

Increased Cognitive Load Enables Unlearning in Procedural Category Learning

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Abstract

Interventions for drug abuse and other maladaptive habitual behaviors may yield temporary success, but are often fragile and prone to relapse. In this paper, we show that increased cognitive load during intervention enables unlearning of category knowledge obtained through procedural systems. In particular, under normal cognitive load, an intervention consisting of random feedback does not interfere with original learning in any way. We have recently proposed that random feedback causes a drop in feedback contingency, defined as the correlation between response confidence and outcome, which in turn causes a gate on further procedural learning to be closed. Our theory assumes that random feedback causes a drop in feedback contingency, which in turn causes a gate on learning to be closed. When this gate is closed, no modification of procedural knowledge can occur. In this paper, we wondered if the neural computation of feedback contingency, and therefore the gate to procedural learning, relies on declarative mechanisms. If so, then increasing cognitive load via an explicit dual-task during random feedback intervention should disrupt the computation of feedback contingency. By disrupting the computation of feedback contingency, we hoped that the gate on procedural learning may not reliably close, thereby leaving learning vulnerable to modification. Our results indicate that this is indeed the case.

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Introduction

Relapse often occurs when an addict returns to the original context of their drug use (Higgins et al., 1995). This may occur because interventions given in clinics do not modify addiction-driving stimulus-response (SR) associations, but instead cause the learning of new clinic-specific associations. Returning to the original context of drug abuse then reactivates the preserved addiction-driving SR associations, causing relapse. If true, then this hypothesis means that the brain has a gating mechanism to protect learning obtained in old contexts from being modified. Our prior work, which was focused on understanding this gating mechanism (Crossley, Ashby, & Maddox, 2013), found that feedback contingency – defined as the correlation between response confidence and outcome – is a principle driver of this gate. The present study is an extension of this earlier work, asking whether the estimation of feedback contingency depends on executive mechanisms. The rest of the introduction proceeds with a brief summary of the key findings reported by (Crossley et al., 2013), followed by the logic of the current study.

Crossley et al. (2013)

Crossley et al. (2013) attempted to understand why the SR associations underlying procedural learning, habits, and addiction are so remarkably resistant to modification. We developed a task that, after initial acquisition of SR associations, attempted to erase the just-formed engram. The results showed promising initial signs of true memory erasure.

Our experiments included three phases of equal duration: acquisition, intervention, and test. During acquisition, all participants were trained on the categories shown in panel C of Figure 1. During intervention, the category structure was unchanged, but feedback about response accuracy was manipulated in an attempt to erase the learning that occurred during the initial acquisition. Our goal was to erase the initially acquired SR associations by overwriting them with random associations.

We investigated the effects of three different types of intervention. All used random feedback (RF) on some percentage of intervention trials. In the RF(.25) conditions, the intervention feedback was random on all trials. Since there are four categories, every intervention response was followed by positive feedback with probability .25 and negative feedback with probability .75. In the RF(.40) conditions, RF was also given on every trial, but the probability of positive feedback was .40 and the probability of negative feedback was .60. Finally, in the mixed feedback conditions, RF was given with probability .75 and true feedback was given with probability .25.

In all conditions, feedback returned to 100% veridical during the test phase. Half the participants in each condition relearned the original categories (the relearning conditions) and half learned new categories that used the same stimuli but permuted the category-response mappings. Thus the study included six conditions created from a 3×2 factorial design where three levels of intervention feedback [RF(.25), RF(.40), mixed feedback] were crossed with two levels of test (relearning, new learning).

Operationally, we require two conditions to conclude that unlearning is successful: (1) the behavior disappears during the intervention, (2) during test, both relearning and new learning occur at the same rate as initial learning. In contrast, if learning is preserved during the intervention, then relearning the original categories should be faster than initial acquisition and learning of new categories should be slower (because of interference).

Results are shown in Fig. 2. In the RF conditions (Fig. 2A and 2C), reacquisition is faster than initial learning, and new category learning is slower, suggesting that RF does not cause unlearning. In contrast, following mixed feedback intervention, reacquisition and new category learning both occur at approximately the same rate as initial learning. Thus, this intervention may have caused true unlearning.

The RF results are incompatible with classic models (see Figure 3A), which assume that procedural skills are learned at cortical-striatal synapses via DA-dependent synaptic plasticity, and that the DA signal is proportional to the reward prediction error ($RPE =$

Obtained Reward – Predicted Reward). Since RF is by definition unpredictable, it generates large RPEs, and therefore classic models predict that RF will cause new learning of random associations, which will overwrite the original category knowledge, causing true unlearning. In contrast, Figure 2A and 2C show that RF did not disrupt the previously acquired category knowledge.

Rapid relearning following RF suggests that **a gating mechanism protects procedural knowledge during RF**. We proposed striatal cholinergic interneurons called TANs (Tonically Active Neurons) as a candidate gate (Ashby & Crossley, 2011; Crossley et al., 2013). In their default state, TANs exert a tonic presynaptic inhibition of cortical inputs to the striatum (Figure 3) (Calabresi, Centonze, Gubellini, Pisani, & Bernardi, 2000). Thus, the default state of the gate is closed. However, TANs learn to pause in response to stimuli that predict reward (Kimura, Rajkowski, & Evarts, 1984), removing the presynaptic inhibition, and allowing striatal neurons to respond to cortical input and cortical-striatal learning to occur (i.e., the gate opens). The TANs are driven by centromedian and parafascicular (CM-Pf) intralaminar thalamic nuclei, which signal salient environmental cues and changes in context (Shimo & Hikosaka, 2001; Yamada, Matsumoto, & Kimura, 2004; Apicella, Legallet, & Trouche, 1997; Ravel, Sardo, Legallet, & Apicella, 2006). The TAN pause occurs only when the CM-Pf–TAN synapse is strong, and learning at both CM-Pf–TAN and cortical-striatal synapses is driven by DA-mediated reinforcement signals (Suzuki, Miura, Nishimura, & Aosaki, 2001; Setyono-Han, Henkelman, Foekens, & Klinj, 1982).

