



A quantitative meta-analysis and review of motor learning in the human brain

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ABSTRACT

Neuroimaging studies have improved our understanding of which brain structures are involved in motor learning. Despite this, questions remain regarding the areas that contribute consistently across paradigms with different task demands. For instance, sensorimotor tasks focus on learning novel movement kinematics and dynamics, while serial response time task (SRTT) variants focus on sequence learning. These differing task demands are likely to elicit quantifiably different patterns of neural activity on top of a potentially consistent core network. The current study identified consistent activations across 70 motor learning experiments using activation likelihood estimation (ALE) meta-analysis. A global analysis of all tasks revealed a bilateral cortical–subcortical network consistently underlying motor learning across tasks. Converging activations were revealed in the dorsal premotor cortex, supplementary motor cortex, primary motor cortex, primary somatosensory cortex, superior parietal lobule, thalamus, putamen and cerebellum. These activations were broadly consistent across task specific analyses that separated sensorimotor tasks and SRTT variants. Contrast analysis indicated that activity in the basal ganglia and cerebellum was significantly stronger for sensorimotor tasks, while activity in cortical structures and the thalamus was significantly stronger for SRTT variants. Additional conjunction analyses then indicated that the left dorsal premotor cortex was activated across all analyses considered, even when controlling for potential motor confounds. The highly consistent activation of the left dorsal premotor cortex suggests it is a critical node in the motor learning network.

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Introduction

Functional neuroimaging studies have been instrumental in determining the neuronal networks that underlie different types of motor learning tasks reviewed in Doyon et al. (2003). There is, however, little consensus regarding which areas of the brain are consistently activated during the acquisition of motor skills. This may be a result of the diverse range of experimental paradigms that have been used to examine motor learning. For instance, neuroimaging studies have examined a variety of sensorimotor paradigms, including learning dexterous skills such as playing musical instruments (Buccino et al., 2004) or tying knots (Tracy et al., 2003), learning visuomotor paradigms such as adapting movements in response to perturbations (Inoue et al., 2000; Nezafat et al., 2001), and phase coordination paradigms where participants learn to perform novel bimanual movement patterns (Puttemans et al., 2005; Rémy et al., 2008). Performance improvements in these sensorimotor tasks occur as participants learn to perform novel kinematics (movement speed and limb geometry) and/or dynamics (muscle forces

and joint coordination). In contrast to sensorimotor tasks, variants of the serial reaction time task (SRTT; Nissen and Bullemer, 1987) are notable as they rely on responding to visual stimuli only by pressing a corresponding button. SRTT variants therefore represent *learning of sequential motor behavior*, yet have relatively *minimal demands on motor execution*, as participants respond through primarily isometric contractions of the finger muscles. Thus, while sensorimotor tasks and SRTT variants are both useful paradigms with which to examine the neural substrates that underlie motor learning, their actual task demands differ considerably; sensorimotor tasks have greater motor demands and emphasize the learning of novel movement kinematics and dynamics, while SRTT variants have relatively minimal motor demands and focus on learning sequential motor behavior. Identifying areas of diverging activation (i.e. those that are activated primarily by sensorimotor tasks or SRTT variants) will thus reveal activations relating to the specific demands of each task type. Conversely, areas that are consistently activated across both sensorimotor tasks and SRTT variants are likely to represent the ‘core’ network of brain structures that are essential for motor learning. Areas identified as being critical to motor learning could then be targeted using neurostimulation techniques, which have been used to modulate the function of brain structures in order to augment skill acquisition (Galea et al., 2011; Reis et al., 2009).

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Previous qualitative reviews have highlighted both similarities and differences between the areas that underlie motor learning for sensorimotor tasks and SRTT variants. Robertson (2007) suggested both paradigms activate the striatum and cerebellum, but that sensorimotor paradigms are more dependent on cortical motor areas while SRTT variants place greater reliance on prefrontal areas. Hikosaka et al. (2002) describe a framework where two cortico-striatal-cerebellar loops underlie motor sequence learning. Performance improves rapidly during initial phases of learning, with changes being driven by an ‘associative’ loop. This loop comprises frontal, parietal and premotor cortical regions, the caudate, and associative cerebellar regions. The gradual increments in performance that occur later, however, are predominantly driven by a ‘motor’ loop. This loop consists of motor areas of the cortex, putamen, and cerebellum. The authors note, however, that this model may not hold for sensorimotor adaptation tasks such as learning to move against curl fields or learning visuomotor rotations. In contrast, Doyon and Benali (2005), Doyon et al. (2003, 2009) propose a single model that can encompass both types of task. Sensorimotor tasks such as motor adaptation primarily recruit a network of cortico-cerebellar structures, while sequence learning tasks instead involve greater contributions from a cortico-striatal system.

