

Context-dependent savings in procedural category learning



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ABSTRACT

Environmental context can have a profound influence on the efficacy of intervention protocols designed to eliminate undesirable behaviors. This is clearly seen in drug rehabilitation clinics where patients often relapse soon after leaving the context of the treatment facility. A similar pattern is commonly observed in controlled laboratory studies of context-dependent savings in instrumental conditioning, where simply placing an animal back into the original conditioning chamber can renew an extinguished instrumental response. Surprisingly, context-dependent savings in human procedural learning has not been carefully examined in the laboratory. Here, we provide the first known empirical demonstration of context-dependent savings in a perceptual categorization task known to recruit procedural learning. We also present a computational account of these savings using a biologically detailed model in which a key role is played by cholinergic interneurons in the striatum.

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1. Introduction

Environmental context plays an essential role in the efficacy of rehabilitation treatments for a variety of behavioral afflictions. For example, relapse of drug addiction is often triggered when the patient leaves the rehabilitation clinic and returns to the original context of their drug use (Higgins, Budney, & Bickel, 1995). Thus, a clear understanding and ability to manipulate the mechanisms underlying context dependence in relapse is of paramount importance to the development of efficacious intervention protocols.

The propensity for relapse is often estimated experimentally by measuring savings in relearning following an intervention protocol that causes some trained behavior to disappear (e.g., a lever press in simple instrumental conditioning paradigms; Bouton, Winterbauer, & Todd, 2012; Marchant, Li, & Shaham, 2013). Savings of the original learning is often inferred by observing that relearning occurs more quickly than original learning (e.g., rapid reacquisition), or that return to the training environmental context can temporarily renew responding (e.g., renewal).

Ashby and Crossley (2011) proposed the first neurobiologically constrained model of savings in instrumental conditioning, and Crossley, Ashby and Maddox (2013) extended this model into the domain of human procedural learning. These models assumed that

learning is instantiated via plasticity at cortical–striatal synapses and that this plasticity is gated by striatal cholinergic interneurons (called TANs for tonically active neurons). As their name implies, the TANs tonically fire in their default state, inhibiting striatal projection neurons (called MSNs for medium spiny neurons), and thereby preventing synaptic plasticity at cortico–striatal synapses. However, the TANs exhibit a pause in firing that is temporally aligned with the midbrain dopamine response (Morris, Arkadir, Nevet, Vaadia, & Bergman, 2004), temporarily releasing MSNs from inhibition and facilitating cortical–striatal plasticity, when they receive strong input from the centromedian and parafascicular (CM–Pf) nuclei of the thalamus. Thus, the efficacy of the CM–Pf–TAN synapse controls whether or not the TANs pause, and whether learning at cortical–striatal synapses is possible.

These models successfully accounted for a broad array of savings-based phenomena, while simultaneously respecting a range of neurobiological constraints. Applied to savings-based paradigms, the models predict that extinction does not entail complete unlearning of the original behavior (presumably implemented at cortical–striatal synapses) because the TANs learn to quit pausing during the extinction treatment, which protects cortical–striatal synapses from alteration. They are also grounded in known basal ganglia anatomy, and they correctly account for single-cell recordings from striatal projection neurons as well as striatal interneurons (TANs) under a range of experimental conditions.

Neither of these previous models, however, was explicitly equipped to account for context-dependent savings. Nevertheless,

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there is preliminary evidence that the gating mechanism in the striatum (i.e., the TANs) could be sensitive to environmental context. Specifically, the input to the TANs (i.e., from the centromedian and parafascicular nuclei of the thalamus) are known to display context-specific firing (i.e., they fire only when specific features of the environment are present; [Matsumoto, Minamimoto, Graybiel, & Kimura, 2001](#)). When endowed with this feature, the [Crossley, Ashby, and Maddox \(2013\)](#) model predicts context-dependent savings in human procedural learning. Surprisingly, to our knowledge, this prediction has never been previously tested. This article therefore makes two main contributions: we provide the first known empirical demonstration of context-dependent savings in human procedural learning, and we extend the [Crossley et al. \(2013\)](#) model to account for our behavioral results.