Our model that includes the TAN gating mechanism accounts for a variety of behavioral and physiological data from simple instrumental conditioning tasks (Ashby & Crossley, 2011; Crossley, Horvitz, Balsam, & Ashby, 2016), including rapid relearning following extinction. However, even this model failed to account for our RF results (Figure 2A and 2C). This is because we still modeled DA release as strictly proportional to RPE, which fluctuates widely during RF. This leads to random fluctuations in the CM-Pf–TAN

synaptic weight, preventing the TANs from reliably closing the gate.

For the TANs to close the gate and protect cortical-striatal plasticity during RF, two conditions must be met: (1) The model must detect RF. Since RF is non-contingent on behavior, the valence of feedback earned after each response is uncorrelated with the confidence that the response was correct (called *response confidence*). Contrast this with veridical feedback, in which negative feedback is typically accompanied by low response confidence. We recently showed that category learning is exquisitely sensitive to this feedback contingency (Ashby & Vucovich, in press). (2) The TANs must close the gate when RF is detected. This only occurs when CM-Pf-TAN synapses undergo consistent weakening. Crossley et al. (2013) modeled this by assuming that the DA response is attenuated and biased below baseline when feedback contingency is low.

With these modifications, the model not only accounts for savings in relearning after RF intervention, but also makes a novel prediction: **If true feedback is given on a small percentage of trials (e.g., 25%), then the correlation between feedback valence and response confidence could be high enough to cause the TANs to pause, allowing the RF on the other (75%) trials to induce true unlearning.** Results from our Mixed Feedback intervention (Figure 2B) are consistent with this prediction.

The Present Study

Crossley et al. (2013) hypothesized that the gate on procedural learning — and therefore the key to procedural modification — is controlled by the degree of feedback contingency, but we made no predictions about how feedback contingency is estimated by the nervous system. This article begins addressing this question — by asking whether the estimation of feedback contingency depends on executive function (e.g., prefrontal networks involved in working memory and executive reasoning). Our rationale is as follows: If feedback contingency is estimated by executive mechanisms, then increasing cognitive load during the intervention phase (by requiring participants to simultaneously perform a dual

task) should disrupt its estimation. This disruption should deprive the TANs gate of the clear signal they require to close the gate during RF, thereby allowing RF to modify the procedural knowledge that was acquired during initial learning.

With this goal in mind, we performed an experiment that mimicked the design of Crossley et al. (2013), except we added a concurrent numerical Stroop task during key classification trials. Previous research suggests that this dual task interferes with category learning that recruits executive function and declarative memory much more than with category learning that recruits procedural memory (Waldron & Ashby, 2001; Crossley, Paul, Roeder, & Ashby, 2016), and that the types of categories used here recruit procedural learning even when the dual task is being performed (Crossley, Paul, et al., 2016).

In the Overlap-150, Overlap-250, and Overlap-350 conditions, the first dual-task trial was 50 trials before the onset of intervention, and continued for 100, 200, or 300 trials, respectively. In the No-Overlap-300 condition, the first dual-task trial was 50 trials after the onset of intervention, and continued for 250 trials. Comparing the three Overlap conditions allows us to look for dose dependency. The No-Overlap condition allows us to assess the importance of disrupting the estimation of feedback contingency during the transition from acquisition to intervention. We also included a control condition in which no concurrent Stroop task was ever performed.

If feedback contingency estimation depends on executive function then two behavioral markers are expected: (1) the dual task should slow the drop in categorization accuracy that occurs with the onset of RF; and (2) reacquisition of the original category learning should be slower in the dual task conditions than in the no dual-task control.

Methods

Design

There were four dual-task conditions (Overlap-150, Overlap-250, Overlap-350, and No-Overlap-300) and one no dual-task control condition. The dual-task conditions differed

on two dimensions, (1) the number of trials on which the dual task was applied, and (2) whether or not the onset of the dual task preceded the onset of intervention.

Participants

163 participants were recruited from the University of Texas at Austin undergraduate population. There were 30 participants in the Overlap-150 condition, 34 participants in the Overlap-250 condition, 32 participants in the Overlap-350 condition, 33 participants in the No-Overlap-300 condition, and 34 participants in the control condition. After exclusions (described in the next subsection), 119 participants were included in the reported analyses. Of these, there were 23 in the Overlap-150 condition, 26 in Overlap-250 condition, 22 in the Overlap-350 condition, 21 in the No-Overlap-300 condition, and 27 in the control condition. All participants completed the study and received course credit for their participation. All participants had normal or corrected-to-normal vision.

Exclusions

Of these 163 participants, 25 were excluded from the reported analyses for failing to reach a an average accuracy of 40% correct during the last 50 trials of the acquisition phase (described below). An additional 19 were excluded for failing to perform the concurrent numerical Stroop task with an average accuracy greater than or equal to 80%.

Stimuli and Categories

Stimuli were black lines that varied across trials only in length (pixels) and orientation (degrees counterclockwise rotation from horizontal). The stimuli are illustrated graphically in Figure 1, and were identical to those used by Crossley et al. (2013).

Procedure

Participants in all conditions were told that they were to categorize lines on the basis of their length and orientation, that there were four equally-likely categories, and that high

levels of accuracy could be achieved. The experiment included three phases: acquisition (300 trials), intervention (400 trials), and reacquisition (150 trials). During acquisition and reacquisition, feedback was based on the participant's response, whereas feedback was random during the intervention. Participants were given no prior instructions about the phases, and the transition from one phase to another occurred without any warning to the participant.

At the start of each non-Stroop trial, a fixation point was displayed for 1 second and then the stimulus appeared. The stimulus remained on the screen until the participant generated a response by pressing the "Z" key for category "A", the "W" key for category B, the "/" key for category C, or the "P" key for category D. Written instructions informed participants of the category label to button mappings. An "invalid key" message was displayed if any other button was pressed. The word "Correct" was presented for 1 second if the response was correct or the word "Wrong" was presented for 1 second if the response was incorrect (except during the intervention phase in which feedback was completely random).

Stroop trials began with a fixation point that was displayed for 1 second. The category stimulus and the Stroop stimuli (numbers flanking the category stimulus) were displayed simultaneously. After 200 ms the Stroop stimuli were replaced by white rectangles which remained on the screen until they made a category response. Responses emitted before the Stroop stimuli were replaced by white rectangles were not accepted. Feedback about the category response was given immediately in the same fashion as on non-Stroop trials. The word "value" or "size" then appeared on the screen prompting participants to indicate which side contained the numerically larger or the physically larger number. Participants pressed the "F" key to choose the number on the left or the "J" key to choose the number on the right. The word "Correct" was then again presented for 1 second if the response to the Stroop task was correct or the word "Wrong" was presented for 1 second if the response was incorrect. See Figure 1 for example trials both including

and excluding the Stroop component. The Stroop task was included on trials 251-350 in condition 1, 251-450 in condition 2, 251-550 in condition 3 and 350-600 in condition 4.

