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Capuchin monkeys' ability to choose beneficial options is inhibited by added complexity

Matthew H. Babb [a, b, *], Laurent Prétôt [c], Redouan Bshary [d], Sarah F. Brosnan [a, b, e]

[a] Department of Psychology, Georgia State University, Atlanta, GA, U.S.A.
[b] Language Research Center, Georgia State University, Atlanta, GA, U.S.A.
[c] Department of Psychology and Counseling, Pittsburg State University, Pittsburg, KS, U.S.A.
[d] Institute of Biology, University of Neuchâtel, Neuchâtel, Switzerland
[e] Department of Philosophy, Center for Behavioral Neuroscience, Georgia State University, Atlanta, GA, U.S.A.

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How does ecological complexity influence decision making? To facilitate interpretation, laboratory studies often focus on decision tasks with limited options, but animals presumably face more variety in the wild. For example, sometimes species must choose between ephemeral and permanent options, as with choosing between mobile prey and stationary food. The optimal choice is to prioritize the ephemeral option, because it will disappear if not selected first, whereas the permanent option will always be available. In experimental tasks with just these two choices, capuchin monkeys (*Sapajus (Cebus) apella*) learn to maximize their rewards. However, in the wild, animals presumably face additional sets of choices, for instance two ephemeral or two permanent options, which may make it more difficult to learn the best way to maximize their payouts. Here we show that adding configurations during learning lowers the capuchins' preference for choosing the ephemeral option first. Because recent theoretical work suggests that this more complex version could be solved by grouping the elements through configural learning, half of our subjects underwent training proposed to aid in the configural learning process prior to experiencing the added complexity. This training did not improve the capuchins' ability to pick the ephemeral option first. We consider both what this means for capuchins' and other species' decision making in more complex environments and how we use experimental results to understand animals' cognition and behaviour.

How do animals make decisions to maximize their outcomes? Research on this topic is critical to understanding everything from cognition (how they make these decisions) to behaviour (the impact of their decisions). One challenge, however, is that in the laboratory, where much of this research is conducted, tasks are often intentionally simplified to focus on the discrimination of interest. This allows for tighter control, but in the wild, animals presumably face multiple options or decisions at the same time, raising questions about the validity of these simplified situations for understanding natural behaviour. Thus, a key question is whether the decisions that we see in the laboratory remain the same when additional diversity of choices is introduced, and what this means for how animals learn to maximize outcomes in more realistic contexts.

One well-studied decision, for which we have data on both the outcomes and the learning strategies, is the so-called biological market task or ephemeral reward task (hereafter, the market task; Bshary & Grutter, 2002; Pepperberg & Hartsfield, 2014; Prétôt et al., 2016a, 2016b, 2020; Salwiczek et al., 2012; Triki et al., 2019; Truskanov et al., 2021; Zentall et al., 2017; Zentall & Case, 2018). In this task, an animal is presented with a choice between two options, both of which provide identical immediate reinforcement, but the availability of each option differs based on whether another selection was made prior. The 'ephemeral' option can only be selected if it is chosen first; however, the 'permanent' option is always available for selection even if the other option is selected before it. In this way, animals need to prioritize the ephemeral option over the permanent option to maximize their rewards. Otherwise, if animals select the permanent option first, then the ephemeral option becomes inaccessible and the animal misses out on the reinforcement that option provides.

* Corresponding author.
E-mail address: matthew.h.babb@gmail.com (M. H. Babb).

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This task was originally designed to test how the bluestreak cleaner wrasse, *Labroides dimidiatus*, a small tropical fish that survives by feeding off the dead tissue, parasites and mucus of two types of 'client' fish, make cooperative foraging decisions on their reefs. In its natural environments, this species must sometimes decide whether to feed from a 'visiting' client fish, which will leave if not serviced quickly (equivalent to the ephemeral option), or a 'resident' client, which has no other servicing options and will therefore wait (equivalent to the permanent option). In the wild, cleaners are adept at this task, servicing the ephemeral visitors first (Bshary, 2001). In the laboratory, when clients were replaced with distinct plastic plates, they also choose the ephemeral plate first (Bshary & Grutter, 2002; Salwiczek et al., 2012; Wismer et al., 2014, 2019).

However, in the wild, cleaners face an additional variety of choices, such as two residents or two visitors. In a recent study, Truskanov et al. (2021) tested cleaners in a more complex version of the market task ('complex market') in which subjects faced the original ephemeral—permanent (EP) choice as well as ephemeral—ephemeral (EE) and permanent—permanent (PP). Cleaners were much less likely to choose the ephemeral option first in the complex market, with a few even developing a preference for the permanent option. This is not necessarily surprising as in the PP configuration, subjects invariably receive two food items, while in the EE configuration they invariably receive only one food item, thus decreasing the value of the ephemeral option by decreasing its average payout relative to the original task with only EP choices and potentially providing a negative value transfer from the EE configurations (Zentall & Sherburne, 1994).

One proposed mechanism for solving the complex market task is configural learning (Prat et al., 2022; Quiñones et al., 2020), or the ability to create compound representations of multiple stimuli that, together, have a different meaning than the individual stimuli alone (Gobet & Simon, 1998; Kolodny et al., 2015; Sutherland & Rudy, 1989). For example, this process is commonly used to learn that the meaning of compound words, like 'butterfly', are different than the individual words themselves, 'butter' and 'fly'. Similarly, if animals use configural learning to learn that the payouts associated with the ephemeral option are different depending on what option it is paired with, then they may be able to choose optimally in the EP configurations and maximize their reinforcement despite the complexity that comes with the additional configurations.

One obvious question is why the additional diversity negatively affects cleaners in the experimental task, but fish can learn to prioritize the ephemeral option in some contexts in the wild, which presumably involves greater diversity than in these experimental contexts. One possibility, then, for failures in earlier experiments, is that the fish used by Truskanov et al. (2021), all of which were wild caught, did not have enough prior experience with making this decision in their natural environment. All the subjects were captured from a reef that had disproportionately small cleaner-to-client ratios because of natural perturbations, which ultimately causes visitors to be less selective towards cleaners (Triki et al., 2018) and may influence how cleaners solve the task (Bshary & Triki, 2022). Another possibility is that although fish show evidence of many impressive cognitive abilities (Beri et al., 2014; Brown et al., 2011; Bshary et al., 2002, 2014), they may need extensive prior experience to use configural learning effectively. In the wild, they receive this experience as they encounter thousands of clients per day (Grutter, 1996), but in the laboratory, they do not get this much experience. One way to test the role of general cognition is to look at other species that have succeeded on the original version of the market task. Thus, for the current study, we replicated Truskanov et al.'s (2021) procedure in tufted capuchin monkeys, *Sapajus (Cebus) apella*, another species who develops a preference for choosing the ephemeral option first in at least some circumstances (Prétôt et al., 2016a, 2016b).

