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 relapse is common. This implies that current interventions do not erase or substantially modify the representations that support the underlying addictive behavior — that is, they do not cause true unlearning. One example of an intervention that fails to induce true unlearning comes from Crossley, Ashby, and Maddox (2013, *Journal of Experimental Psychology: General*), who reported that a sudden shift to random feedback did not cause unlearning of category knowledge obtained through procedural systems, and they also reported results suggesting that this failure is because random feedback is non-contingent on behavior. These results imply the existence of a mechanism that (1) estimates feedback contingency, and (2) protects procedural learning from modification when feedback contingency is low (i.e., during random feedback). This article reports the results of an experiment in which increasing cognitive load via an explicit dual-task during the random feedback period facilitated unlearning. This result is consistent with the hypothesis that the mechanism that protects procedural learning when feedback contingency is low depends on executive function.

Keywords: Feedback Contingency; category learning; Unlearning; Declarative Memory; Procedural Memory

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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 during intervention. 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 attempted to erase recently formed SR associations. 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, the mixed feedback conditions included RF(.25) feedback on a random 75% of trials and true feedback on 25% of the trials.

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, and (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 centremedian 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) Some neural network 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(.25) feedback 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 unlearning — 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 that support 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 perform a simultaneous dual task) should disrupt its estimation. This disruption should deprive the TANs of the clear signal they require to close the gate during RF. If the gate remains open during RF, then random SR associations should overwrite the recently acquired procedural knowledge, thereby allowing RF to cause true unlearning.

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

IRB Approval

All methods were approved by the University of Texas at Austin IRB, with study title "The Unlearning of Human Procedural Skills" and Human Subjects Assurance Number: 00002030.

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 251-400 in the Overlap-150 condition, 251-500 in the Overlap-250 condition, 251-600 in the Overlap-350 condition, and 350-650 in the No-Overlap-300 condition.

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 seperately 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 × 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 × 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 is the first article to 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 attention should interfere with the gate the normally protects procedural learning during random feedback. This should should consequently cause the random feedback to strengthen random SR associations, thereby inducing true unlearning of the original category structure. In our experiments, behavioral signatures of this unlearning include: (1) a slowed decrease in classification accuracy during intervention, and (2) slower relearning of the categories 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 – 150 trials of dual task were just as effective as 350 trials of dual task. On the other hand, intuition suggests that some dose effects must exist. Surely a single dual-task trial, or even a few dual-task trials would not have the same effect as 150 dual-task trials. If not, then all the doses explored in this article were past the saturation point at which all doses are equally effective. Testing this hypothesis will require further experimentation.

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 true unlearning requires the increase in cognitive load to precede the onset of the random feedback intervention. The idea 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 feedback contingency estimation (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 it 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.