Participants were instructed to try their hardest on both task components but to prioritize performance on the Stroop task. Both the category-learning task and the Stroop task were explained to participants prior to beginning the experiment, and on screen messages warned them when the Stroop component would begin, and again when it would end. These messages read, “You will now perform both the categorization task and the paired numbers task simultaneously. Keep trying your hardest!” and “You have now finished the section with the paired numbers task. You will now be shown only the line categorization task. Keep trying your hardest.” 85% of Stroop trials the numerically larger number was physically smaller. The proportion of Stroop trials that prompted “size” or “value” was split 50/50. Accuracy on the numerical Stroop task was indicated at the top of the screen when they received feedback regarding their performance on the concurrent task on each trial. This score was displayed in green if it was above 80% and red if it was below 80%. Note that when we refer to the “dual-task”, we are referring to the Stroop task just described.

Statistical Analyses

All t-tests comparing effects between conditions use the Welch-Satterthwaite approximation to the degrees of freedom to account for violations of homogeneity of variance.

Results

Numerical Stroop Accuracy

Figure 4 shows histograms characterizing mean dual-task performance separately for each condition. Overall, mean accuracy on the dual-task was very good, with mean proportion correct at 0.88 in the Overlap-150 condition, 0.87 in the Overlap-250 condition,

0.84 in the Overlap-350 condition, and 0.82 in the No-Overlap-300 condition. Participants that failed to perform the dual-task with an average accuracy greater than or equal to 80% were excluded from further analyses (see the “Exclusions” section above).

Classification Accuracy

Figure 5 shows the mean accuracy in each block of 25 trials across the duration of the experiment. Recall that if feedback contingency is estimated via executive mechanisms, then (1) dual-task trials should slow the change in classification performance during intervention, and (2) dual-task conditions should show reduced savings relative to the no dual-task control. We see evidence for both features in our data.

Acquisition. All conditions are identical for the first 250 trials (10 blocks) of acquisition (before dual-task onset), and so we expect performance during these blocks to be the same across conditions. However, Figure 5 shows modest differences between some of the conditions. A 5 Condition \times 10 Block repeated-measures ANOVA revealed a significant main effect of Condition $F(4, 1180) = 8.29, p < 0.01, \Omega = 0.02$, and a significant main effect of Block $F(1, 1180) = 250.83, p < 0.01, \Omega = 0.17$, but no significant interaction $F(4, 1180) = 1.95, p = 0.10, \Omega = 0.01$. Posthoc t-tests indicated that the main effect of Condition was driven by the Overlap-150 condition being significantly less than the No-Overlap-300 condition [$t(39) = -2.26, p < 0.05, d = 0.81$] and the Overlap-350 condition being significantly less than the No-Overlap-300 [$t(41) = 2.30, p < 0.05, d = 0.82$].

Intervention. If the estimation of feedback contingency depends on executive function, then we expect change in performance during intervention to be slowed during the simultaneous performance of the dual task. This is clearly seen in the first four blocks of the intervention phase (visual inspection of Figure 5), and is supported by the results of a 5 condition \times 4 block repeated-measures ANOVA. A significant effect of Condition [$F(4, 466) = 17.34, p < 0.001, \Omega = 0.11$] primarily reflected an overall difference in intervention performance in dual-task conditions relative to the no dual-task control. The

effect of Block and the interaction between Condition and Block were also significant [Block: $F(1, 466) = 59.37, p < 0.001, \Omega = 0.10$; Condition: $F(4, 466) = 2.41, p < 0.05, \Omega = 0.02$]. The directional interpretation of the omnibus test is supported by several planned comparisons on the overall mean accuracies during the first four blocks of the intervention phase. Early intervention accuracy in all dual-task conditions in which the dual-task was introduced before the onset of the intervention phase was significantly different from intervention accuracy in the no dual-task control [Overlap-150 vs no dual-task control: $t(41) = 5.34, p < 0.01, d = 4.44$; Overlap-250 vs no dual-task control: $t(47) = 4.99, p < 0.01, d = 3.61$; Overlap-350 vs no dual-task control: $t(36) = 2.87, p < 0.05, d = 1.38$; No-Overlap-300 vs no dual-task control: $t(31) = 0.88, p = 0.38, d = 0.14$].

Savings. If the computation of feedback contingency depends on executive function, then we expect the dual-task conditions to exhibit less savings than the no dual-task control – that is, we expect reacquisition of the original categories to be slower under dual-task conditions. This is apparent via visual inspection of Figure 6, which shows the mean savings per condition.

There was no significant savings in any of the dual-task conditions [Overlap-150: $t(22) = -0.27, p = 0.79, d = 0.02$; Overlap-250: $t(25) = -0.95, p = 0.35, d = 0.18$; Overlap-350: $t(21) = 0.39, p = 0.70, d = 0.03$; No-Overlap-300: $t(20) = -0.49, p = 0.63, d = 0.05$;], but there was significant savings in the no dual-task control condition [$t(26) = 2.57, p < 0.05, d = 1.29$].

Moreover, the savings observed in the no dual-task control condition was significantly greater than in all dual-task conditions except the Overlap-350 condition. [Overlap-150 < no dual-task control: $t(43) = -1.78, p < 0.05, d = 0.48$; Overlap-250 < no dual-task control: $t(51) = -2.47, p < 0.05, d = 0.86$; Overlap-350 < no dual-task control: $t(45) = -1.45, p = 0.08, d = 0.31$; No-Overlap-300 < no dual-task control: $t(38) = -1.88, p < 0.05, d = 0.58$], and was significantly greater than the savings pooled

across all dual-task conditions [$t(26) = 2.57, p < 0.05, d = 1.29$].

Recall that our design was constructed to allow for an examination of dose-dependency between the Overlap conditions. To answer this question, we performed a 1-way ANOVA asking if savings is different between these conditions. There was no significant difference between these conditions [$F(1, 69) = 0.22, p = .64, \Omega = 0.003$], indicating that we did not observe a dose-dependency.