Capuchins are an excellent species for this because they have been tested on the original version of the task (Prétôt et al., 2016a, 2016b; Salwiczek et al., 2012). This allowed us to design our procedure to maximize the possibility for learning and to determine how a relatively more cognitively sophisticated species would perform on the task. Capuchins have relatively large brains, even when compared to other primates (Isler et al., 2008; Stephan et al., 1988), which may suggest enhanced cognitive ability (Byrne & Corp, 2004; Jerison, 1973; but see Deaner et al., 2007; van Schaik et al., 2021) and should be useful if cognitive ability is essential for succeeding in the task. In addition, capuchin monkeys have shown some circumstantial evidence of configural learning. For example, capuchins have a greater ability to organize size seriation in a categorical rather than a linear way, suggesting a capacity for chunking sequences together (McGonigle et al., 2003).

The current study was based on a computerized version of the market task for which capuchins learned to maximize outcomes in previous work (Prétôt et al., 2016a). The computerized modality minimized the potential influence of extraneous cues (i.e. the presence of the experimenter: Prétôt et al., 2016a; Smith et al., 2018; the presence of visible food: Boysen & Berntson, 1995; Boysen et al., 1999; Murray et al., 2005; Prétôt et al., 2016b) and reduced the possible interference from being unable to simultaneously grab two foods at once (Pepperberg & Hartsfield, 2014). For this task, we utilized two different choice conditions, the 'simple market' condition, in which subjects were presented with only the ephemeral—permanent (EP) configuration, as in the original version of the task (Bshary & Grutter, 2002; Salwiczek et al., 2012), and the 'complex market' condition (Truskanov et al., 2021), which included the EP configuration and two additional configurations: ephemeral—ephemeral (EE) and permanent—permanent (PP). This complex market was presumably closer to the variety of choice configurations animals could see in their natural environments, allowing us to test how this added complexity impacted capuchins' ability to learn to prioritize the ephemeral option.

We used a within-subjects design in which all subjects underwent both conditions so that we could compare how individual capuchins performed on the market task under different learning environments. This also allowed a qualitative comparison with the cleaners (Truskanov et al., 2021), which is interesting as both species learned to prioritize the ephemeral option in the simple task (Bshary & Grutter, 2002; Prétôt et al., 2016a, 2016b; Salwiczek et al., 2012; Wismer et al., 2014, 2019). In addition, to explore whether prior experience with the EP configuration can help animals maximize their rewards in the complex market (Triki et al., 2018; Wismer et al., 2014), we divided our subjects into two groups; half of our subjects experienced the simple market condition first followed by the complex market condition, and the other half experienced the reverse. Lack of prior experience is one of the potential explanations for the reduced performance of cleaners in the earlier study (Bshary & Triki, 2022; Triki et al., 2018, 2019; Truskanov et al., 2021), and repeated exposure of the EP configuration has been proposed to aid in the configural learning process (Goldstein et al., 2010), which is argued to help animals prioritize the ephemeral option (Prat et al., 2022; Quiñones et al., 2020). Thus, we predicted that if this type of experience is helpful for learning the complex task, then the monkeys with experience would outperform those without.

We had no a priori hypotheses regarding how demographic factors would affect performance on the task, but the theoretical studies predicted that factors such as rank, sex or life stage could affect how individuals learn and perceive the task (Prat et al., 2022; Quiñones et al., 2020). However, in our capuchin social groups, all subjects were adults and all males were always higher ranking than females (thus making sex and rank colinear), so we only included rank as a secondary explanatory factor in our analysis. Finally, although our goal was not to compare the monkeys with the cleaners, and a statistical analysis was impossible due to procedural differences, we did qualitatively compare the capuchins' and cleaners' performance.

METHODS

Subjects and Housing

We tested 20 tufted capuchin monkeys (7 males, 13 females, age: mean ± SD = 19 ± 6.55 years, range 8–34 years) at Georgia State University's Language Research Center (LRC) in Atlanta, Georgia, U.S.A. Information regarding group demographics is given in the Appendix, Table A1. The capuchins were socially housed in mixed-sex groups, each with their own large indoor/outdoor enclosure with enrichment and climbing structures. The capuchins at the LRC had previously been trained to voluntarily separate from their social group into testing boxes attached to their indoor enclosure, where they routinely completed noninvasive behavioural and cognitive testing, including computer-based studies using a hand-controlled joystick (Evans et al., 2008). Since participation in testing was voluntary, not all subjects chose to complete the task. Within the first five sessions, three subjects completed on average fewer than half (20 out of the possible 40) of the trials per session and were dropped from participation in the study, leaving us with 17 subjects, eight of which had prior experience with a computerized version of the original market task (Prétôt et al., 2016a).

Ethical Note

All studies at the LRC are noninvasive and subjects voluntarily choose to participate. Regardless of participation in tasks, the subjects were never deprived of food, water, treats, outdoor time or social contact to motivate testing and there were no consequences for choosing not to participate, other than not being able to take part in the task. Throughout the duration of each trial, water was available ad libitum. After completion of the subjects' daily testing (approximately 4 h), they were released back into their social group.

Georgia State University is fully accredited by the Association for Assessment and Accreditation of Laboratory Animal Care (AAALAC), and the Georgia State University Institutional and Animal Care and Use Committee approved all procedures in this study (IACUC number A20018). Additionally, the research was conducted in accordance with the laws of the United States and by the standards for the treatment and use of animals in research established by the ASAB Ethical Committee/ABS Animal Care Committee (2023) and the American Society of Primatologists (2021).

General Procedure

In the market task, the subjects were presented with two options, 'permanent' and 'ephemeral'. For both permanent and ephemeral options, the reinforcement was identical and immediate, but the contingency of each option differed. The ephemeral option disappeared immediately if it was not chosen first, which means the only way for a subject to receive reinforcement from this option was to choose it first. In contrast, the permanent option was always available for selection, even if another option was selected before it (Bshary & Grutter, 2002; Prétôt et al., 2016a; Salwiczek et al., 2012). Based on these contingencies, subjects needed to choose the ephemeral option first (when it was present) to maximize their rewards.