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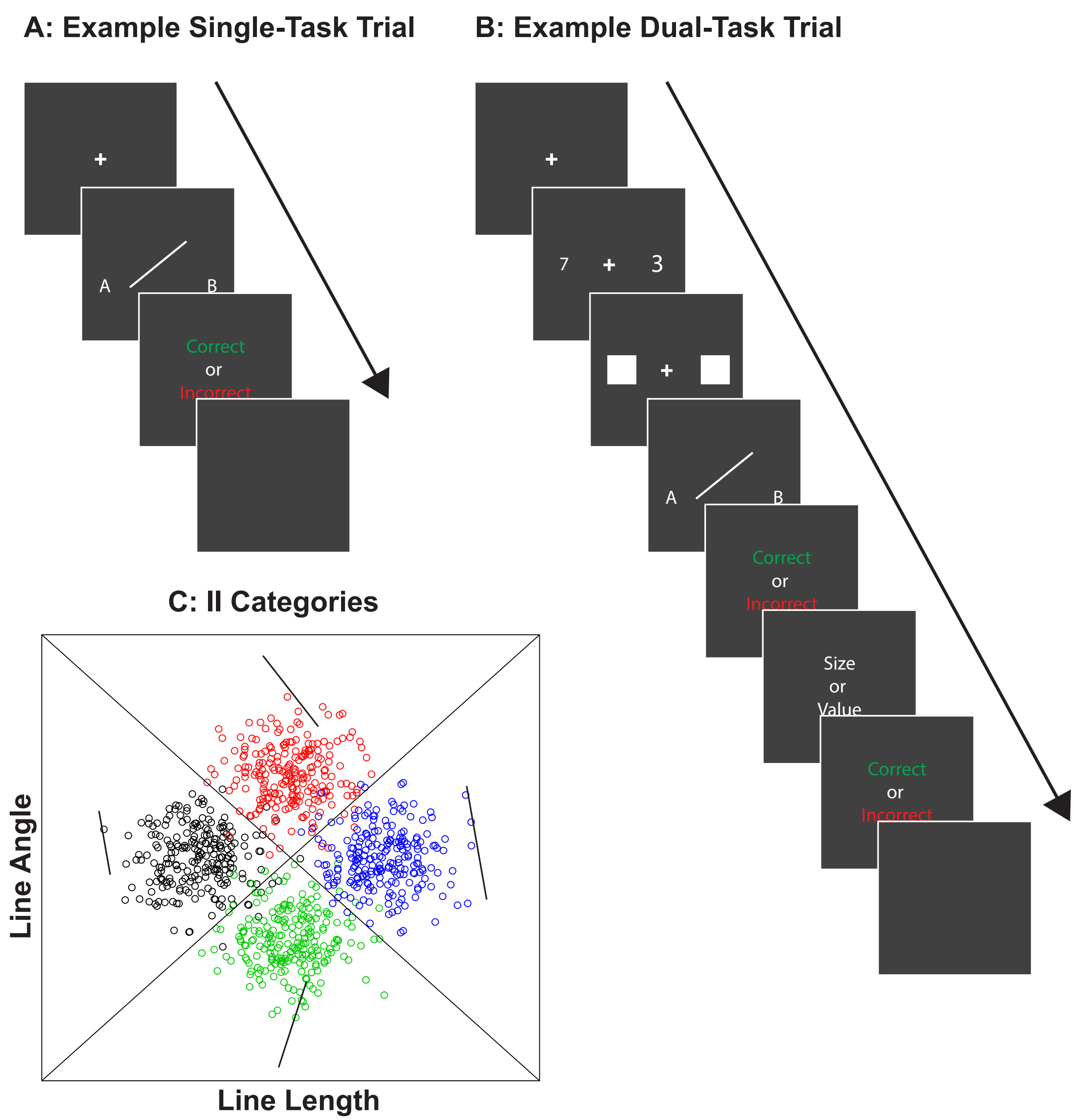

Figure 1. **A:** An Example trial during single-task conditions. **B:** An example trial during dual-task conditions. **C:** The categories used during the acquisition phase of Crossley et al. (2013).

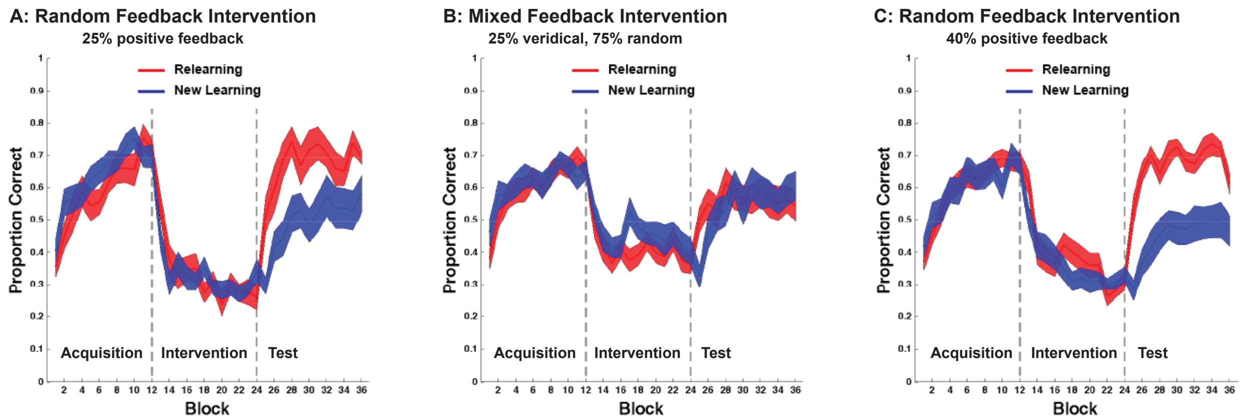

Figure 2. Crossley et al. (2013) behavioral results with different interventions. **A:** Random feedback intervention with 25% positive feedback. Accuracy drops to near chance during intervention, but is reacquired faster than original learning in the Relearning condition (red). In contrast, a lasting 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.