We also designed our experiment to investigate the importance of placing the dual-task on the transition from acquisition to intervention. Since the No-Overlap-300 condition is significantly greater than the Overlap-150 and Overlap-350 Conditions, we can only examine this question by comparing the Overlap-250 condition to the No-Overlap-300 condition. A t-test revealed no significant difference [$t(41) = .18, p = .86, d = 0.06$], indicating that we found no evidence suggestion that the placement of the dual-task matters.

Discussion

Summary

Our results support our earlier conclusion (Crossley et al., 2013) that feedback contingency, defined as the correlation between response confidence and feedback valence, may be key to controlling a gate that prevents or permits the modification of procedural SR associations. To our knowledge, this article reports results from the first behavioral experiments that investigate the cognitive mechanisms that estimate feedback contingency. Specifically, our goal was to determine whether executive function and declarative memory mechanisms mediate contingency estimation. If they do, then a dual task that depends on working memory and executive function should make it more difficult for participants to recognize the sudden onset of random feedback. In our experiments, behavioral signatures of this difficulty would include (1) a slowed decrease in classification accuracy during intervention, and (2) decreased savings in relearning relative to a no dual-task control. Our

results were consistent with both of these predictions.

Dose Dependency and Intervention Onset

Our design allowed us to ask not just whether contingency estimation relies on executive function, but also whether the effects of disrupted contingency estimation are dose dependent (i.e., whether effects increase with dual-task exposure). We did not find dose effects. The absence of a dose effect indicates that 150 trials of dual-task was equally effective as 350 trials of dual-task. Could it be that 50, 10, or even a single trial of dual-task could again be equally effective? A true absence of dose effect would imply that this is indeed the case, though this prospect seems intuitively unlikely to be true. More likely, all the doses explored in this paper were past a saturation point, at which point dose effects are washed out. In the absence of further data, we are left only to our speculations.

Finally, our design also allowed us to ask whether it is important for the dual task to overlap with the transition from acquisition to intervention. One possibility is that in order for procedural learning to remain vulnerable to modification, the increase in cognitive load would need to precede the onset of random feedback intervention. The thinking here is that the gate that protects procedural learning during random feedback may be sensitive to *changes* in feedback contingency. Another possibility is that any disruption in the computation of feedback contingency at any time can cause the gate on learning to open. This possibility predicts that any increased cognitive load during intervention, regardless where it is placed should enable unlearning via random feedback. We found no evidence that the overlap was important.

Category Learning as a Procedural Skill

A natural question for readers unfamiliar with the category-learning literature is whether our behavioral paradigm is a good choice for studying procedural behaviors. In other words, how can a task with such simple motor demands (e.g., push a button) possibly recruit procedural networks that are strongly tied to motor processes? In fact, the

empirical evidence is strong that performance improvements in the classification task used here are mediated via procedural learning and memory (Ashby & Maddox, 2005, 2010; Ashby & Valentin, in press). Nevertheless, a limitation of the present study is that we did not directly probe the learning to ensure that was procedural in nature.

Therapeutic Relevance

The old adage of “it’s like riding a bike” is a surprisingly accurate description of procedural knowledge, reflecting its remarkable retention over years without practice. Paradigms designed to study procedural learning in the lab have echoed this adage, reporting savings in learning up to a year after training (Romano, Howard, & Howard, 2010; Turner, 2012). However, the stability of procedural memory comes at the cost of remarkable inflexibility. For example, changing any stimulus or response parameter that was present during training can prove catastrophic to performance (Rozanov, Keren, & Karni, 2010; Dienes & Berry, 1997). While resilience and inflexibility are desirable traits when a useful skill has been sufficiently learned, they can also lead to persistent maladaptive behaviors that have serious negative consequences, and in some cases may prove detrimental to a person’s health (e.g., drug abuse). Unfortunately, neither the potential for modification of procedural knowledge, nor a method to do so, are well understood.

Our previous research identified the interplay between striatal cholinergic interneurons and the midbrain dopamine system in controlling the eligibility of procedural knowledge for modification (Ashby & Crossley, 2011; Crossley et al., 2013). Directly targeting this network for improved interventions is unfortunately challenging, due to the difficulty of manipulating and measuring subcortical networks. Here, insofar as increasing cognitive load via a dual-task taps into prefrontal networks, we looked for more easily accessible cortical substrates that may control the striatal mechanism. Our results indicate that prefrontal networks likely do play an important role in controlling the estimation of

feedback contingency, and therefore may provide an accessible cortical target for electrical or magnetic intervention.

References

- Apicella, P., Legallet, E., & Trouche, E. (1997). Responses of tonically discharging neurons in the monkey striatum to primary rewards delivered during different behavioral states. *Experimental brain research*, 116(3), 456–466. Retrieved 2016-09-15, from <http://link.springer.com/article/10.1007/PL00005773>
- Ashby, F. G., & Crossley, M. J. (2011). A computational model of how cholinergic interneurons protect striatal-dependent learning. *Journal of Cognitive Neuroscience*, 23(6), 1549–1566.
- Ashby, F. G., & Maddox, W. T. (2005). Human category learning. *Annual Review of Psychology*, 56, 149-178.
- Ashby, F. G., & Maddox, W. T. (2010). Human category learning 2.0. *Annals of the New York Academy of Sciences*, 1224, 147-161.
- Ashby, F. G., & Valentin, V. V. (in press). Multiple systems of perceptual category learning: Theory and cognitive tests. In H. Cohen & C. Lefebvre (Eds.), *Handbook of categorization in cognitive science, second edition* (p. ?). New York: Elsevier.
- Ashby, F. G., & Vucovich, L. E. (in press). The role of feedback contingency in perceptual category learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, ?(?), ?
- Calabresi, P., Centonze, D., Gubellini, P., Pisani, A., & Bernardi, G. (2000). Acetylcholine-mediated modulation of striatal function. *Trends in neurosciences*, 23(3), 120–126. Retrieved 2016-09-15, from <http://www.sciencedirect.com/science/article/pii/S0166223699015015>
- Crossley, M. J., Ashby, F. G., & Maddox, W. T. (2013). Erasing the engram: The unlearning of procedural skills. *Journal of Experimental Psychology: General*, 142(3), 710. Retrieved 2016-09-18, from <http://psycnet.apa.org/journals/xge/142/3/710/>
- Crossley, M. J., Horvitz, J. C., Balsam, P. D., & Ashby, F. G. (2016). Expanding the role