In prior research (Bshary & Grutter, 2002; Prétôt et al., 2016a, 2016b, 2020; Salwiczek et al., 2012), subjects were always presented with both an ephemeral and a permanent option in every trial (the EP configuration), but in the current study, we presented subjects with this configuration and two additional configurations, two ephemeral choices (Table 1; ephemeral–ephemeral, or EE) and two permanent choices (Table 1; permanent–permanent, or PP). This allowed us to examine how the more complex contexts influence which options they choose.

All subjects participated in two experimental conditions: the 'simple market' and the 'complex market'. The simple market included only the original EP configuration, whereas the complex market included all three choice configurations (EP, EE and PP) within the same session (Table 1). To keep sessions the same length (to control for food acquisition) while also ensuring that subjects did not receive more EP trials in one condition than the other, we added single-option control trials (C) to the simple market condition in which only one icon was present (described below and in Fig. 1).

Computerized Task Design

The task was run on a computer using a program coded in the Python 3 programming language (van Rossum & Drake, 2012), based on the first two versions of the computerized task used in Prétôt et al. (2016a). At the start of every trial, a green start button appeared at the centre of the white screen. Simultaneous with the appearance of the start button, a short ding sound occurred to signify the start of another trial and to capture subjects' attention (this was important because not all subjects finished the previous task; Prétôt et al., 2016a). After subjects used the joystick to move the cursor to the start button, icons representing each of the two options appeared on opposite sides of the computer screen (Fig. 1). To select an option, the subjects then had to move their cursor and touch the icon of choice. All options rewarded the subject with one 45 mg banana-flavoured pellet (Bio-Serv, Frenchtown, NJ, U.S.A.). There was an intertrial interval (ITI) of 60 s between trials because this duration resulted in learning in previous work using this task in this species (Prétôt et al., 2016a).

All subjects were tested on a minimum of 480 trials in each market condition, half of which (range 240–380) were trials that contained the ephemeral–permanent configuration (EP trials). We used a greater number of EP trials than previous work because several subjects from Prétôt et al. (2016a) failed to learn the task after only 100 EP trials; thus, more trials gave them additional opportunity to learn. This was particularly important since we designed this task to be more challenging. Each testing session consisted of 40 total trials, of which 20 were EP trials, and subjects completed only one session per day. Sessions were capped at 100 min, or roughly twice the amount of time needed to complete all 40 trials in a session, to avoid collecting data once subjects stopped paying attention. Because some individuals did not complete all 40 trials in every session, it took our subjects 12–24 sessions (median: 18) to complete all 480 trials in each market condition.

Although 480 trials was the minimum, we did not halt a session once a subject achieved 480 trials (and because subjects could stop earlier trials part way through, the end of a session did not always coincide with an even 480 trials). In addition, data was exported biweekly and some subjects were not removed from the testing program until their data was checked. To ensure these additional trials did not change the overall conclusions of our results, we conducted two separate analyses, one that only included the

Table 1
Payout matrix for the contingencies of the task

Condition	Choice configuration	First choice	Reward sequence	Total reward amount
Simple market	EP	E	E → P	2
		P	P	1
	C	C	C	1
Complex market	EE	E	E	1
	EP	E	E → P	2
		P	P	1
	PP	P	P → P	2

In the simple market condition, subjects experienced either the ephemeral–permanent (EP) or the control (C) choice configuration. In the complex market condition, individuals experienced either ephemeral–ephemeral (EE), ephemeral–permanent (EP) or permanent–permanent (PP) choice configurations.

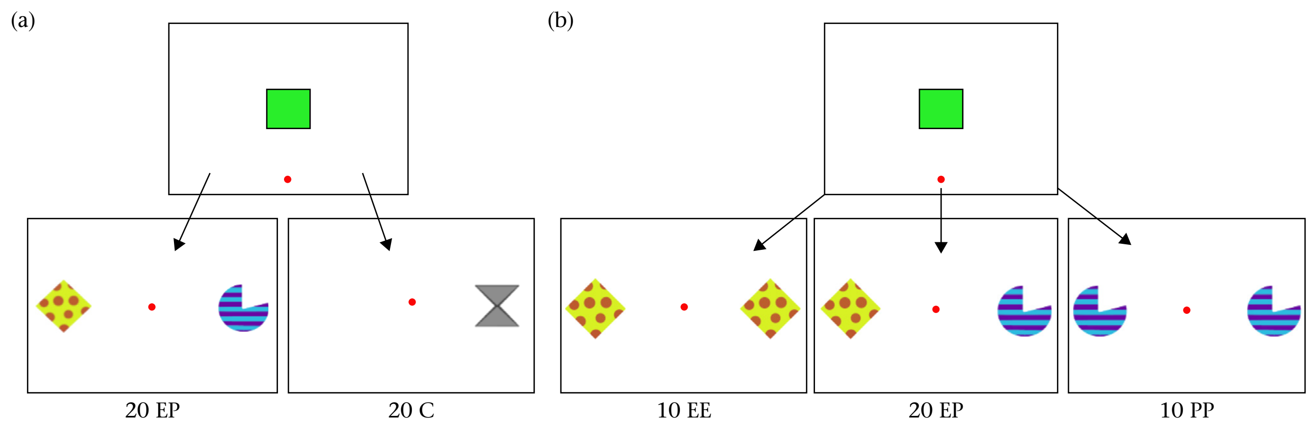

Figure 1. Computerized market task and icons. Prior to each trial, a green square, representing the start button, and a red circle, which was a cursor controlled by the subject, appeared in the middle and bottom of a white screen, respectively. To start each trial, the subjects had to move their cursor upwards to touch the green start button, after which the trial began. (a) In the simple market condition, subjects experienced 20 ephemeral–permanent (EP) trials and 20 control (C) trials per session. (b) In the complex market condition, subjects experienced 10 ephemeral–ephemeral (EE) trials, 20 ephemeral–permanent (EP) trials and 10 permanent–permanent (PP) trials per session. Stimulus identity was counterbalanced so that half of the monkeys were trained to learn that the yellow/orange diamond was the ephemeral option and the other half were trained to learn that the yellow/orange diamond was the permanent option.

monkeys' first 240 EP trials for each condition and one that included all EP trials. We found no significant differences between the analyses (Appendix, Table A2) so for consistency we chose to focus on the results using only the first 240 EP trials in each condition.