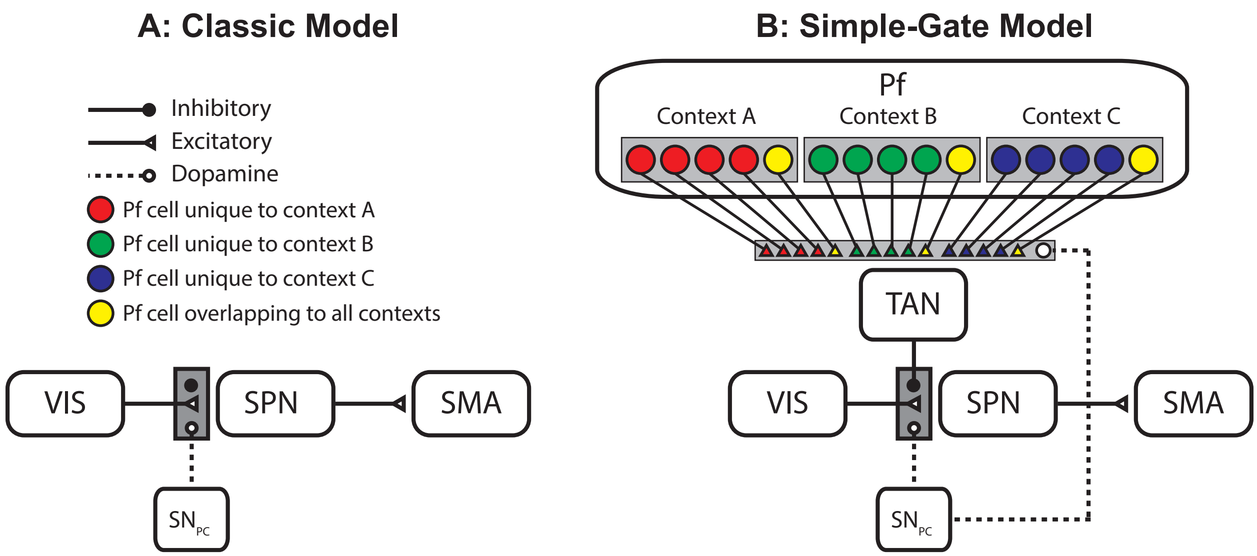

Figure 3. **A: The Classic Model.** A classic model of procedural learning based on a greatly simplified representation of the "direct pathway" through the basal ganglia. S-R associations are learned at cortical-striatal synapses, which are modified via dopamine-dependent reinforcement learning. The 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)

