW, Krebs JR. 1986. Foraging Theory. Princeton University Press, Princeton.
6. Paglieri F. 2013 The costs of delay: waiting versus postponing in intertemporal choice. *J. Exp. Anal. Behav.* **99**, 362–377. (doi: 10.1002/jeab.18)
7. Navarick D. 2004 Discounting of delayed reinforcers: Measurement by questionnaires versus operant choice procedures. *Psychol. Rec.* **54**, 85-94. (doi: 10.1007/bf03395463)
8. Jimura K, Myerson J, Hilgard J, Braver T, Green L. 2009 Are people really more patient than other animals? Evidence from human discounting of real liquid rewards. *Psychon. Bull. Rev.* **16**, 1071–1075. (doi: 10.3758/pbr.16.6.1071)
9. Jimura K, Myerson J, Hilgard J, Keighley J, Braver T, Green L. 2011 Domain independence and stability in young and older adults' discounting of delayed rewards. *Behav. Process.* **87**, 253–259. (doi: 10.1016/j.beproc.2011.04.006)
10. Logue AW, King GR. 1991 Self-control and impulsiveness in adult humans when food is the reinforcer. *Appetite* **17**, 105-120. (doi: 10.1016/0195-6663(91)90066-2)
11. Rosati AG, Stevens JR, Hare B, Hauser MD. 2007 The evolutionary origins of human patience: temporal preferences in chimpanzees, bonobos, and human adults. *Curr. Biol.* **17**, 1663-1668. (doi: 10.1016/j.cub.2007.08.033)
12. Addessi E, Bellagamba, F, Delfino A, De Petrillo F, Focaroli V, Macchitella L, Maggiorelli V, Pace B, Pecora G, Rossi S, Sbaffi A, Tasselli MI, Paglieri F. 2014 Waiting by mistake: Symbolic representation of rewards modulate intertemporal choice in capuchin monkeys (*Cebus apella*), preschool children and adult humans. *Cognition* **130**, 428-441. (doi: 10.1016/j.cognition.2013.11.019)
13. Mischel W, Shoda Y, Rodriguez ML. 1989 Delay of gratification in children. *Science* **244**, 933–938. (doi: 10.1126/science.2658056)
14. Mischel W, Ebbesen EB, Zeiss AR. 1972 Cognitive and attentional mechanisms in delay of gratification. *J. Personal. Soc. Psychol.* **21**, 204–18. (doi: 10.1037/h0032198)
15. Mischel W, Shoda Y, Peake PK. 1988 The nature of adolescent competencies predicted by preschool delay of gratification. *J. Personal. Soc. Psychol.* **54**, 687–99. (doi: 10.1037/0022-3514.54.4.687)

16. Grosch J, Neuringer A. 1981 Self-control in pigeons under the Mischel paradigm. *J. Exp. Anal. Behav.* **35**, 3–21. (doi: 10.1901/jeab.1981.35-3)
17. Evans T, Beran M. 2007 Chimpanzees use self-distraction to cope with impulsivity. *Biol. Lett.* **3**, 599–602. (doi: 10.1098/rsbl.2007.0399)
18. Shettleworth SJ, Jordan V. 1986 Rats prefer handling food to waiting for it. *Anim. Behav.* **34**, 925–927. (doi: 10.1016/s0003-3472(86)80079-3)
19. Addessi E, Paglieri F, Focaroli V. 2011 The ecological rationality of delay tolerance: insights from capuchin monkeys. *Cognition* **119**, 142–147. (doi: 10.1016/j.cognition.2010.10.021)
20. De Petrillo F, Gori E, Micucci A, Ponsi G, Paglieri F, Addessi E. 2015 When is it worth waiting for? Food quantity, but not food quality, affects delay tolerance in tufted capuchin monkeys. *Anim. Cogn.* **18**, 1019–1029. (doi: 10.1007/s10071-015-0869-x)
21. Paglieri F, Focaroli V, Bramlett J, Tierno V, McIntyre J, Addessi E, Evans TA, Beran MJ. 2013 The hybrid delay task: can capuchin monkeys (*Cebus apella*) sustain a delay after an initial choice to do so? *Behav. Process.* **94**, 45–54. (doi: 10.1016/j.beproc.2012.12.002)
22. Stephens D W, Anderson D. 2001 The adaptive value of preference for immediacy: when shortsighted rules have farsighted consequences. *Behav. Ecol.* **12**, 330–339. (doi: 10.1093/beheco/12.3.330)
23. Addessi E, Paglieri F, Beran M, Evans T, Macchitella L, De Petrillo F, Focaroli V. 2013 Delay choice vs. delay maintenance: Different measures of delayed gratification in capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.* **27**, 392–398. (doi: 10.1037/a0031869)
24. Bramlett JL, Perdue BM, Evans TA, Beran MJ. 2012. Capuchin monkeys (*Cebus apella*) let lesser rewards pass them by to get better rewards. *Anim. Cogn.* **15**, 963–969 (doi: 10.1007/s10071-012-0522-x)
25. Genty E, Karpel H, Silberberg A. 2012 Time preferences in long-tailed macaques (*Macaca fascicularis*) and humans (*Homo sapiens*). *Anim. Cogn.* **15**, 1161–1172.