The simple market condition was the control condition and most closely resembled the original task (Prétôt et al., 2016a). In each session, half of the trials (20 trials) were the EP configuration and the other half were control trials (20 trials) in which only one icon appeared, on either the left or right side of the screen (Fig. 1), and the subject was rewarded for selecting it. To reduce the possibility of our subjects developing a side bias, the control icon appeared on both sides of the screen an equal number of times per session. The control icon differed in shape and pattern from both the ephemeral and the permanent icons to prevent carryover effects. The complex market condition also included 20 EP trials, but in lieu of control trials, each complex market session included 10 EE and 10 PP trials. Thus, in the simple market condition, subjects completed (at least) 240 EP and 240 control trials, and in the complex market, subjects completed (at least) 240 EP, 120 EE and 120 PP trials.

In both conditions, the configurations were presented in a pseudorandomized order within each session, with no more than three of the same configurations occurring in a row. Additionally, since capuchin monkeys develop side biases in some experimental contexts (Brosnan & de Waal, 2009; Prétôt et al., 2016a; Tecwyn et al., 2017; Ventricelli et al., 2013), we pseudorandomized the position of both the ephemeral and the permanent options in EP trials, so that no option appeared on the same side more than three times in a row. Lastly, in case there was some inherent preference for either of the icons, we counterbalanced the identity of each icon so that the purple/blue icon was the ephemeral option to half of the subjects and the yellow/orange icon was the ephemeral option to the other half.

A goal of this study was to test whether prior experience with the EP configuration would help the capuchins learn to pick the ephemeral option first. Theoretical work on the configural learning process predicts that repeated exposure of relevant configurations over a brief amount of time may aid in learners' ability to chunk individual units into compound units (Goldstein et al., 2010). To test this, we compared the performance of eight subjects that completed the simple market condition first (three of which had previous experience with a similar computerized task; Prétôt et al., 2016a), thus giving them repeated exposure to only the relevant EP configuration, and nine subjects that completed the complex market condition first (five of which had previous experience with a similar computerized task; Prétôt et al., 2016a).

Statistical Analysis

The focus of our analysis was to determine whether the ephemeral or permanent option was prioritized in the heterogeneous trial type (EP trials). To analyse the likelihood of prioritizing the ephemeral option, we fitted a logistic mixed effects model predicting the capuchins' binary choice in all EP trials ('glmer' function from R package lme4; Bates et al., 2015). To ensure that the eight subjects that also participated in Prétôt et al.'s (2016a) study several years prior did not change our results, we also fitted an identical model with only the 11 naïve subjects. The overall trends of our findings did not change (for analysis, please see Appendix, Table A4), so we focus on the results from the model with all 17 subjects.

In our model, we included subject identity as a random effect and for the fixed effects, we included market type (simple market being the referent), trial number within each market (range 1–240), the market experienced first (simple market first being the referent) and all two-way interactions to determine how performance changed within each condition. We also included the two-way interaction between market type and relative rank score (range 0.00–1.00) because theoretical work has indicated that social factors may also influence how individuals learn this task, but no experimental studies have tested this (Prat et al., 2022; Quiñones et al., 2020). We did not include sex because all the male subjects were higher ranking than all females in their groups (thus making rank and sex colinear), and we did not include age because our subjects were all adults. All numeric predictors were z-centred to facilitate convergence (for more information on how we calculated relative rank scores, see Appendix).

We assessed the statistical significance of our logistic model by comparing its fit to a null model that included only the intercept and the random effects ('anova' function from R package car). We checked the models' diagnostics using residual plots and examined the normality of residuals for the random effects using a Q–Q plot and a Shapiro–Wilk test (Model 1: $W = 0.90311$, $P = 0.0766$). There were also no problems with collinearity for any of the predictors in the model (variance inflation factor, VIF < 1.1). All data were analysed using R statistical programming language in RStudio (R version 3.6.0; R Core Team, 2019).

In addition to our model, we conducted two-sided exact binomial tests on each subject's EP trials to determine which individuals had a significant preference for choosing the ephemeral option first. We examined each monkey's preferences across all 240 of their EP trials in each condition (Appendix, Table A3); however, because our model indicated that the subjects' preferences were changing significantly over time as they learned the contingencies of the task, we also examined their preferences in their final 40 trials, since this was likely a better indicator of what they learned throughout the task (Table 2; trial numbers 200–240). In line with this finding, we also reran our model using only the last 40 EP trials from each subject and removed the fixed effect of session number and all interactions. The results from this model aligned with our original model (Appendix, Table A5).

RESULTS

Ephemeral Preferences in the Market Task

In total, we analysed 8160 total trials, 4080 from each market condition (simple and complex). Overall, the monkeys prioritized the ephemeral option in 3283 (40.2%) of trials, choosing it first in 1914 (46.9%) of the simple market trials and 1369 (33.6%) of the complex market trials. The binomial tests for each monkey's final 40 EP trials revealed that seven monkeys preferred selecting the ephemeral option first in the simple market condition and no monkeys preferred selecting it first in the complex market condition. However, four monkeys preferred the permanent option first in the simple market condition and 12 monkeys preferred it first in the complex market condition (Table 2, Fig. 2).

Learning Over Time

Compared to the random effects-only model (Akaike's information criterion: AIC = 8871.9; Bayesian information criterion: BIC = 8885.9), our model, which included subject identity, market type, the market experienced first, trial number, rank score and all two-way interactions, showed significant improvement in predicting the likelihood of an ephemeral selection (AIC = 8208.4, BIC = 8278.5, $\chi^2_8 = 679.41$, $P < 0.001$). The capuchins' likelihood of prioritizing the ephemeral option varied significantly as a function of the market type and the trial number interaction ($b = -1.07$, odds ratio = 0.34, SE = 0.02, $P < 0.001$; Fig. 3, Table 3) such that the capuchins' preferences for the ephemeral option increased as more trials were completed under simple market conditions, while their preferences for the ephemeral option decreased as more trials were completed under the complex market conditions. This indicates that over time, the capuchins were learning to choose the ephemeral option first in the simple condition but learning to choose the permanent option first in the complex condition.