Despite the conflicting nature of these models, there is a degree of consensus regarding the specific roles that individual brain areas contribute to motor learning. The cerebellum is widely considered to maintain a ‘forward model’ of the motor apparatus, used to predict the sensory consequences of actions and detect errors in these predictions (Hikosaka et al., 2002; Krakauer and Mazzoni, 2011; Penhune and Steele, 2012; Shadmehr and Krakauer, 2008). Despite some controversy, it is widely suggested that the basal ganglia are implicated in probabilistic calculations and reward for optimal action selection (Hikosaka et al., 2002; Krakauer and Mazzoni, 2011; Penhune and Steele, 2012; Shadmehr and Krakauer, 2008). The primary motor cortex (M1) is consistently implicated in the use dependent acquisition and storage of muscle synergies required for faster and more precise movements (Krakauer and Mazzoni, 2011; Penhune and Steele, 2012; Shmuelof and Krakauer, 2011). The relatively consistent interpretations of the roles of the cerebellum, basal ganglia and motor cortex may stem from their highly preserved architecture in vertebrate species, which afford multiple converging sources of evidence as to their function (Shmuelof and Krakauer, 2011).

The roles of the parietal cortex and medial temporal lobe (MTL), however, are a matter of conjecture. Shadmehr and Krakauer (2008) suggest the parietal lobe combines the expected sensory consequences of movements (produced by the cerebellum; Miall and King, 2008; Miall et al., 2007) with actual sensory feedback to generate state estimations (see also Desmurget et al., 1999). Similarly, while Shadmehr and Krakauer (2008) indicate that the MTL is independent to the acquisition of motor skills, Robertson proposes that MTL engagement increases with temporal task demands, and that it is involved in learning ‘higher order’ components of sequences (see Robertson, 2007). It is, however, notable that Shadmehr and Krakauer (2008) primarily considered sensorimotor tasks, while Robertson (2007) was specifically reviewing SRTT variants. Task specific differences both between these experimental paradigms and within their specific demands may therefore explain the presence or absence of activity in the MTL and SPL.

Thus, previous reviews highlight consistent roles for the basal ganglia, cerebellum and M1, while bringing forth conflicting views on the roles of the parietal cortex and MTL. It should be considered that these reviews, though informative, are primarily qualitative in nature, usually drawing inference from the results of relatively few key studies. This leaves scope for quantitative techniques that examine evidence from a broader spectrum of studies to be utilized to assess which areas of the brain consistently contribute to motor learning.

Coordinate based meta-analyses can integrate the results of multiple neuroimaging studies across a field of research in a quantitative,

unbiased fashion. Pooling data from multiple investigations provides opportunities to address several of the problems inherent to individual neuroimaging studies, such as their typically limited sample sizes (10–20 participants). Combining results from multiple investigations thus provides an opportunity to combat their relatively low statistical power. Individual neuroimaging studies are also sensitive to specific aspects of paradigm implementation and the particular contrasts examined. This can lead to diverging patterns of results between studies due to subtle differences in experimental design. Summarizing their results in a quantitative manner provides results that are less influenced by such study-specific ‘noise’. Activation Likelihood Estimation (ALE) provides a well established technique for quantitative voxelwise random effects meta-analysis (Eickhoff et al., 2009, 2012; Laird et al., 2005; Turkeltaub et al., 2002, 2012). This approach determines areas of significant spatial convergence based on peak activation coordinates reported in previous neuroimaging investigations. A key advantage of this coordinate-based approach is its principled statistical testing procedure against a null distribution to provide quantitative results.

The current investigation therefore utilized ALE to summarize the existing functional neuroimaging literature on motor learning and identify brain areas consistently activated during motor learning tasks. We hypothesized that an integration across all experiments would primarily reveal activations in motor cortical and cerebellar brain structures. Controlling for motor execution and for hand use during the tasks would allow further specification of areas that are involved in the higher level aspects of motor learning (as opposed to those simply involved in motor control). Furthermore, we hypothesized that while both sensorimotor and SRTT variant tasks would elicit activity in brain areas relating to motor preparation and execution, sensorimotor tasks would elicit greater activations in areas utilized to sense or predict the current state of the body and control movements. Finally, we hypothesized that areas that were demonstrated to be consistently activated across both sensorimotor and SRTT variant tasks would represent the ‘core’ areas essential to the motor learning network.

Material and methods

Data used for the meta-analysis

Studies to be integrated in the current meta-analysis were obtained via PubMed literature searches (www.pubmed.org, search strings “motor learning” or “sequence learning”) on functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) experiments. Citations within these papers and previous qualitative reviews were examined to identify additional functional imaging studies to include in the analysis. Only publications reporting whole-brain analyses in standard reference space (Talairach/Tournoux, MNI) were included (coordinates reported in Talairach space were transformed into MNI coordinates using the Lancaster transformation; Laird et al., 2010; Lancaster et al., 2007). Only results from group analyses of healthy adult participants were considered for further analysis; single subject reports and between-group comparisons were excluded. In cases where studies reported data from patient populations, only data from healthy controls was used. The sample was further restricted to examine only manual motor learning tasks, as the number of studies examining training with other effectors (e.g. the legs) was insufficient for meaningful analysis. As an examination of the eligible studies revealed that relatively few experiments presented data on training related decreases in activity associated with motor learning, the meta-analyses presented here examined only training related increases in activation. We do, however, present a summary of the data from analyses of training related decreases in activity in the supplementary materials, as it has been proposed that they may reflect important changes in the

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