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Research Report

Neural mechanisms for learning actions in context

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ABSTRACT

The transition from actions that require effortful attention to those that are exercised automatically reflects the progression of learning. Full automaticity marks the performance of the expert. Research on changes in brain activity from novice to skilled performance has been consistent with this behavioral characterization, showing that a highly practiced skill often requires less brain activation than before practice. Moreover, the decrease in brain activity with practice is most pronounced in the general or executive control processes mediated by frontal lobe networks. Consistent with these human cognitive neuroscience findings, animal neurophysiological evidence suggests that two elementary learning systems support different stages of skill acquisition. One system supports rapid and focused acquisition of new skills in relation to threats and violations of expectancies. The other involves a gradual process of updating a configural model of the environmental context. We collected dense array electroencephalography as participants performed an arbitrary associative ("code learning") task. We predicted that frontal lobe activity would decrease, whereas posterior cortical activity would increase, as the person gains the knowledge required for appropriate action. Both predictions were confirmed. In addition, we found that learning resulted in an unexpected *increase* in activity in the medial frontal lobe (the medial frontal negativity or MFN). Although preliminary, these findings suggest that the specific mechanisms of learning in animal neurophysiology studies may prove informative for understanding the neural basis of human learning and executive cognitive control.

1. Introduction

When experts become skilled in a given task domain, they perform routine tasks automatically, thereby freeing up cognitive resources for more executive tasks, such as organizing situational awareness (Fitts, 1964). Psychological studies of expert cognition have emphasized the importance of *controlled processes*, which are limited by the capacity of working memory, require active attention, and can be directed consciously in new task situations (Schneider and Shiffrin, 1977; Shiffrin and Schneider, 1977). These are contrasted with *automatic processes*, which result from learning and are not strongly limited by the capacity of working memory, and which, when engaged in the appropriate context, may be carried out unconsciously with minimal distraction of conscious attention (Chein and Schneider, 2005).

NeuroImaging studies have suggested there may be direct neural correlates of the reduced demands for controlled processes, as evidenced by decreased demands on brain activity resulting from increasing practice with task performance. Given that frontal lobe activity is thought to be particularly important to goal representations and providing control-

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related outputs (Miller and Cohen, 2001), it is theoretically important that both meta-analysis of fMRI studies and new experiments have suggested a specific decrease in frontal lobe activity (bilateral dorsal frontal, left ventral prefrontal, anterior cingulate cortex, left insular regions) as participants become more practiced in task performance (Chein and Schneider, 2005).

In attempting to link the more elementary neurophysiology of action regulation to the development of expert control of human cognition, we looked to the literature on neurophysiological models of animal learning. In research on discriminant learning in mammals, two cortico-limbic-thalamic circuits have been identified, each providing a unique strategic control on the learning process (Gabriel et al., 2002). The first system is responsible for rapid discriminant learning (both avoidance and conditional). This system includes the anterior cingulate cortex (ACC), amygdala, and mediodorsal nucleus of the thalamus. The unique properties of the fast learning system, e.g., its contribution to overcoming habitual responses, led Gabriel and colleagues (2002) to suggest this circuit is integral to what has been called the executive control of cognition (Posner and DiGirolamo, 1998). Bussey and colleagues (2001) have shown that the ventral and orbital prefrontal cortices should also be included as part of this fast learning system.

A second circuit, centered on the posterior cingulate cortex (PCC) and anterior thalamic nucleus, is involved in the late stages of learning (Bussey et al., 1996; Keng and Gabriel, 1998). In these late stages, a contextual model is formed, and minor changes that are consistent with the contextual model can be made with minimal attentional demands. This late stage learning process can be described as forming the basis of habits (Bussey et al., 1996).

If this neurophysiological model is correct, learning is achieved by circuits with qualitative strategic biases, toward either (1) gradual updating of a valued context model or (2) rapid, focused changes of associations under conditions of threat or context violation (Tucker and Luu, 2006). In extending this model to expertise in human learning, the rapid, focused learning system would be required as participants learn new arbitrary associations, such as in visuomotor mapping of an arbitrary visual stimulus to a particular response (Bussey et al., 2001; Wise and Murray, 2000). Researchers studying arbitrary visuomotor mapping (also referred to as conditional visuomotor mapping) regard the underlying processes as indicative of the remarkable capability of mammals to associate any arbitrary stimulus with a motor response, and thus to behave appropriately in any given context.

Functional neuroimaging studies of hemodynamic responses during arbitrary visuomotor association learning have identified the involvement of the anterior cingulate sulcus, parahippocampal gyrus, caudate nucleus (i.e., dorsal striatum), inferior frontal gyrus, middle temporal gyrus, dorsal premotor cortex, and parietal cortex (Toni and Passingham, 1999; Toni et al., 2001; Wise and Murray, 2000). These regions appear to overlap substantially with the neural networks implicated in controlled cognitive processes by Chein and Schneider (2005), and certain of these structures are closely related to the fast learning cortico-thalamic-limbic circuit implicated by Gabriel and colleagues in the early stages of discriminant learning.

Although we have emphasized the importance of the ACC in action monitoring (Luu and Tucker, 2003), many of the human findings of error-related negativities (response-locked ERNs) or medial frontal negativities (stimulus-locked MFN or N2) have shown strong responses in medial frontal cortex when the subject's expectancies are violated. These results may be consistent with more elementary learning processes; discrepancy or conflict detection is a requirement for behavioral adjustments. Indeed, it is through the detection of discrepancies between what is expected, given a particular action, and what actually happened that new learning occurs (Rescorla and Wagner, 1972). According to an influential theory of medial frontal control of cognitive conflict, the ERN reflects the activity of a learning system that relies on prediction errors (Holroyd and Coles, 2002).

In the present study, we presented participants with an arbitrary associative ("code learning") task, in which they needed to discover an arbitrary mapping of stimuli (digits or spatial location) with key presses of the correct hand and finger, or with no response. We hypothesized, broadly, that the learning process would engage frontal lobe activity implicated in controlled cognitive processes. More specifically, in line with the neurophysiologic model of action regulation, we hypothesized that the demands on rapid learning early in the task would engage activity of the anterior ventral network. In contrast, we hypothesized that as participants learned this task, the consolidation of a cognitive context for performance would be indexed by an increasingly robust P300 or Late Positive Complex (LPC), generated in medial temporal, posterior cingulate, and parietal cortices, thus reflecting the more automatic process typical of expert performance. For both the frontal, ventral contribution to early learning, and the posterior, dorsal contribution to late learning, we hypothesized that the digit code task would result in greater activity in left hemisphere networks and the spatial code task would result in greater activity in right hemisphere networks.

2. Results

2.1. Behavioral data

The following factors were considered in repeated measures ANOVA models: task (digit, spatial), accuracy (error, correct), target (go, nogo), and learning (pre, post). Although learning is a likely to be a dynamic and continuous phenomenon, for analytic purposes, it is convenient to determine a cutoff that marks when participants have fully acquired the target–response mapping. There are several methods for determining when learning has occurred (Smith et al., 2004). We use the simplest method, the fixed-number of consecutive correct responses method[1] (FCCR). In this method, a learning

[1] For several subjects, we compared the fixed-number of consecutive correct responses method against a dynamic state–space method for determination of a learning thershold (Smith et al., 2004). On average, the state–space method identified the occurrence of learning to be two trials earlier, consistent with what Smith et al. (2004) reported. Because analyses of the behavioral and ERP data are based on subject averages, it is unlikely that the reported results were affected by this small difference.