- of striatal cholinergic interneurons and the midbrain dopamine system in appetitive instrumental conditioning. *Journal of Neurophysiology*, 115(1), 240–254.
- Crossley, M. J., Paul, E. J., Roeder, J. L., & Ashby, F. G. (2016). Declarative strategies persist under increased cognitive load. *Psychonomic bulletin & review*, 23(1), 213–222.
- Dienes, Z., & Berry, D. (1997). Implicit learning: Below the subjective threshold. *Psychonomic Bulletin & Review*, 4(1), 3–23.
- Higgins, S. T., Budney, A. J., Bickel, W. K., Badger, G. J., Foerg, F. E., & Ogden, D. (1995). Outpatient behavioral treatment for cocaine dependence: one-year outcome. *Experimental and Clinical Psychopharmacology*, 3(2), 205. Retrieved 2016-09-18, from <http://psycnet.apa.org/journals/pha/3/2/205/>
- Kimura, M., Rajkowski, J., & Evarts, E. (1984). Tonicly discharging putamen neurons exhibit set-dependent responses. *Proceedings of the National Academy of Sciences*, 81(15), 4998–5001.
- Ravel, S., Sardo, P., Legallet, E., & Apicella, P. (2006). Influence of spatial information on responses of tonically active neurons in the monkey striatum. *Journal of neurophysiology*, 95(5), 2975–2986.
- Romano, J. C., Howard, J. H., & Howard, D. V. (2010). One-year retention of general and sequence-specific skills in a probabilistic, serial reaction time task. *Memory*, 18(4), 427–441. Retrieved from <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=2894701&tool=pmcentrez&rendition=full> doi: 10.1080/09658211003742680
- Rozanov, S., Keren, O., & Karni, A. (2010, may). The specificity of memory for a highly trained finger movement sequence: Change the ending, change all. *Brain Research*, 1331, 80–7. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/20298683> doi: 10.1016/j.brainres.2010.03.019
- Setyono-Han, B., Henkelman, M., Foekens, J., & Klinj, J. (1982). Effect of the nigrostriatal

- dopamine system on acquired neural responses in the striatum of. *Nature*, 298, 686.
- Shimo, Y., & Hikosaka, O. (2001). Role of tonically active neurons in primate caudate in reward-oriented saccadic eye movement. *The Journal of Neuroscience*, 21(19), 7804–7814.
- Suzuki, T., Miura, M., Nishimura, K.-y., & Aosaki, T. (2001). Dopamine-dependent synaptic plasticity in the striatal cholinergic interneurons. *Journal of Neuroscience*, 21(17), 6492–6501.
- Turner, B. O. (2012). *Long-term retention in the cortical and subcortical procedural category-learning systems*. University of California, Santa Barbara. Retrieved 2016-02-10, from <http://gradworks.umi.com/35/45/3545135.html>
- Waldron, E. M., & Ashby, F. G. (2001). The effects of concurrent task interference on category learning: Evidence for multiple category learning systems. *Psychonomic Bulletin & Review*, 8(1), 168–176.
- Yamada, H., Matsumoto, N., & Kimura, M. (2004). Tonically active neurons in the primate caudate nucleus and putamen differentially encode instructed motivational outcomes of action. *The Journal of neuroscience*, 24(14), 3500–3510. Retrieved 2016-09-18, from <http://www.jneurosci.org/content/24/14/3500.short>