Table 2
The proportion of ephemeral–permanent (EP) trials in which each subject selected the ephemeral option first

Subject	Market experienced first	Simple market		Complex market	
		Proportion of EP trials	95% CI	Proportion of EP trials	95% CI
Albert	Simple	1.000[a]	0.912–1.000	0.250[b]	0.127–0.412
Applesauce	Simple	0.975[a]	0.868–0.999	0.500	0.338–0.662
Atilla	Complex	0.500	0.338–0.662	0.250[b]	0.127–0.412
Bias	Complex	0.525	0.361–0.685	0.475	0.315–0.639
Gabe[c]	Simple	0.000[b]	0.000–0.088	0.125[b]	0.042–0.268
Gambit[c]	Complex	0.550	0.385–0.707	0.525	0.398–0.626
Gretel	Complex	0.950[a]	0.831–0.994	0.650	0.361–0.685
Griffin[c]	Complex	0.000[b]	0.000–0.088	0.075[b]	0.016–0.204
Ingrid	Simple	0.875[a]	0.732–0.958	0.400	0.249–0.567
Irene	Complex	0.700[a]	0.535–0.834	0.225[b]	0.108–0.385
Liam[c]	Complex	0.000[b]	0.000–0.088	0.000[b]	0.000–0.088
Lily[c]	Simple	0.450	0.293–0.615	0.050[b]	0.006–0.169
Lychee	Simple	0.700[a]	0.535–0.834	0.200[b]	0.091–0.356
Nala[c]	Complex	0.550	0.385–0.707	0.075[b]	0.016–0.204
Paddy	Simple	0.375	0.227–0.542	0.200[b]	0.091–0.356
Widget[c]	Simple	0.950[a]	0.831–0.994	0.125[b]	0.042–0.268
Wren[c]	Complex	0.425[b]	0.270–0.591	0.000[b]	0.000–0.088

Only the final 40 EP trials of each subject within each market condition are shown. Confidence intervals (CIs) were calculated as a part of two-sided exact binomial tests.
[a] Significant preference for selecting ephemeral (E) first.
[b] Significant preference for selecting permanent (P) first.
[c] Previously tested on a computerized market task in Prétôt et al. (2016a).

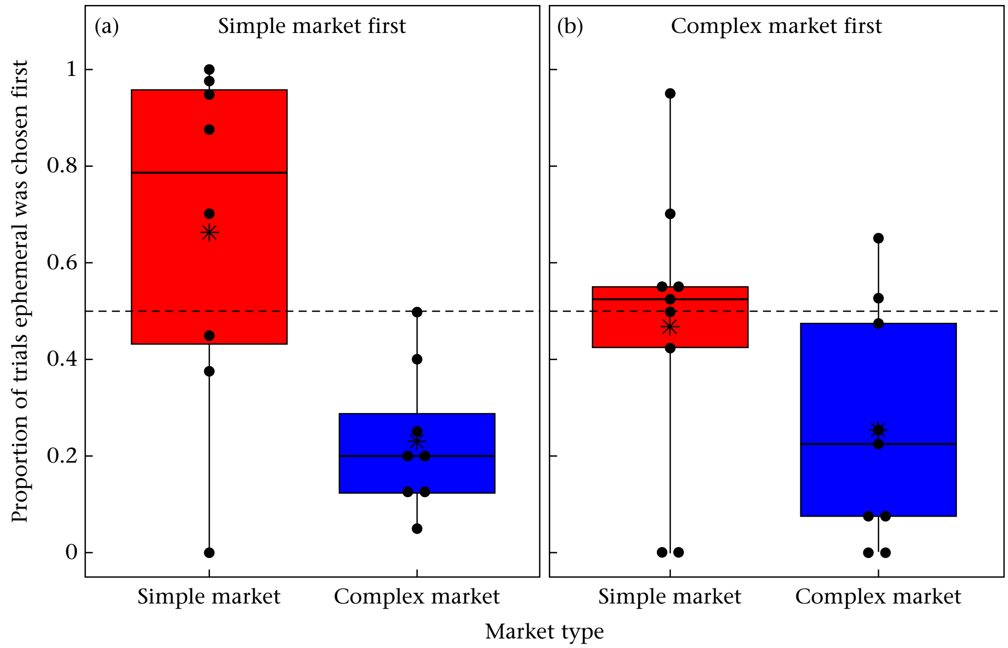

Figure 2. Proportion of final 40 ephemeral–permanent (EP) trials that each subject selected the ephemeral option first for (a) individuals who received the simple market condition first ($N = 8$) and (b) individuals who received the complex market condition first ($N = 9$). Points represent the proportion of EP trials in which each individual selected the ephemeral option first in their final 40 EP trials of each condition (0.00–1.00). Boxes represent the interquartile range with the vertical lines representing the minimum and maximum. The solid horizontal lines within each box represent the median proportion of EP trials per condition and the stars represent the mean proportion of EP trials per condition. The dashed line indicates the preference expected by chance (0.50).