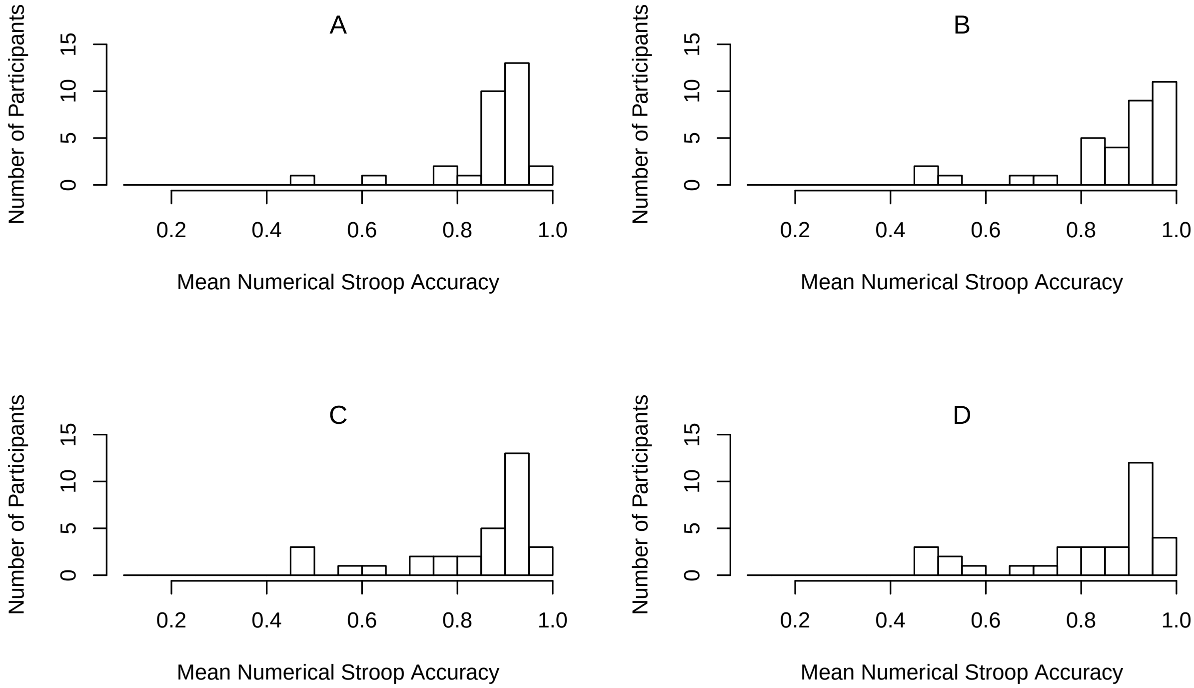

Figure 4. Histograms showing distribution of mean Numerical Stroop accuracy seperately for each condition. **A:** Overlap-150. **B:** Overlap-250. **C:** Overlap-350. **D:** No-Overlap-300.

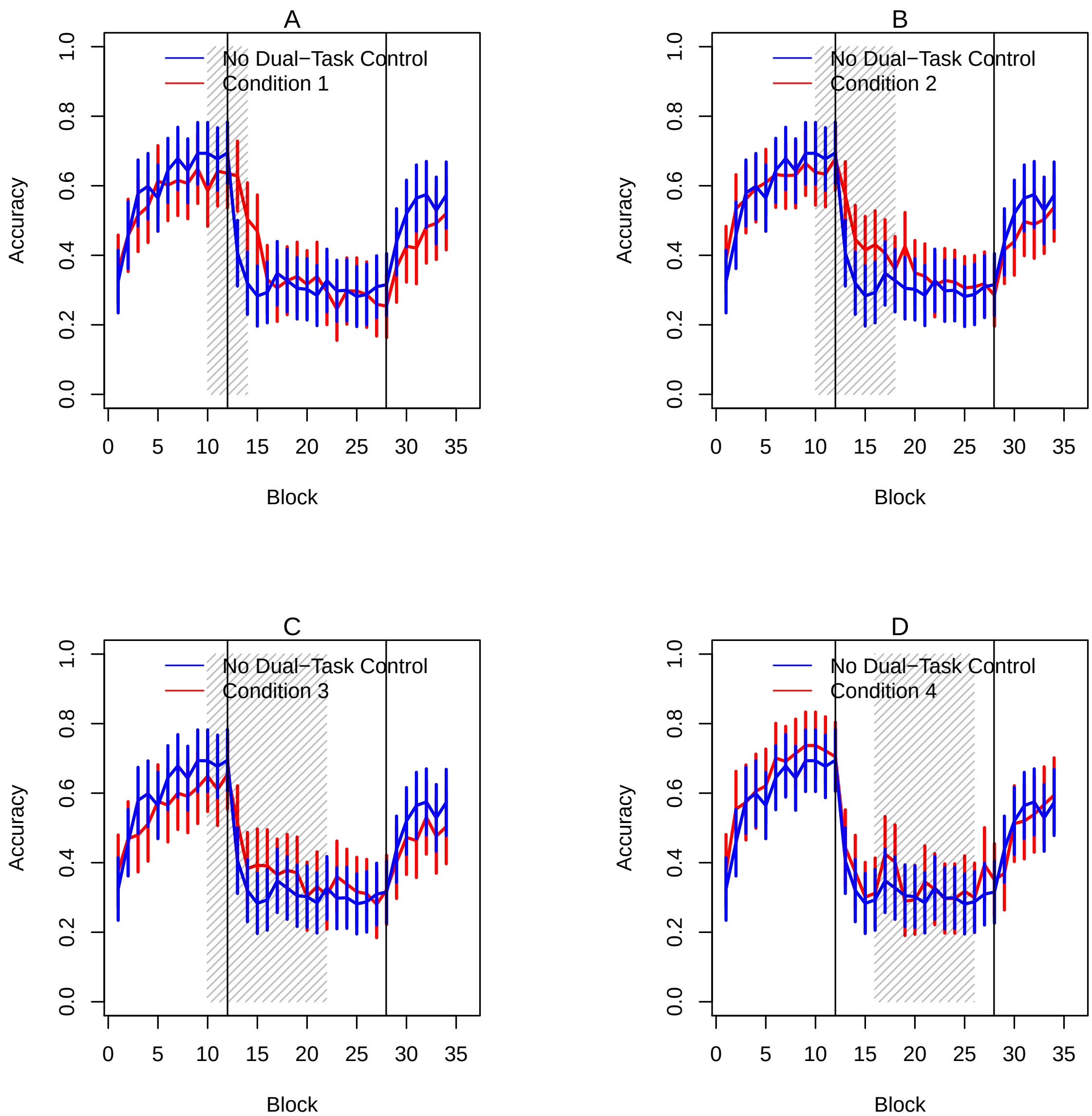

Figure 5. Mean accuracy per 25 trial block. The blue line in each panel is the no dual-task control condition. The hatch marks indicate dual-task trials. The key features are (1) dual-task slows the change in classification strategy (seen in this plot as "accuracy" decline), and (2) the dual-task conditions 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.

