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In search of the engram, 2017

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Based on evidence from lesion and imaging studies, some authors have suggested that the 'motor engram' — a representation underlying skillful behavior — becomes more localized with learning. We critically review the evidence in favor of this view pointing out several caveats with the interpretation, most of which have been raised in Karl Lashley's classical paper from 1950. We argue that motor skills are likely not stored in a single area, but are instead encoded across multiple representations in both cortical and subcortical areas. To better understand these distributed neural changes with learning, we need a richer description of skilled performance and testable process models of skill acquisition.

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Introduction

Motor learning is the remarkable process by which the brain can improve performance of movements through practice. While we can readily observe the resulting behavioral changes, it remains unclear what neural processes underlie learning, and where in the brain the newly acquired skills are represented. Searching for the location of the 'motor engram' has been the central agenda of many neuroscientists from the very beginnings of our discipline. Many of the fundamental issues with this quest were already eloquently exposed in Karl Lashley's seminal paper from 1950 [1••], and despite dramatic improvements in our ability to record and manipulate neural circuits, these questions have largely remained the same in 2017. Reviewing modern evidence from neuroimaging, lesion, and electrophysiological studies, we reiterate here Lashley's argument that the search for a motor engram will in most cases not have a simple, localized answer. We discuss the conceptual advances in the analysis of neural and neuroimaging data that are needed to understand how movement skills are represented across different brain areas. We also argue that we need behavioral theories that characterize motor learning not as a monolith, but as an emergent property of parallel, interacting processes. We focus our discussion on acquisition of complex motor skills, using sequence learning as one paradigmatic example of skill development.

There is no single motor engram

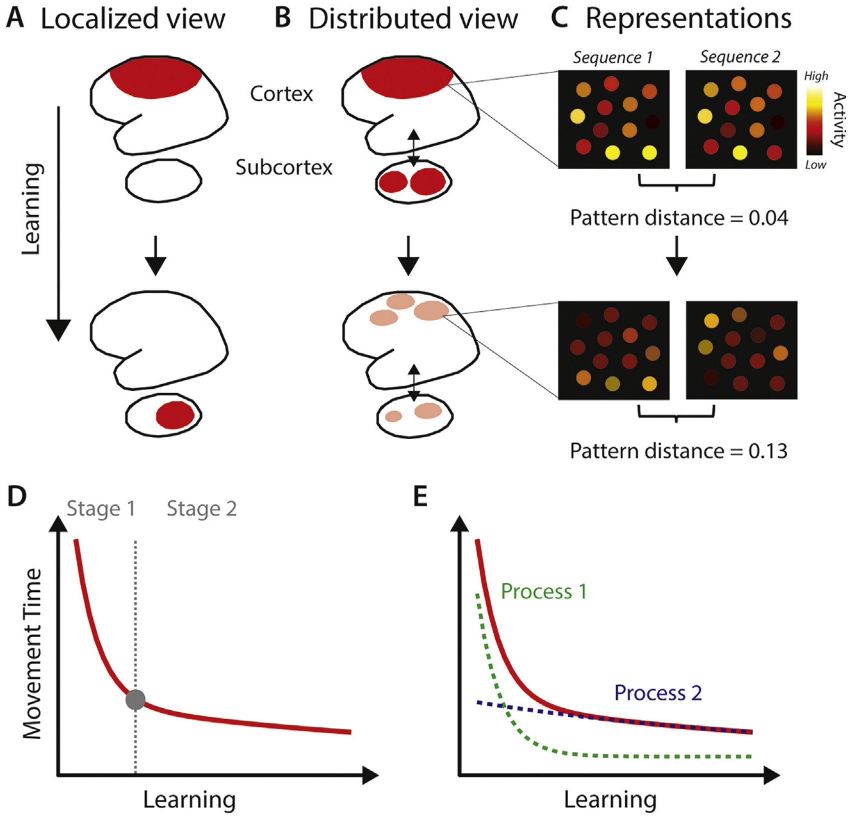
A widely-held view is that early in motor learning, skills are controlled by a wide network of cortical areas, but with time and practice the representation is transferred to a more narrow set of subcortical structures [2–4] (Figure 1a). The simplicity of this account is attractive because it follows our intuition of the roles of the cortex and the subcortex. However, the intuition can easily lead to false inferences about the representation of highly trained skills. Lashley summarized this argument as follows:

> 'Consciousness is a function of the cerebral cortex; long-practiced habits become automatic and are performed without conscious control; therefore they are no longer mediated by the cerebral cortex. Both premises of this syllogism are probably false, and the conclusion would not follow if they were true [1••].'

Of course, the view of increasing subcortical control with learning is based on more than an ill-conceived argument about flexibility, attention or conscious control. In the following section, we will review some of the main empirical results in favor of a localized subcortical storage of acquired motor memories, and point out the main problems in their interpretation. Ultimately, we will argue that there is no firm evidence for the exclusive storage of a motor engram in subcortical structures.

Numerous functional magnetic resonance imaging (fMRI) studies have attempted to study motor learning by correlating improvements in performance with changes in the overall activity in different brain areas with learning (see [5] for a review). One common observation is that early in learning, the production of motor sequences evokes extended activity in a network of cortical motor, pre-motor and association regions. This activity commonly decreases with time in the majority of cortical regions, while focal activation increases have been observed in sensorimotor regions of the cerebellum [6], basal ganglia [7] and the spinal cord [3]. This has been

Figure 1



(a,b) Localized versus distributed view of neuronal changes with learning. (a) The localized view proposes that motor skills transfer from widespread recruitment of cortical areas to a circumscribed subcortical locus with learning. (b) The distributed view suggests that both cortical and subcortical regions are involved at all stages of learning, with overall decreasing activation levels and more efficient encoding. **(c)** Changes in representational structure with learning. Neuronal population in a given area might respond very similarly during two finger tapping sequences at the beginning of learning (indicated by similar pattern of activation of activation units and a low pattern distance). With training, units become less active, but also differentially recruited for each of the two sequences. Thus, early in learning a downstream-connected area would receive identical input for production of either sequence, but later on it receive a unique input for each of them, further leading to recruitment of specific motor pools for each action. **(d,e)** Stage versus process models of behavioral changes with learning. (d) The stage model divides motor learning into distinct stages — an initial fast learning stage (often within-session), and a late slow learning stage with more incremental improvements until performance asymptotes. Translating the stage model into a neural mechanism, this would require a switching mechanism regulating the transition between stages (the 'switch' is indicated by the gray dot). (e) The same behavioral improvement can be explained by two continuous (and possibly independent) processes, where the process with a greater exponential improvement dominates in the early learning, while a slower process gains importance later on.

interpreted as evidence that well-learnt motor sequences are stored subcortically, with a decreasing cortical role in the skilled behavior (Figure 1a). The fundamental problem with this argument, however, is that decreases in fMRI activation do not necessarily reflect that an area is no longer involved in the task. It could be that the region still performs the same function, but does so more efficiently, which would result in lower fMRI activation [8]. Therefore, such results do not provide conclusive evidence for a disengagement of the cortex in performance of skilled movements.

Lesion studies are considered to be the gold standard for establishing causal relationships between regional activation and behavior. One possible outcome of a lesion experiment is that skilled performance remains unimpaired or recovers rapidly after the lesion [9•,10,11]. This is taken as an indication that the disrupted region is not strictly necessary for performing skilled behavior. But should we conclude that the region does not causally contribute to the skill at all? It is very well possible that there is no area that would lead to circumscribed deficits of skilled performance without impairing motor output in general. This would arise from a situation in which skill is represented in a distributed fashion across the brain, and where disruption of one region can be immediately compensated with activity coming from other areas. Such a behavior was recently observed in the mouse during a delayed response task, where temporary disruptions of one premotor cortex were immediately corrected by