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Research Report

Selective role for striatal and prefrontal regions in processing first trial feedback during single-trial associative learning

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ABSTRACT

Discrete jumps in knowledge, as exemplified by single-trial learning, are critical to survival. Despite its importance, however, one-trial learning remains understudied. We sought to better understand the brain activity adaptations that track punctuated changes in associative knowledge by studying visual–motor associative learning with functional magnetic resonance imaging. Human and primate neurophysiological studies of feedback-based learning indicate that performance feedback elicits high activity at first that diminishes rapidly with repeated success. Based on these findings we hypothesized a network of brain regions would track the importance of feedback, which is large early in learning and diminishes thereafter. Specifically, based on neurophysiological findings, we predicted that frontal and striatal regions would show a large activation to first trial feedback and a subsequent reduction selective to performance feedback but not stimulus cue presentation. We observed that the striatum and frontal cortex as well as several other cortical and subcortical sites exhibited this pattern. These findings match our prediction for activity in frontal and striatal regions. Furthermore, these observations support the more general hypothesis that a large network of regions participates in the associative process once the behavioral goal is definitively identified by first trial performance feedback. Activity in this network declines upon further rehearsal but only for feedback presentation. We suggest that, based on the timing of this process, these regions participate in binding together stimulus cue, motor response, and performance feedback information into an association that is used to accurately perform the task on after the first trial.

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1. Introduction

Associative learning plays a key role in survival by providing a mechanism for behavioral adaptation. This reinforcement learning mechanism allows organisms to learn through experience how to respond to environmental contexts that promote or threaten survival. When an organism's response is highly consequential to survival learning may occur in one trial. Despite its importance, however, the neural correlates of one-trial learning remain understudied.

Identifying single-trial learning effects on the brain depends upon the precise experimental control of learning. Of the two basic approaches to the study of instrumental associative learning, deterministic and probabilistic, deterministic paradigms are better suited to identify single-trial learning effects. Deterministic paradigms use fixed feedback rules such that positive feedback is always given for the correct response and negative feedback is always given for the incorrect response. Probabilistic paradigms use stochastic feedback rules that can randomly vary from trial to trial according to a predetermined proportion but that on average indicate that one response is better than another. Although probabilistic paradigms contribute to our understanding of striatal, prefrontal and medial temporal lobe involvement in associative learning (Aron et al., 2004; Cools et al., 2002; Poldrack et al., 2001), probabilistic approaches cannot address one-trial learning because associative knowledge accumulates gradually over many trials. Complex deterministic category learning paradigms also yield gradual learning effects (Boettiger and D'Esposito, 2005), but simple deterministic tasks are well suited to examine discrete changes in brain activation. This is because associations can be conclusively learned in a few trials and remain fixed thereafter. In spite of this, most deterministic paradigms, our own included, provide less than the ideal control of the learning process that is needed to examine one-trial learning (Bedard and Sanes, 2009; Brovelli et al., 2008; Eliassen et al., 2003). In particular, successful learning can be defined by the occurrence of the first correct response to a stimulus cue. This first correct trial, when followed by only correct responses, indicates a definitive knowledge of the cue–response–outcome association. Deterministic paradigms often use multiple response alternatives or rules, however, which allows learning to occur on error trials preceding the first correct response through a process of elimination. These preliminary errors provide information to guide future behavior by identifying the remaining possible response alternatives. Often, the correct response can be learned before being selected, as in the Wisconsin Card-Sorting Test and similar paradigms (Barcelo et al., 2000, 2002; Monchi et al., 2001; Zanolie et al., 2008). This allows definitive associative knowledge to be obtained before the first correct trial. In that case, analyses that aggregate across preliminary errors or that examine only the first correct response provide an incomplete description of the changes associated with single-trial learning.

Instrumental associations can only be learned on the basis of feedback. As associations become learned by trial and error, feedback begins to convey less critical information about how to conduct future behavior. Feedback becomes completely predictable, especially if the associations are uncomplicated and deterministic. Electrophysiological correlates of this change in feedback predictability have been observed in both primate and human studies. These changes provide the basis for our hypothesis that brain activation in single-trial learning will track the importance, or utility, of feedback to future task performance. In human event-related potential (ERP) EEG studies, researchers have identified activity changes associated with unexpected feedback following a rule switch. Specifically, Barcelo et al. (2002) observed an increase in the frontally located P300A waveform in response to feedback presentation after a rule-switch compared to before. This activity diminishes quickly with repeated successes following a switch. Primate single-unit studies of the reward system show that activity in dopaminergic ventral tegmental area neurons also tracks changes in feedback utility. The so-called reward response of this system initially reacts to the presentation of unpredicted positive performance feedback. As the positive feedback becomes predictable with learning this reaction diminishes (Schultz et al., 1995, 1997). The frontal targets of the reward system also exhibit activity correlated with feedback utility in a probabilistic paradigm (Aron et al., 2004). However, deterministic human learning studies to date provide only indirect evidence of a single-trial feedback-specific change in striatal activity with learning. Brovelli et al. (2008) show that the striatum is more active early in learning. The relationship of this activity to trial-by-trial changes in knowledge remains unclear, though, because they use a paradigm in which learning is defined across several trials through a modeling procedure that defines a prediction error signal. Using a trial-based analysis strategy, Bedard and Sanes (2009) observe that Parkinson's Disease patients differ from controls more early in learning than later, indirectly suggesting a more prominent striatal role early in learning in healthy individuals. Altogether, this research suggests that performance feedback activation should decrease following single-trial learning in the striatum and prefrontal cortex. Such activity changes would correlate with the declining utility of feedback to guiding future performance.

In the current study we investigated this question using a one-trial visual–motor associative learning paradigm. The paradigm required participants to learn associations between pictures and responses. The task used easily nameable color pictures and a two-alternative choice response. Trials were classified by the pattern of performance, and the analysis included only associations where no errors occurred after the first trial. We predicted that stimulus cue representations and performance feedback representations would be differentially altered by associative learning on the first trial. Specifically, in the transition from learning on the first trial to rehearsal on the second trial there would be reductions in feedback activation in frontal and striatal regions but not similar changes in stimulus activation.

2. Results

2.1. *Behavior*

The analysis of reaction times indicated the presence of learning related reductions. There was a significant effect of experience ($F(5,95)=11.46$, $P<0.001$), whereby reaction time