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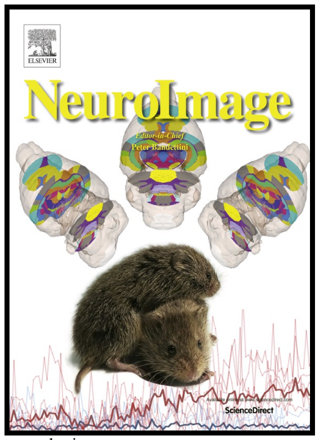

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Hierarchical control of procedural and declarative category-learning systems

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Abstract

Substantial evidence suggests that human category learning is governed by the interaction of multiple qualitatively distinct neural systems. In this view, procedural memory is used to learn stimulus-response associations, and declarative memory is used to apply explicit rules and test hypotheses about category membership. However, much less is known about the interaction between these systems: how is control passed between systems as they interact to influence motor resources? Here, we used fMRI to elucidate the neural correlates of switching between procedural and declarative categorization systems. We identified a key region of the cerebellum (left Crus I) whose activity was bidirectionally modulated depending on switch direction. We also identified regions of the default mode network (DMN) that were selectively connected to left Crus I during switching. We propose that the cerebellum—in coordination with the DMN—serves a critical role in passing control between procedural and declarative memory systems.

Keywords: cognitive control, functional connectivity, dual systems

1. Introduction

Evidence that humans have multiple memory systems (Eichenbaum & Cohen, 2001; Squire, 2004; Tulving & Craik, 2000) inspired theories that humans also have multiple, qualitatively distinct category-learning systems (Ashby et al., 1998; Erickson & Kruschke, 1998). According to this view, procedural memory is used to form many-to-one stimulus-to-response mappings (S-R associations), whereas declarative memory is used to apply rules and test explicit hypotheses about category membership. Much of the neuroimaging evidence supporting these distinctions depends on prior research with rule-based (RB) and information-integration (II) category-learning tasks (Hélie et al., 2010a; Nomura et al., 2007; Soto et al., 2013; Waldschmidt & Ashby, 2011). In RB tasks, the categories can be learned via an explicit hypothesis-testing procedure (Ashby et al., 1998). In the simplest variant, only one dimension is relevant (e.g., bar width), and the task is to discover this dimension and then map the different dimensional values to the relevant category responses. In II tasks, accuracy is maximized only if information from two or more stimulus dimensions is integrated perceptually at a pre-decisional stage (Ashby & Gott, 1988). In most cases, the optimal strategy in II tasks is difficult or impossible to describe verbally (Ashby et al., 1998). Verbal rules may be (and sometimes are) applied, but they lead to suboptimal performance. Example II and RB categories are illustrated in panels A and B of Figure 1.

Much evidence suggests that II tasks recruit procedural memory, whereas RB tasks recruit declarative mechanisms. Even so, a natural question for readers unfamiliar with the category-learning literature is how any classification task can be a good choice for studying procedural behaviors. For instance, 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 some types of classification tasks are mediated via procedural learning and memory. At least 25 different behavioral dissociations tie II learning to procedural memory and RB learning to declarative memory (for reviews, see Ashby & Maddox, 2005, 2010; Ashby & Valentin, 2017b).

This hypothesis is further supported by a variety of investigations into the neural underpinnings of successful II and RB learning. Specifically, success in RB tasks depends on a broad neural network that includes the prefrontal cortex (PFC), anterior cingulate, the head of the caudate nucleus, and medial temporal lobe structures—regions that are also frequently associated with declarative memory and executive attention (Brown & Marsden, 1988; Filoteo et al., 2007; Muhammad et al., 2006; Seger & Cincotta, 2006). Arguably, the most important region in this network is the PFC, where rules are thought to be initially represented (Miller & Cohen, 2001; Wallis et al., 2001). Success in II tasks, on the other hand, depends on regions that have been implicated in procedural memory, including the striatum, premotor cortex, and the associated sensorimotor basal ganglia loop (Ashby & Ennis, 2006; Filoteo et al., 2005; Knowlton et al., 1996; Nomura

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