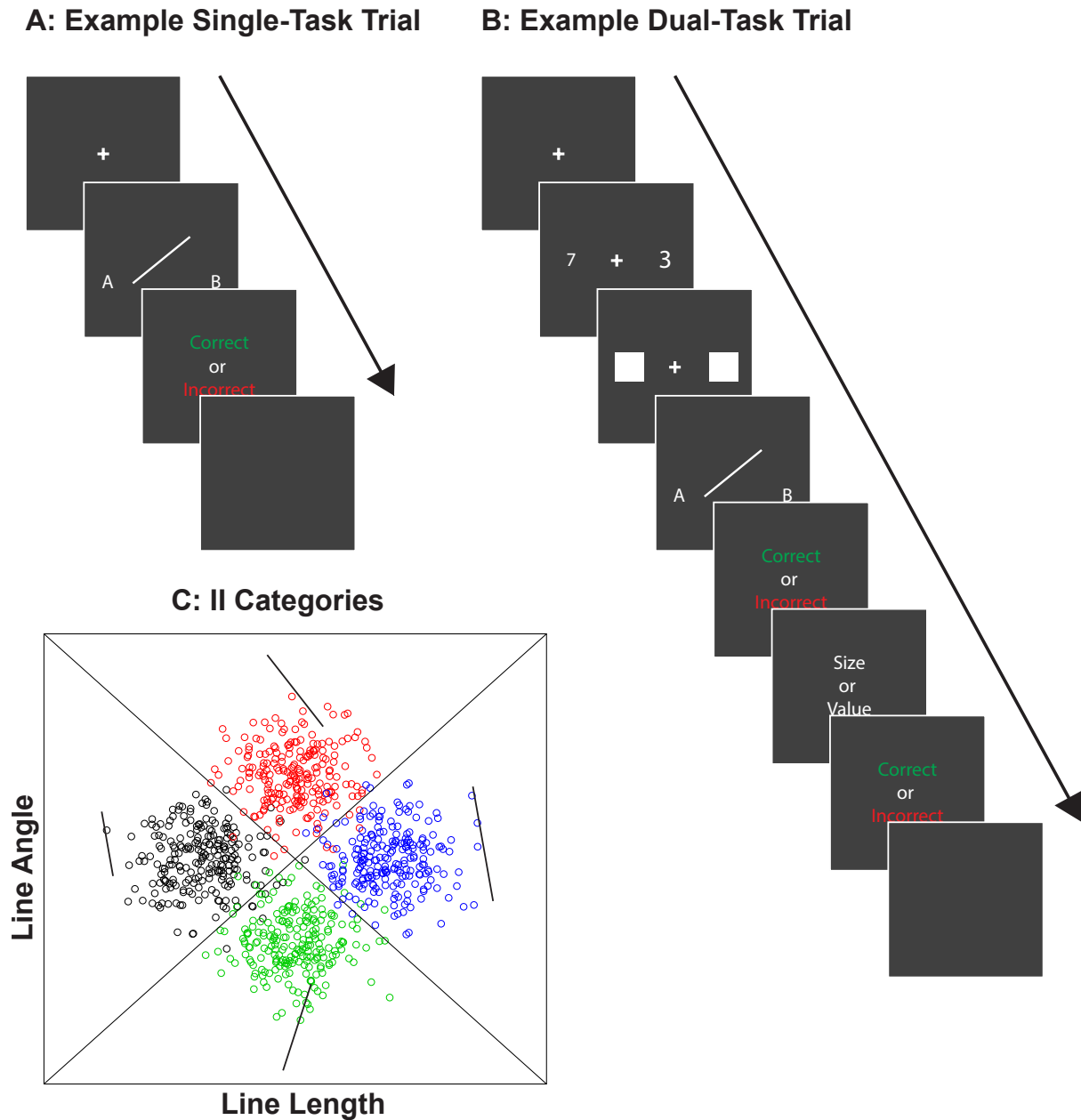


Figure 1. **A:** An Example trial during single-task conditions. **B:** An example trial during dual-task conditions. **C:** The categories used during the acquisition phase of Crossley et al. (2013).

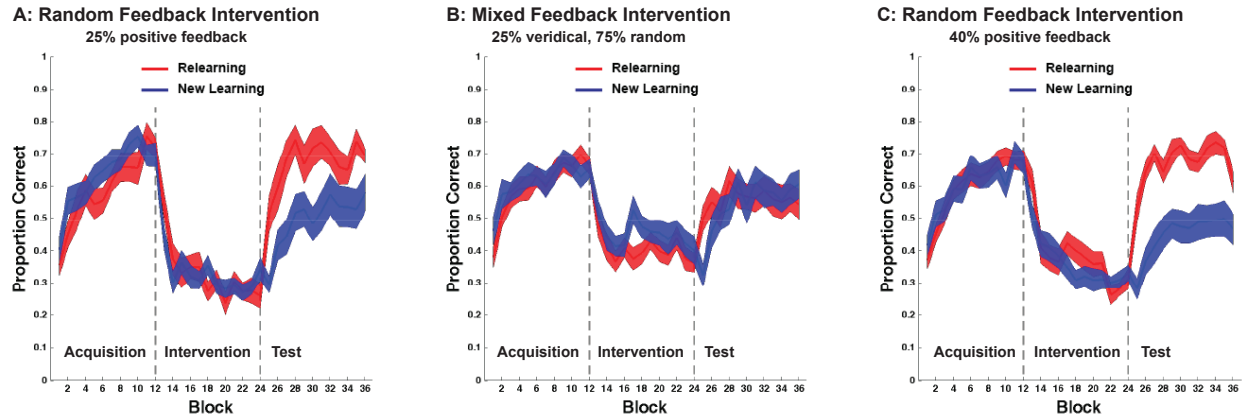


Figure 2. Crossley et al. (2013) behavioral results with different interventions. **A:** Random feedback intervention with 25% positive feedback. Accuracy drops to near chance during intervention, but is reacquired faster than original learning in the Relearning condition (red). In contrast, a lasting interference is observed in the New Learning condition (blue). Both results are consistent with the hypothesis that initial learning was not overwritten by random feedback. **B:** Mixed feedback intervention. Accuracy drops during intervention – though not to chance (i.e., 25%) – but subsequent learning proceeds at approximately the same rate and to the same extent as initial learning when either the original category-response mappings (red) or new category-response mappings (blue) are introduced. These results are consistent with the hypothesis that initial learning was overwritten during the intervention. **C:** Random feedback intervention with 40% positive feedback. Results are qualitatively identical to random feedback intervention with 25% positive feedback, implying that the mixed feedback results were driven by feedback contingency and not by positive feedback.