26. Wagenmakers EJ (2007) A practical solution to the pervasive problems of p values. *Psychon. Bull. Rev.* **14**, 779–804. (doi: 10.3758/bf03194105)
27. R Core Team. 2020 R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
28. Maestriperi, D., Schino, G., Aureli, F., Troisi, A. 1992 A modest proposal: displacement activities as an indicator of emotions in primates. *Anim. Behav.* **44**, 967–979. (doi: 10.1016/s0003-3472(05)80592-5)
29. Stevens JR 2010 Intertemporal choice. In Breed MD, Moore J (eds) Encyclopedia of Animal Behaviour. Academic Press, Oxford, pp 203–208.
30. Vander Wall SB. 1990 Food hoarding in animals. University of Chicago Press, Chicago.
31. Bateson M, Kacelnik A. 1996 Rate currencies and the foraging starling: The fallacy of the averages revisited. *Behav. Ecol.* **7**, 341–352.
32. Stevens JR, Hallinan EV, Hauser MD. 2005 The ecology and evolution of patience in two New World primates. *Biol. Lett.* **1**, 223–226. (doi: 10.1098/rsbl.2004.0285)
33. Stevens JR, Stephens DW. 2010 The adaptive nature of impulsivity. In Madden GJ, Bickel WK (eds) Impulsivity: the Behavioral and Neurological Science of Discounting. APA Press, Washington, DC, pp. 361–387.
34. Stephens DW, Kerr B, Fernández-Juricic E. 2004 Impulsiveness without discounting: the ecological rationality hypothesis. *Proc. R. Soc. B* **271**, 2459–2465. (doi: 10.1098/rspb.2004.2871)
35. Todd PM, Gigerenzer G. 2000 Precipitous of simple heuristics that make us smart. *Behav. Brain Sci.* **23**, 727–780. (doi: 10.1017/s0140525x00003447)
36. Fawcett TW, McNamara JM, Houston AI. 2012 When is it adaptive to be patient? A general framework for evaluating delayed rewards. *Behav. Process.* **89**, 128–136. (doi: 10.1016/j.beproc.2011.08.015)
37. Amici F, Aureli F, Call J. 2008 Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. *Curr. Biol.* **18**, 1415–1419. (doi: 10.1016/j.cub.2013.06.020)
38. Hayden BY. 2016 Time discounting and time preference in animals: a critical review. *Psychon. Bull. Rev.* **23**, 39–53. (doi: 10.3758/s13423-015-0879-3)
39. Killen P. 2009 An additive-utility model of delay discounting. *Psychol. Rev.* **116**, 602–619. (doi: 10.1037/a0016414)
40. Stephens DW. 2002 Discrimination, discounting and impulsivity: a role for an informational constraint. *Philos. Trans. R. Soc. B* **357**, 1527–1537. (doi: 10.1098/rstb.2002.1062)
41. Animal Behavior Society. 2015 Guidelines for the treatment of animals in behavioural research and teaching. *Anim. Behav.* **83**, 301–309. (doi: 10.1016/s0003-3472(14)00451-5)