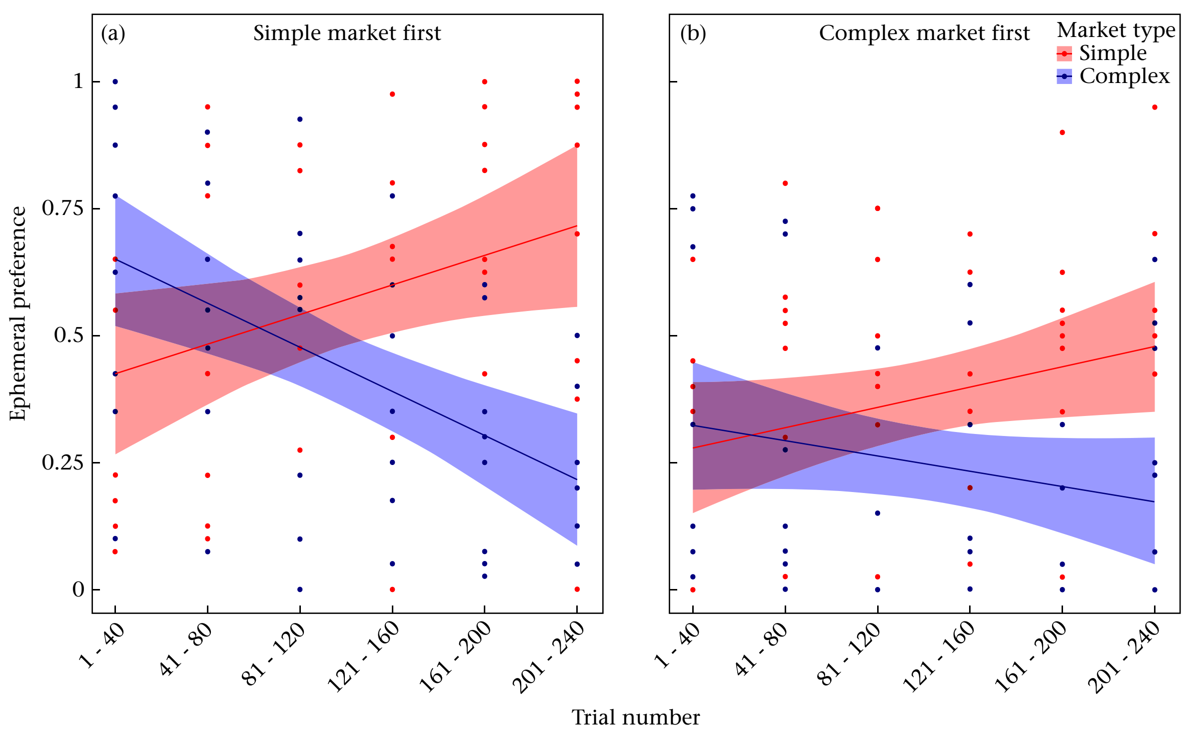

Figure 3. Preference for the ephemeral option throughout each condition for (a) subjects who received the simple market condition first and (b) subjects who received the complex market condition first. Points represent each subject's preference for choosing the ephemeral option first. To calculate preferences, trials were grouped by chunks of 40 trials for a total of six groups. Lines represent average preference for the ephemeral option ± 1 SE.

Effect of Prior Experience

Contrary to our predictions, experiencing the simple market condition prior to the complex market condition did not help capuchins solve the complex condition. There was a significant interaction between market type and condition order ($b = -0.279$, odds ratio $= 0.76$, SE $= 0.09$, $P = 0.014$; Fig. 2, Table 3), indicating that individuals who underwent the simple market first were more

Table 3
Mixed effects logistic regression predicting the likelihood of prioritizing the ephemeral option ($N = 17$ subjects, paired design)

Predictor	Coefficient	Odds ratio	SE	Z	P
Intercept	−0.003	1.00	0.38	−0.007	0.994
Market type[a]	−0.499	0.61	0.05	−5.942	**<0.001**
Market order[a]	−0.604	0.55	0.29	−1.140	0.254
Trial number[a]	0.435	1.54	0.08	8.780	**<0.001**
Rank score[a]	−1.156	0.31	0.08	−4.327	**<0.001**
Market type*market order	−0.279	0.76	0.09	−2.452	**0.014**
Market type*trial number	−1.069	0.34	0.02	−18.885	**<0.001**
Market order*trial number	0.097	1.10	0.06	1.740	0.082
Market type*rank score	0.586	1.80	0.12	8.451	**<0.001**

[a] Due to significant interactions, the main effects are not interpretable and are only presented for statistical completeness. Significant outcomes are shown in bold.

likely to prioritize the ephemeral option in the complex condition; however, a closer look at Fig. 3 suggests that the difference was largely driven by a carryover effect from the simple market condition that led to initially high performance in the complex market condition. By the final 40 EP trials, preferences for the ephemeral option in the complex market were similar between the two groups and no individuals chose the ephemeral option first significantly more than chance in the complex market, regardless of the market they experienced first (Table 2).

Effect of Dominance

The interaction between rank score and market type was a significant predictor of subjects' preferences in the model ($b = 0.586$, odds ratio = 1.80, SE = 0.12, $P < 0.001$; Fig. 4, Table 3), with subordinate capuchins being significantly more likely to prioritize the ephemeral option than dominant capuchins. This effect was more pronounced in the simple market condition; however, closer examination of Fig. 4 indicates the difference between the two conditions was too small to be meaningful.

DISCUSSION

Much experimental work on decision making focuses on highly structured tasks so that researchers can maximize control, but natural contexts may involve more diversity. Capuchin monkeys can learn to choose an ephemeral option, which disappears if not chosen immediately, preferentially over a permanent one, which always remains available, when all choices are between only those two options (Prétôt et al., 2016a, 2016b), but to explore how additional diversity impacts their responses, we tested them with this choice as well as the choice between two ephemeral or two permanent options. None of our monkeys learned to pick the ephemeral first when additional ephemeral−ephemeral and permanent−permanent configurations were present. Furthermore, it has been proposed that exposure to the original ephemeral−permanent choice helps individuals learn it (through the configural learning process; Prat et al., 2022; Quiñones et al., 2020), but we found no such effect.

Considering our results in more detail, no individuals in our study developed a significant preference for the ephemeral option in the complex market condition, although several developed a preference for the permanent one. This is an interesting situation, both because the capuchins learned to prioritize the ephemeral option in earlier work and because in natural settings, cleaner fish presumably experience more diversity in their available choices than simply an ephemeral versus permanent client, yet they learn to solve the task (Bshary, 2001). Because our task was designed to measure the capuchins' choices, rather than the mechanism underpinning them, we cannot determine the specific proximate mechanisms that may have caused this; however, it is worth considering some of the possibilities, none of which are mutually exclusive.

One possibility is that individuals rely on the associative value of each option to determine which option they prefer, which is an effective strategy in the simple market, with only the ephemeral−permanent configuration (Prat et al., 2022; Quiñones et al., 2020), but not in the more complex one, with all three configurations available. This is because in the permanent−permanent configuration, subjects invariably receive two food items, which increases the average value of the permanent option and may elicit a positive value transfer onto the permanent option that was not present when the EP configuration was presented alone (Zentall & Sherburne, 1994). Similarly, in the ephemeral−ephemeral configuration, subjects invariably receive only one food item (because the second ephemeral option disappears when the first is chosen, which cannot be avoided), which decreases the average value of the ephemeral option and may elicit a negative value transfer onto the ephemeral option (Zentall & Sherburne, 1994). This asymmetry in value likely causes the subjects to prefer the permanent option.

It is also possible that the monkeys may prefer the consistency of the permanent option over the apparent stochasticity of the ephemeral one. The permanent option always resulted in a reward on every trial, whereas the ephemeral option only gave a reward if it was chosen first (otherwise it disappeared). This is fairly easy to track when subjects are exposed only to one configuration, but once we added the ephemeral−ephemeral choice (in which it was impossible to get both ephemeral rewards), the monkeys may have been frustrated by the fact that they could never get both rewards, thus leading some of our subjects to use a rule of thumb of choosing the option that was consistent, whether or not it was always the optimal choice.

