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Research Report

Corticolimbic mechanisms in the control of trial and error learning

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ABSTRACT

As learning progresses, human and animal studies suggest that a frontal executive system is strongly involved early in learning, whereas a posterior monitoring and control system comes online as learning progresses. In a previous study, we employed dense array EEG methodology to delineate the involvement of these two systems as human participants learn, through trial and error, to associate manual responses with arbitrary digit codes. The results were generally consistent with the dual-system learning model, pointing to the importance of both systems as learning progressed. In the present study, we replicate and extend the previous findings by examining the brain responses to error trials as well as examine the activity of these two systems' response to feedback processing. The results confirmed the role of these two systems in learning but they also provide a more complex view of their makeup and function. The frontal system includes ventral (inferior frontal gyrus, ventral anterior cingulate cortex, anterior temporal lobe) corticolimbic structures that are involved early in learning whereas the posterior system includes dorsal (anterior and posterior cingulate and medial temporal lobe) corticolimbic circuits that are engaged later in learning. Importantly, the engagement of each system during the course of learning is dependent on the nature of the events within the learning task.

1. Introduction

Regulating behavior requires learning appropriate actions in the context of environmental events. The outcome of successful learning reflects the integrated function of self-regulatory processes (such as regulation of motives, action monitoring, memory encoding and retrieval etc.) that are controlled by specific corticolimbic networks. Electrophysiological and imaging studies have converged to identify differential engagement of these networks during different stages of learning. For example, the prefrontal lobes (including the inferior frontal gyrus, dorsolateral prefrontal cortex, and medial prefrontal cortex), and anterior cingulate cortex (ACC) have been observed to be strongly engaged early in the learning cycle when stimulus-response mappings are actively being established (Chein and Schneider, 2005; Luu et al., 2007; Toni et al.,

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1998). In later stages of learning, however, once contingency mappings have become consolidated, these frontal structures exhibit a reduction in activity. In contrast, posterior regions, including the posterior cingulate cortex (PCC), precuneus, cuneus, superior parietal lobule, and intraparietal sulcus demonstrate increased activity during these later stages (Chein and Schneider, 2005; Luu et al., 2007; Toni and Passingham, 1999). The reduction of activity observed in frontal structures in later stages of learning appear to represent reduced reliance on top-down control systems once learning has been established, while the increased activity observed in posterior structures may represent the establishment and automatization of the learned action patterns as well as continued monitoring of performance (Chein and Schneider, 2005; Toni and Passingham, 1999).

These findings, based on human studies, are consistent with animal research identifying two separable circuits underlying discriminative learning: one that supports the rapid acquisition of new skills through regulation of 'executive' control systems, and a second system that supports the habitual automatization of learned behavior (Gabriel et al., 2002). These two systems allow learning to be graded: moving from intensive monitoring and control early in the learning cycle, when stimulus–response contingencies remain undeveloped, to reduced reliance on these resource-demanding processes and automated performance once these contingencies have been sufficiently mapped (see Gabriel et al., 2002 for additional discussion). Bringing the animal learning model to human learning studies, we hypothesized that initial learning requires greater executive control from frontolimbic networks, whereas in later stages of learning, when performance becomes more automated, processing in posterior corticolimbic networks dominates both performance and the continued adjustments of learning (Luu et al., 2007).

In that research, we examined the activity of cortical and limbic systems during visuomotor learning in humans using dense-array EEG methodology. The task employed is amenable to automated performance once learning has been achieved because the stimulus–response mappings are constant (see Chein and Schneider, 2005). We found that posterior cortical regions (including parietal, PCC, and parahippocampal cortices, as indexed by the P3) became progressively engaged as participants discovered and learned stimulus–response mappings (Luu et al., 2007). However, the pattern of neural activity in learning was more complex for frontal components. We identified a frontal component of the averaged event-related potential (ERP) that was localized to ventral corticolimbic networks (anterior temporal pole and inferior frontal cortex). Furthermore, this component was lateralized according to the stimulus (to the left frontal lobe for digit codes and to the right frontal lobe for spatial locations). The analysis showed that, although it could be confused with the inferior dipole inversion of the P3 or "Late Positive Complex", this component showed not only a unique source but a unique time course as well.

We described this component as the Lateralized Inferior Anterior Negativity (LIAN). Although the LIAN was differentially lateralized for verbal and spatial stimuli, it showed a gradual deactivation during learning only for spatial location–response mappings. Under the hypothesis that early control of learning engages greater control from frontal executive networks, we would predict that the decrease in the LIAN after learning would be observed for both the digit code and spatial pattern learning conditions. On the other hand, a right-lateralized frontal decrease with learning is consistent with a meta-analytic study, based on fMRI findings that revealed right-lateralized biases for learning-related deactivations of the lateral ventral prefrontal cortex (Chein and Schneider, 2005).

In contrast, the LIAN for digit–response mappings showed a slight, although not significant, increase as learning progressed. A possible explanation for the sustained LIAN after learning is that participants may not have achieved automated levels of performance. A second explanation, though not exclusive of the first, involves the observation by Chein and Schneider (2005) that the left ventral prefrontal cortex remains strongly engaged during practice performance of word pair association tasks, which suggested to them that this region may be involved in representational functions that are not immediately associated with cognitive control.

In the Luu et al. (2007) study, we also examined a component reflecting activity in dorsal frontolimbic networks, described as the medial frontal negativity (MFN), localized to the medial prefrontal cortex, including the ACC. The MFN has been shown to be important to aspects of the executive monitoring of the learning process (Gehring and Willoughby, 2002). The hypothesis that frontal control decreases as learning progressed was not supported by the measures of the MFN in the Luu et al. study; the MFN actually increased as subjects gained knowledge of the correct stimulus–response mapping, and as they demonstrated consistent performance guided by this knowledge.

In the present study, we replicated and extended the findings by Luu et al. (2007) in a separate sample of subjects. The replication involved analysis of target-locked brain responses on correct trials. The extension involves analysis of target-locked brain responses to error trials and feedback-locked brain responses. The analysis of target-locked brain responses on error trials permits further examination of the nature of the MFN increase we previously observed. The analysis of feedback-locked responses will permit determination of how corticolimbic structures involved in learning are affected by informational content, providing us with a more complete picture of how their activity is moderated during different learning stages.

Based on our previous explanation that the MFN increase may reflect development of action context representations (thus leading to opportunities for response conflicts), we predict that target-locked MFN amplitudes would be particularly large for error trials that occur after learning. We hypothesize that activity of the frontal circuit (i.e., fast learning system) would be reduced in response to feedback as learning progressed because the accuracy of actions are internally represented once learning is established (see Holroyd and Coles, 2002). Specifically, we predict the feedback-related negativity (FRN; Luu et al., 2003), which indexes frontolimbic evaluative mechanisms, would decrease in amplitude with learning. Similarly, we predict that the LIAN would appear in evaluation of the feedback to integrate the