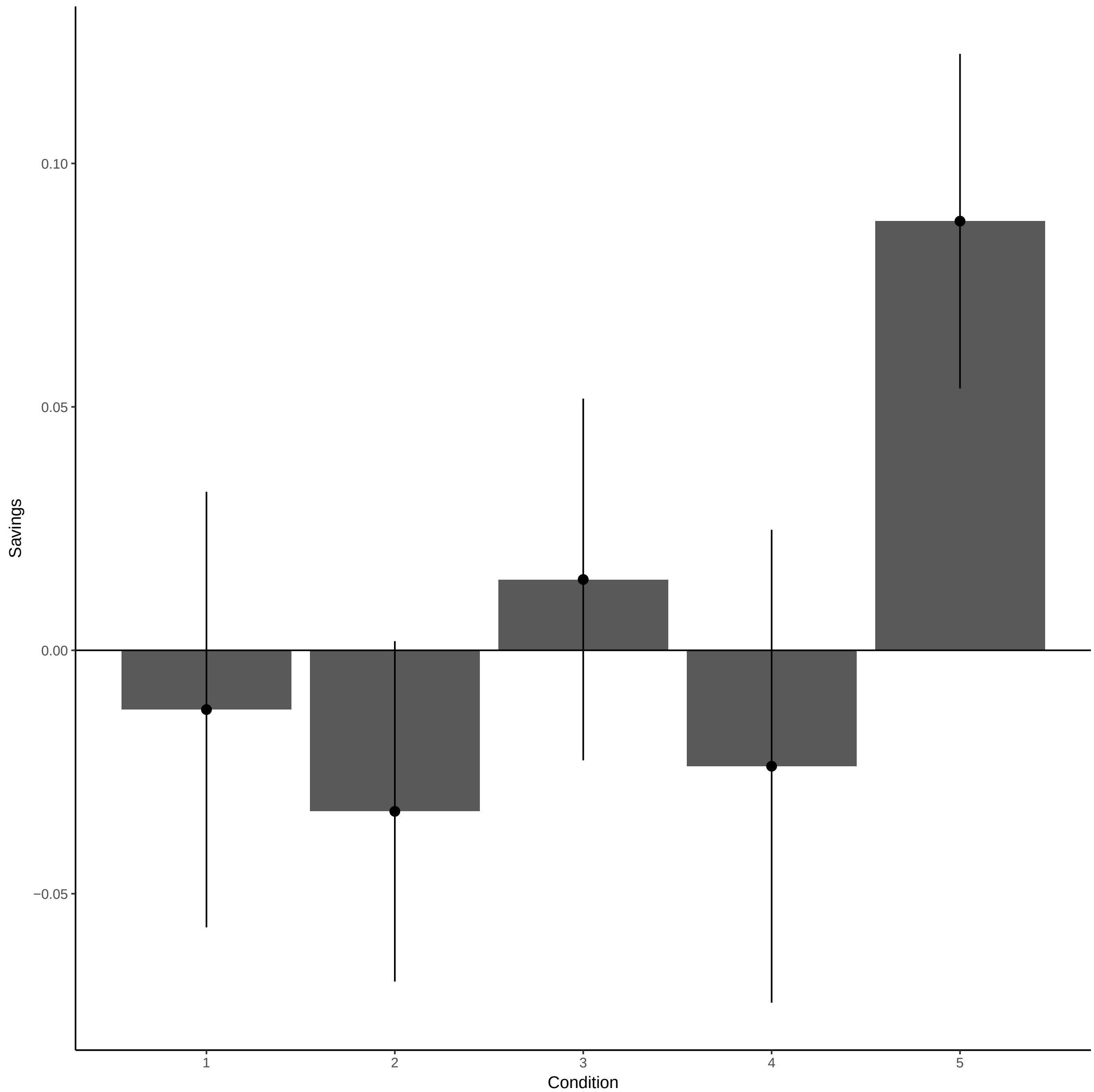

Figure 6. Savings (mean of the first 50 reacquisition trials - mean of the first 50 acquisition trials) in all conditions of the present experiment. Error bars are SEM.