Another possibility is that configural learning is required but capuchins do not readily use it. The current evidence that capuchins can use this cognitive process is limited, with only one study inferring it based on how they performed in a size seriation task (McGonigle et al., 2003). Given that several other taxa, including chimpanzees, *Pan troglodytes* (Gao et al., 2018), macaques (Japanese macaque, *Macaca fuscata*, and rhesus macaque, *Macaca mulatta*: Nejime et al., 2015), Guinea baboon, *Papio papio* (Tosatto et al., 2022), rats (Alvarado & Rudy, 1992) and pigeons (Couvillon & Bitterman, 1996; Wynne, 1996), have shown convincing evidence

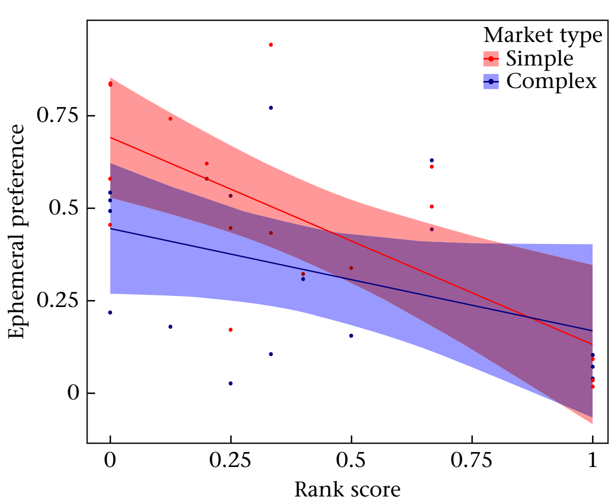

Figure 4. Effect of rank on performance. The preference for selecting the ephemeral option first in the simple market condition (in red) and the complex market condition (in blue) as a function of rank score. Shaded areas represent ± 1 SE.

that they use configural learning in experimental tasks, it seems likely that capuchins can also do so, but the design of the current task was not conducive for allowing capuchins to be aided by configural learning. Future research that specifically tests for configural learning in capuchins will help clarify whether they lack this ability or whether it is not used in this context.

For any of the above mechanisms, there is also the issue that this task may not be as ecologically relevant for the capuchins. It was designed to match the ecology of cleaner fish, and monkeys do not regularly experience the same choice in their natural environment. Capuchins do consume insects and small vertebrates (i.e. ephemeral food sources that can try to escape), but they do not face the decision between a guaranteed food item (a piece of fruit) and an escaping one (an insect or small vertebrate) thousands of times a day, as do cleaners (Grutter, 1996). Therefore, there may have been little pressure for this discrimination to evolve, suggesting that even if capuchins do have the requisite cognitive mechanisms, they may not easily learn it.

Interestingly, we found little evidence that experience improved the monkeys' performance. For capuchins, like cleaners, experiencing the simple market first did not improve performance in the complex market condition (Truskanov et al., 2021). Only five of eight subjects developed a preference for the ephemeral option in the simple market task and of these, none of them maintained this preference in the complex market. Moreover, eight of our subjects had participated in a previous study nearly 5 years prior in which they did prefer the ephemeral option on a simple market task (Prétôt et al., 2016a), yet failed to do so here. Perhaps experiencing only 240 EP trials was simply not enough for them to learn the configuration, although the possibility of value transfer and the fact that they actually decreased their performance over time suggests that increased experience may not improve it.

Although we had no a priori hypotheses for how social factors would influence performance on the market task, theoretical studies (Prat et al., 2022; Quiñones et al., 2020) suggest that these factors may influence how individuals prioritize the ephemeral option by changing the way they learn or perceive the task. Indeed, in our study, social rank significantly affected the monkeys' performance in both conditions, with subordinate individuals preferring the ephemeral option more often than dominant individuals. This finding aligns with capuchin social dynamics, as dominant capuchins have more access to preferred food than do subordinates (Fragaszy et al., 2005), who may therefore be under greater pressure to learn to optimize their opportunities to obtain resources than dominants.

Lastly, although the methodologies were slightly different, it is worth comparing the monkeys' performance to the fish. In a previous study, some fish did learn to solve the complex version of the task, although like the monkeys, many did not (Truskanov et al., 2021). Thus, it is interesting to consider why neither those wild-caught cleaners nor the monkeys do well on the task, despite the fact that in the wild, cleaners appear to be able to overcome the natural complexity. First, it could be that subjects in the laboratory are not receiving enough experience to understand the contingencies of the task. In the wild, cleaners experience the decision between clients thousands of times per day (Grutter, 1996), but in both studies, we limited subjects to only 28 or 40 trials per day (Truskanov et al., 2021), and at most 240 test trials overall. Moreover, in the case of the cleaners specifically, the fish from Truskanov et al. (2021) were all caught from reefs that were still recovering from a sudden decrease in client densities (associated with coral bleaching; Triki et al., 2018), so they likely did not have the same amount of experience with this decision in the wild as other fish did in previous studies (Bshary & Grutter, 2002; Salwiczek et al., 2012; Triki et al., 2019). Second, although the more complex market is meant to resemble an animal's natural interactions more closely than the simple market, it still does not truly model all the complexity involved in the decision, especially for cleaners. Undoubtedly there are nuances to this decision in the wild that we are failing to replicate in the laboratory setting. As just one example (and there are certainly others), in the laboratory task, subjects always experience the simultaneous presentation of two options, but in the wild, the decision likely does not always present itself as a simultaneous dichotomous choice. Therefore, animals may need additional cues to successfully learn to pick the ephemeral option first.

Overall, the capuchin monkeys failed to learn the market task on which they had previously succeeded when additional choice configurations were introduced. What this means for their decision making in natural contexts is an interesting question. Cleaner fish are clearly making this discrimination in some contexts in nature (Bshary, 2001), suggesting that they can learn it despite the inherent complexity. Perhaps, if given enough time, capuchins too could learn this discrimination, or perhaps it is so distinct from any similar decision that they make in the wild that there has been no selective pressure for them to develop the ability to solve it. It would be particularly interesting to know how they use configural learning in other contexts to determine whether they might be using it in the current task, as well as what other mechanisms may be inhibiting or enhancing their ability to learn. Most importantly, the fact that increasing the complexity so dramatically changed subjects' behaviour, now in two species, suggests that while carefully controlled experimental tasks remain an important tool for understanding behaviour and cognition, these results must be considered with respect to context and ecology, and when possible, tested with additional variants to determine how relatively small changes may be affecting responses.