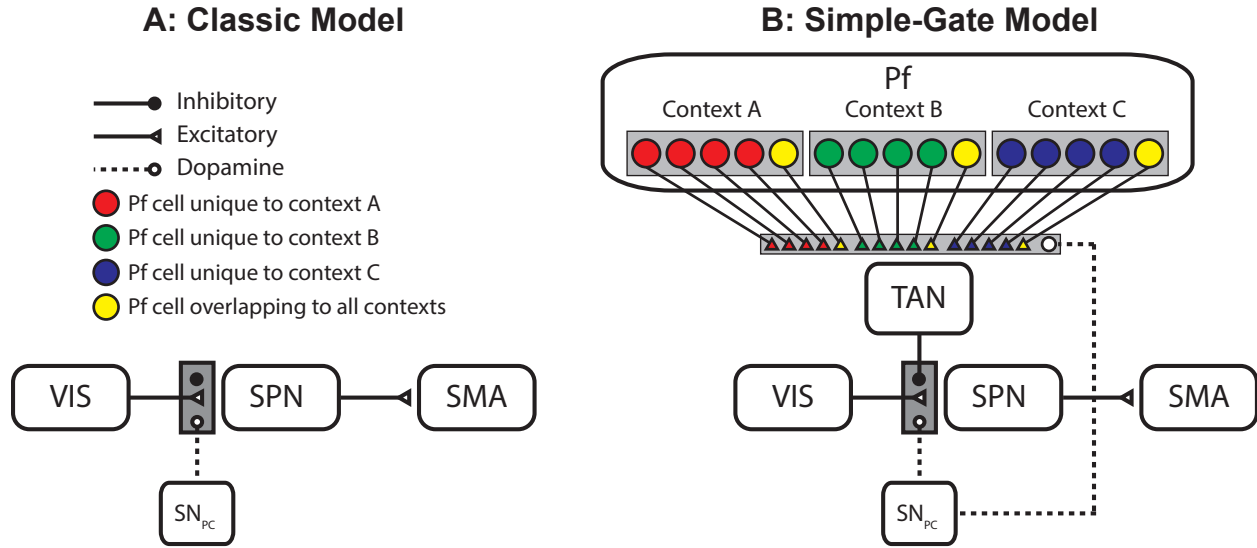


Figure 3. A: The Classic Model. A classic model of procedural learning based on a greatly simplified representation of the “direct pathway” through the basal ganglia. S-R associations are learned at cortical-striatal synapses, which are modified via dopamine-dependent reinforcement learning. The likelihood of repeating actions that lead to *unexpected* positive outcomes is gradually increased, and the likelihood of repeating actions that lead to *unexpected* negative outcomes is gradually decreased. **B: The TANs Model.** The classic model of procedural learning with the addition of a context-specific Pf-TAN pathway. This pathway acts as a gate on cortical-striatal synaptic plasticity, permitting or preventing the learning and expression of procedural knowledge. (SPN - spiny projection neuron of the striatum. D1 - Direct pathway SPN expressing the D1 DA receptor. D2 - Indirect pathway SPN expressing the D2 DA receptor. SMA - Supplementary Motor Area. SNpc - substantia nigra pars compacta. Pf - parafascicular nucleus of the thalamus. VIS - visual cortex)

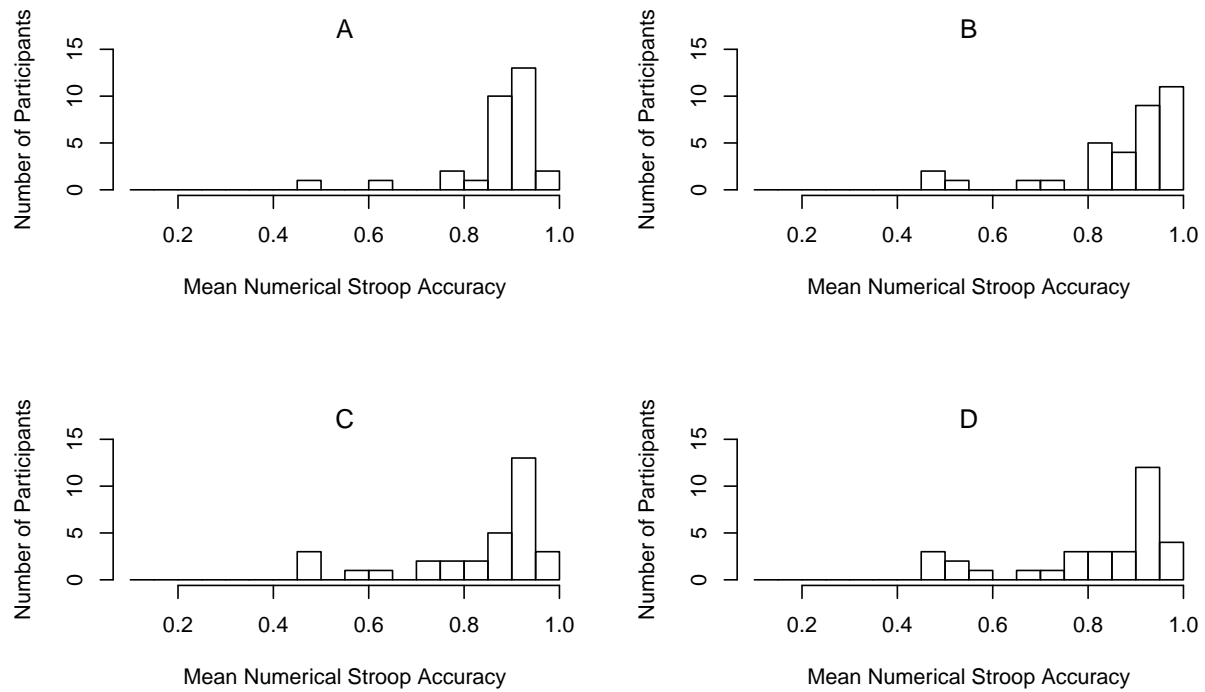


Figure 4. Histograms showing distribution of mean Numerical Stroop accuracy separately for each condition. **A:** Overlap-150. **B:** Overlap-250. **C:** Overlap-350. **D:** No-Overlap-300.