2. Materials and methods

We examined savings in relearning in an information–integration (II) category-learning task. In II categorization tasks, stimuli are assigned to categories in such a way that accuracy is maximized only if information from two or more non-commensurable stimulus dimensions is integrated at some pre-decisional stage ([Ashby & Gott, 1988](#)). Typically, the optimal strategy in II tasks is difficult or impossible to describe verbally (which makes it difficult to discover via logical reasoning). An example of an II task is shown in [Fig. 1](#). In this case the four categories are each composed of single black lines that vary in length and orientation. The diagonal lines denote the category boundaries. Note that no simple verbal rule correctly separates the lines into the four categories. Nevertheless, many studies have shown that with enough practice, people reliably learn such categories, and the evidence is good that II category learning uses procedural memory and requires dopamine-dependent reinforcement learning in the striatum (e.g., [Ashby & Maddox, 2005](#)).

The II task used here included acquisition, intervention, and reacquisition phases of 300 trials each. These three phases were all identical except in the nature of the feedback provided after each response. During acquisition and reacquisition, feedback indicated whether each response was correct or incorrect. During the intervention phase, the feedback was random – that is, participants were informed that their response was correct with probability 1/4 and incorrect with probability 3/4, regardless of what response they actually made. The same protocol was used in Experiment 1 of [Crossley et al. \(2013\)](#).

The present experiment diverges from [Crossley et al. \(2013\)](#) in that the acquisition, intervention, and reacquisition phases could occur in different environmental contexts, where the context was defined by the background color displayed on the computer screen during presentation of the categorization stimulus. We examined

savings in four different experimental conditions – AAA, ABA, AAB, and ABC. The three letters in each condition name indicate the context used during acquisition, intervention, and reacquisition, respectively. Context A always occurred with a green background, context B with a blue background, and context C with a red background.

Every stimulus in all three phases of Experiment 1 was a black line (as in [Fig. 1](#)) that varied across trials in length and orientation. Identical II category structures were used in all three phases. These are represented abstractly in [Fig. 1](#). Also note that the categories overlap slightly such that the best possible accuracy with these categories is 95%.

The transition from the acquisition to the intervention phase occurred without the participant's knowledge or any additional cue in the AAA and AAB conditions, but in the ABA and ABC conditions the transition coincided with a change in the background color. No participants in any condition were told that this transition indicated that feedback would be random. Similarly, the transition from the intervention phase to the reacquisition phase occurred without the participant's knowledge in the AAA condition, but coincided with a background color change in the AAB, ABA, and ABC conditions.

2.1. Participants

There were 26 participants in the AAA condition, 18 participants in the ABA condition, 25 participants in the AAB condition, and 23 participants in the ABC condition. All participants completed the study and received course credit for their participation. All participants had normal or corrected to normal vision. To ensure that only participants who performed well above chance were included in the post-acquisition phase, a learning criterion of 40% correct (25% is chance) during the final acquisition block of 100 trials was applied. Using this criterion, no participant in any condition was excluded.

2.2. Stimuli and procedure

All stimuli and procedures were identical to those used in [Crossley et al. \(2013\)](#), with the exception of the different background colors in the different experimental phases. Example stimuli, as well as the complete category distributions are shown in [Fig. 1](#) and specified in [Table 1](#). Example trials for each context are shown in [Fig. 2](#).

2.3. Theoretical modeling

We previously proposed a neurobiologically detailed computational model that describes a mechanism in the striatum that

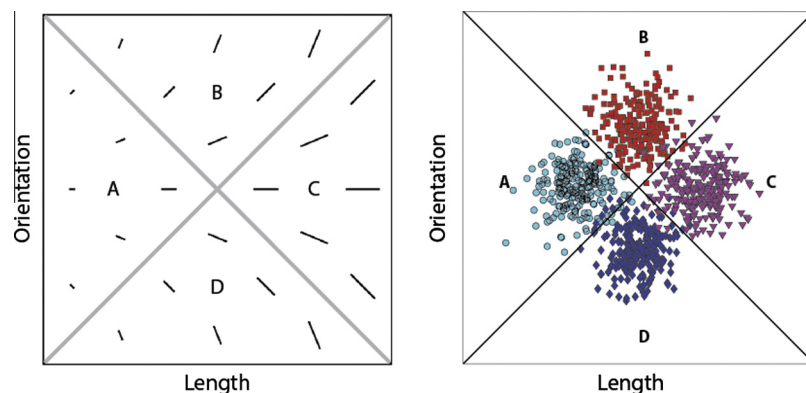


Fig. 1. (Left) A few examples of stimuli that might be used in an information–integration (II) category-learning experiment. (Right) The category distributions used here.

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