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Reviews and perspectives

Motor skill acquisition across short and long time scales: A meta-analysis of neuroimaging data $^{\bigstar}$

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ABSTRACT

In this systematic review and meta-analysis, we explore how the time scale of practice affects patterns of brain activity associated with motor skill acquisition. Fifty-eight studies that involved skill learning with healthy participants (117 contrasts) met inclusion criteria. Two meta-contrasts were coded: decreases: peak coordinates that showed decreases in brain activity over time; increases: peak coordinates that showed increases in activity over time. Studies were grouped by practice time scale: short (≤ 1 h; 25 studies), medium (>1 and \leq 24 h; 18 studies), and long (>24 h to 5 weeks; 17 studies). Coordinates were analyzed using Activation Likelihood Estimation to show brain areas that were consistently activated for each contrast. Across time scales, consistent decreases in activity were shown in prefrontal and premotor cortex, the inferior parietal lobules, and the cerebellar cortex. Across the short and medium time scales there were consistent increases in supplementary and primary motor cortex and dentate nucleus. At the long time scale, increases were seen in posterior cingulate gyrus, primary motor cortex, putamen, and globus pallidus. Comparisons between time scales showed that increased activity in M1 at medium time scales was more spatially consistent across studies than increased activity in M1 at long time scales. Further, activity in the striatum (viz. putamen and globus pallidus) was consistently more rostral in the medium time scale and consistently more caudal in the long time scale. These data support neurophysiological models that posit that both a cortico-cerebellar system and a cortico-striatal system are active, but at different time points, during motor learning, and suggest there are associative/ premotor and sensorimotor networks active within each system.

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1. Introduction

Numerous, non-systematic reviews have been conducted on the behavioural and physiological changes that accompany practice and the acquisition of motor skills (e.g., Hikosaka, Nakamura, Sakai, & Kakahara, 2002; Willingham, 1998). The main focus of past work has been on changes in brain activity that underlie improved speed and accuracy in sequence learning or visuomotor adaptations (e.g., Dayan & Cohen, 2011; Doyon et al., 2009; Wadden, Borich, & Boyd, 2012). Based on data from neuroimaging (e.g., fMRI, PET) and cortically-induced perturbations (e.g., TMS), neurophysiological theories of motor learning advance the idea that skill acquisition and ultimately long term learning is supported by cortico-thalamic-cerebellar and cortico-thalamic-striatal systems (e.g., Hikosaka et al., 2002; Doyon et al., 2009).

Experimental evidence from individual studies also demonstrate distinct "associative/premotor" (AP) and "sensorimotor" (SN) networks that operate within the cortico-cerebellar and cortico-striatal systems. The AP network includes the dorsolateral prefrontal cortex, rostral premotor areas, the inferior parietal cortex, cerebellar cortex, and rostral basal ganglia. The SN network consists of supplementary and primary motor cortices, caudal basal ganglia, and the dentate nucleus (Coynel et al., 2010; Lehéricy et al., 2005; see also Hikosaka et al., 2002). These networks operate on different time scales with AP areas contributing to early-stage performance and SN regions supporting performance at later stages of practice. However, the time course of shifts within and between the networks that support motor learning remains to be determined. Recently, a meta-analysis was performed to distinguish brain areas associated with learning two types of motor tasks: sensorimotor adaptation versus the serial reaction time (SRT) task (Hardwick, Rottschy, Miall, & Eickhoff, 2013). However, a limitation in this work was the omission of time-dependent analyses.

Motor learning has been defined as "relatively permanent changes in the capability for skilled behaviour" resulting from practice or experience that is typically assessed by a delayed retention test (Schmidt & Lee, 2005, p. 302). The need to differentiate performance and learning effects is based on a substantial body of research showing differences in behaviour when it is assessed at the end of a practice session as compared to following a delay (typically 24 h to 1 week after practice has concluded; Kantak & Winstein, 2012). Group differences noted during practice have been shown to disappear (e.g., Feijen, Hodges, & Beek, 2010; Winstein, Pohl, & Lewthwaite, 1994), appear (Abe et al., 2011), or even reverse following a retention interval (Lee & Simon, 2004). Indeed, as many as 63% of studies show a lack of consistency in performance effects between immediate and delayed testing sessions, when those testing sessions are delayed by > 24 h (Kantak & Winstein, 2012). There are also empirical demonstrations of change in both behavioural and neural data when a delay is introduced between practice and retention testing, referred to as motor memory consolidation (Debas et al., 2010; Robertson, Pascual-Leone, & Miall, 2004; Shadmehr & Holcomb, 1997). Thus, changes in behavior that occur within a session could represent early stages of learning and/or transitory changes in performance (what Doyon et al., 2009 have referred to as "fast learning processes"), making it important to distinguish this early or "fast" learning from more permanent "slow" learning processes which take place over longer time spans.

In view of these distinctions, the duration of practice was the primary variable of interest in our meta-analysis. Operationally, we divided practice into three time scales: short (< 1 h). medium $(>1 h to \le 24 h)$, and long (>24 h to 5 weeks). Dividing practice sessions within a single day into short and medium time scales is motivated by similar distinctions made by Karni et al. (1998), who noted behavioural and neurophysiological changes across these time scales. Changes observed over long time scales meet the criterion of inclusion of a delayed retention test and therefore are more likely to reflect brain activity associated with learning. By controlling for the time scale of practice and combining large numbers of studies, we can delineate which brain regions are active following relatively short to moderate time scales of practice from more long-term changes and resolve some of the heterogeneous results in neuroimaging studies of skill acquisition.

2. Method

2.1. Literature search

We searched for studies published in or translated to English in the following databases: PsycINFO (EBSCO), Google Scholar, and PubMed. Search terms included combinations of "motor learning" and "skill acquisition" with one of the following, "neuroimaging", "fMRI", and "PET". The initial search was conducted in February 2013 and updated until January 2014. Further literature was obtained through reference lists of included papers.

2.2. Inclusion criteria

Analysis was restricted to experimental studies, but all time scales of learning were considered. Time scales were calculated based on methodological information provided in the study. Two coders (KRL and KW) calculated the time scale of practice for each study based on the time between first and last measurements of brain activity. When there was disagreement the authors discussed the study in question until consensus was reached. There were three time scales: short-term studies (*short*) which were ≤ 1 h (the shortest of which was ~ 12 min; Inoue et al., 1997); medium-term studies (*medium*) which were > 1 h and ≤ 24 h (the longest

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