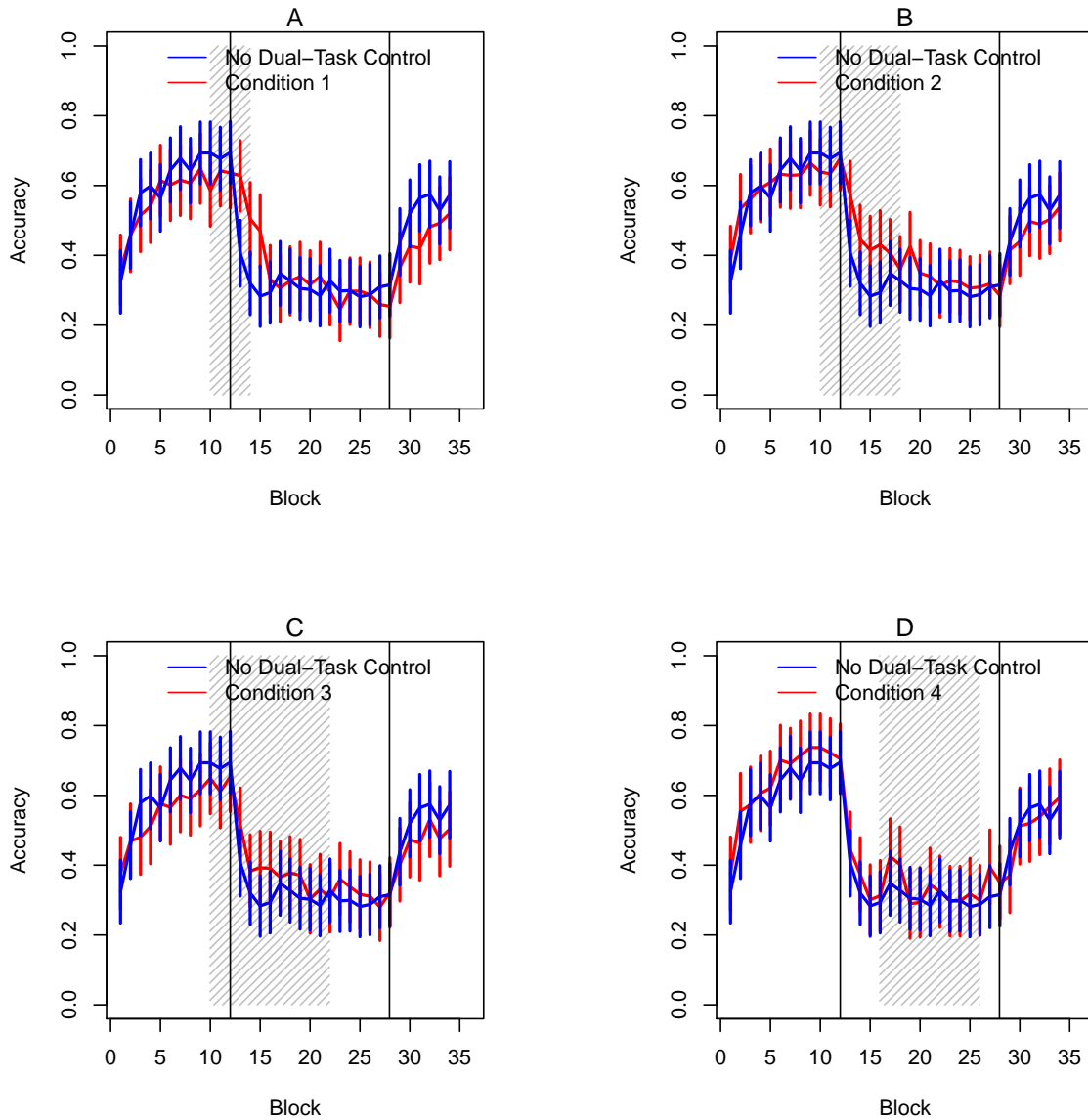


Figure 5. Mean accuracy per 25 trial block. The blue line in each panel is the no dual-task control condition. The hatch marks indicate dual-task trials. The key features are (1) dual-task slows the change in classification strategy (seen in this plot as “accuracy” decline), and (2) the dual-task conditions show less savings than the no dual-task control. There is no obvious dose-dependent effect of the dual task, nor is there an obvious difference between dual-task conditions. **A:** Overlap-150 (dual-task applied on trial 251 through trial 350). **B:** Overlap-250 (dual-task applied on trial 251 through trial 450). **C:** Overlap-350 (dual-task applied on trial 251 through trial 550). **D:** No-Overlap-300 (dual-task applied on trial 351 through trial 650). Error bars are SEM.

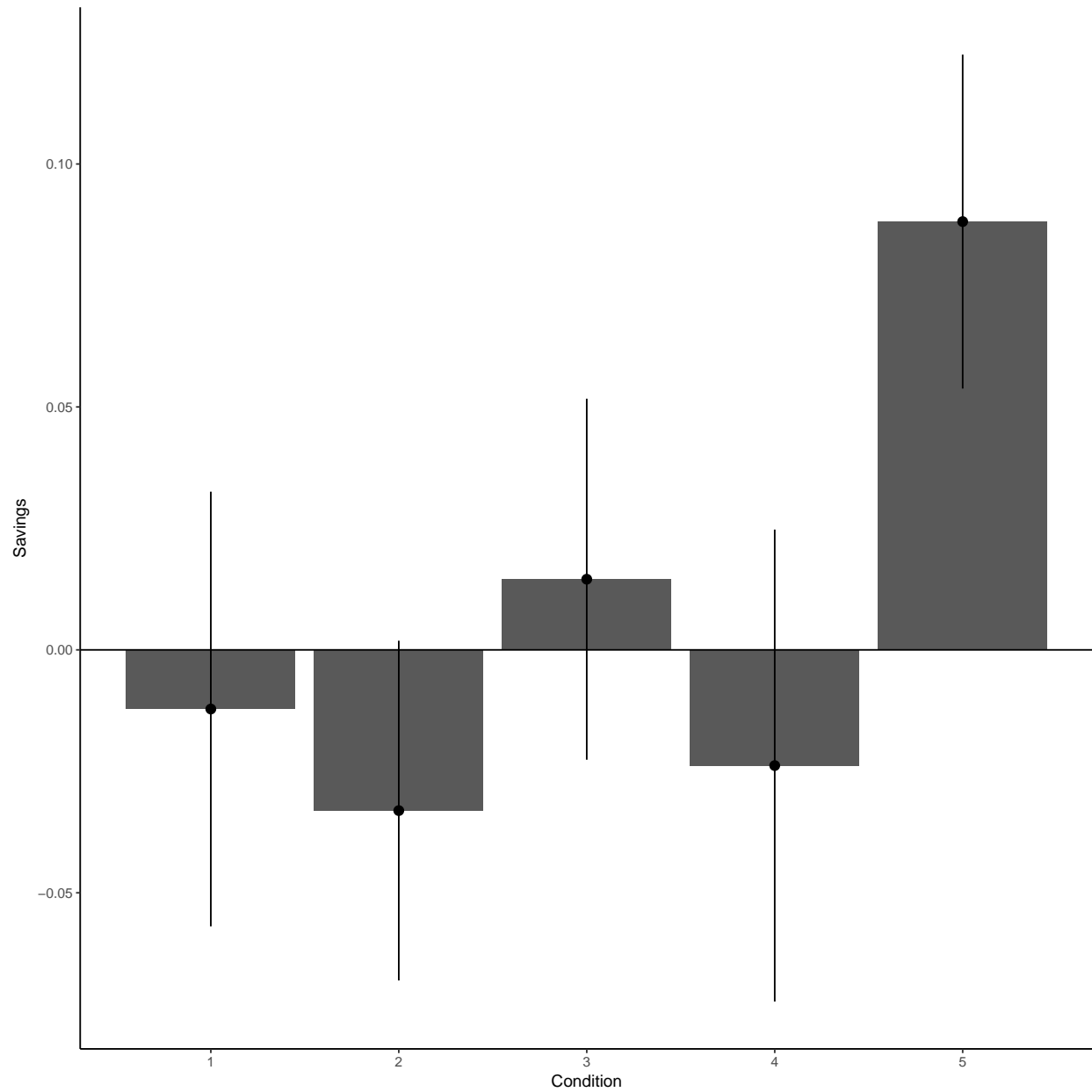


Figure 6. Savings (mean of the first 50 reacquisition trials - mean of the first 50 acquisition trials) in all conditions of the present experiment. Error bars are SEM.