Author Contributions

R.B. and S.F.B. conceived the study and all authors contributed to the study's design. M.H.B. conducted the study with logistical support from S.F.B.; M.H.B. analysed the data and led the writing with support from S.F.B.; all authors discussed the results and approved the final manuscript.

Data Availability

The data sets analysed during the current study are available in online repositories. The names of the repositories can be found at https://github.com/mattbabb97/ComplexMarketData.git.

Declaration of Interest

The authors declare that they have no conflict of interest.

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Appendix

Relative Dominance Rank Calculation

To determine the dominance rank of each individual, we used the results from another study conducted concurrently in our laboratory on the same population of monkeys. Using nearly 2 years of observational data, this study calculated the cardinal rank of each individual based on the number of social encounters that the individual won or lost. We took these rankings, which were originally calculated in Elo-ratings (see Franz et al., 2015), and converted them to a rank score using the following equation:

$$\text{Rank score}_i = \frac{r_i}{n-1},$$

where r represents the number of group members that individual i outranks within their group of size n. Therefore, a value of 1 represents the highest-ranking individual and a value of 0 represents the lowest-ranking individual. Since our group sizes range from four to nine individuals, this proportion of animals outranked helps account for different group sizes (Vandeleest et al., 2016).

Table A1
Demographic information about subjects

Subject name	Sex	Age	Rank score
Albert	M	10	0.00
Applesauce	F	17	0.33
Atilla	M	9	0.67
Bias	F	34	0.25
Gabe	M	23	1.00
Gambit	F	25	0.67
Gretel	F	17	0.13
Griffin	M	24	1.00
Ingrid	F	9	0.20
Irene	F	19	0.00
Liam	M	18	1.00
Lily	F	24	0.50
Lychee	F	22	0.00
Nala	F	19	0.33
Paddy	F	11	0.40
Widget	F	13	0.00
Wren	F	19	0.25

Table A2
Logistic mixed model results with all trials included

Predictor	Coefficient	Odds ratio	SE	*Z*	*P*
Intercept	0.071	1.07	0.41	0.189	0.850
Market type	−0.786	0.46	0.04	−9.756	**<0.001**
Market order	−0.519	0.60	0.31	−0.982	0.326
Trial number	0.494	1.64	0.09	9.346	**<0.001**
Rank score	−1.181	0.31	0.08	−4.409	**<0.001**
Market type*market order	−0.229	0.80	0.09	−2.124	**0.034**
Market type*trial number	−1.206	0.30	0.02	−21.394	**<0.001**
Market order*trial number	0.202	1.22	0.07	3.620	**0.015**
Market type*rank score	0.566	1.76	0.12	8.632	0.255

Significant outcomes are shown in bold.

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Table A3
Proportion of ephemeral—permanent (EP) trials in which each subject selected the ephemeral option first

Subject	Market experienced first	Simple market		Complex market	
		Proportion of EP trials	95% CI	Proportion of EP trials	95% CI
Albert	Simple	0.833[a]	0.780–0.878	0.521	0.456–0.586
Applesauce	Simple	0.942[a]	0.904–0.968	0.771[a]	0.712–0.822
Atilla	Complex	0.504	0.439–0.569	0.442	0.378–0.822
Bias	Complex	0.446	0.382–0.511	0.533	0.468–0.598
Gabe[c]	Simple	0.092[b]	0.058–0.135	0.100[b]	0.065–0.145
Gambit[c]	Complex	0.613[a]	0.548–0.674	0.629[a]	0.565–0.690
Gretel	Complex	0.742[a]	0.681–0.796	0.179[b]	0.133–0.234
Griffin[c]	Complex	0.033[b]	0.014–0.065	0.038[b]	0.017–0.070
Ingrid	Simple	0.621[a]	0.556–0.682	0.579	0.424–0.642
Irene	Complex	0.454	0.390–0.519	0.217[b]	0.166–0.274
Liam[c]	Complex	0.017[b]	0.005–0.042	0.071[b]	0.042–0.111
Lily[c]	Simple	0.338[b]	0.278–0.401	0.154[b]	0.111–0.206
Lychee	Simple	0.579	0.424–0.642	0.492	0.427–0.557
Nala[c]	Complex	0.433[b]	0.370–0.499	0.104[b]	0.069–0.150
Paddy	Simple	0.321[b]	0.262–0.384	0.308[b]	0.251–0.371
Widget[c]	Simple	0.838[a]	0.785–0.882	0.542	0.476–0.606
Wren[c]	Complex	0.171[b]	0.125–0.225	0.025[b]	0.009–0.054

Includes all 240 EP trials for each subject within each market condition. Confidence intervals (CIs) were calculated as a part of two-sided exact binomial tests.
[a] Significant preference for selecting ephemeral (E) first.
[b] Significant preference for selecting permanent (P) first.
[c] Previously tested on a computerized market task in Prétôt et al. (2016a).

Table A4
Mixed effects logistic regression predicting the likelihood of prioritizing the ephemeral option ($N = 9$ subjects, paired design)

Predictor	Coefficient	Odds ratio	SE	*Z*	*P*
Intercept	0.650	1.91	0.74	1.673	0.094
Market type	−0.206	0.81	0.10	−1.758	0.079
Market order	−0.579	0.56	0.26	−1.227	0.220
Trial number	0.423	1.53	0.09	7.129	**<0.001**
Rank score	−0.225	0.80	0.31	−0.585	0.559
Market type*market order	−0.426	0.65	0.09	−3.047	**0.002**
Market type*trial number	−1.026	0.36	0.02	−14.751	**<0.001**
Market order*trial number	0.114	1.12	0.08	1.644	0.100
Market type*rank score	0.642	1.90	0.21	5.770	**<0.001**

All subjects who previously participated in Prétôt et al. (2016a) removed. Significant outcomes are shown in bold.

Table A5
Mixed effects logistic regression predicting the likelihood of prioritizing the ephemeral option in each subject's final 40 EP trials ($N = 17$ subjects, paired design)

Predictor	Coefficient	Odds ratio	SE	*Z*	*P*
Intercept	0.21	1.23	0.48	0.54	0.587
Market type	−1.86	0.16	0.02	−12.86	**<0.001**
Market order	−0.06	0.94	0.50	−0.11	0.912
Rank score	−1.29	0.28	0.08	−4.56	**<0.001**

Significant outcomes are shown in bold.

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