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Abstract

Attempting to understand the neurophysiological underpinnings of learned behaviors and the process of learning itself has yielded interesting findings relating to what happens in the brain and across the nervous system when learning a new skill. The nervous system displays several structural, functional and neurochemical adaptations to motor learning which have been highlighted through the use of neuroimaging techniques such as fMRI, EEG and TMS. This review attempts to outline the neural adaptations governing the acquisition and retention of motor skills, as well as build a timeline for these adaptations following Fitt's model of motor learning (Fitts and Posner 1967). As one moves across the stages of learning (cognitive, associative, autonomous) the nervous system displays an initial increase in activity and plasticity in the frontal associative regions, motor cortical regions, parietal cortices, sensorimotor striatum, associative striatum, cerebral cortices and nuclei and hippocampus (Doyon et al., 2008), as well as the basal ganglia thalamocortical loops, medial cerebellum, anterior cingulate cortex, inferior frontal gyrus and the visual and parietal cortical areas (Seidler 2011). These neuro-plastic adaptations and activation patterns cement and refine themselves in later stages, indicating a more efficient circuitry and decreased cognitive load when performing the skill (Poldrack et al., 2005). In terms of practical applications of these findings, manipulation of the training principles involved in specific contexts of motor skill learning such as training specificity, duration and intensity, may yield improved neural adaptations and in turn performance on the skill in question.

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Introduction

Much effort has gone into attempting to unravel the neural underpinnings of motor learning (Xiong et al., 2009, Ma et al., 2010, Coynel et al., 2010). The behavioral adaptations to motor learning have long been described as pertaining to three stages; the cognitive, associative and autonomous stages following Fitt's model of motor learning (Fitts and Posner 1967). As one moves across these stages, movement becomes more accurate, stable and smooth as well as replicable. Interestingly, the neural adaptations underpinning these behavioral stages also seem to vary with training duration (Ma et al., 2011). When attempting to study the way humans learn motor skills, one must consider the vital role of these neural adaptations. Many advancements have been made in the field including novel data acquisition tools such as transcranial magnetic stimulation (TMS) and fMRI that have allowed researchers to map neural adaptations to a higher degree of accuracy (Jensen et al., 2005, Ma et al., 2011, Hlustik et al., 2004, Lehericy et al., 2005, Karni et al., 1995). When repeated, controlled actions are performed, various adaptive responses take place across the nervous system, both centrally and peripherally. An attempt to map the neural adaptations across the stages of motor skill acquisition could improve the practical applications of collecting data on neural activity, as one could map progression across training. The ample literature on the topic raises questions such as; When, on a neural level, can a skill be considered learned? Can any factors affect the rate of neural adaptations to skill acquisition? What are the differences between short- and long-term neural adaptations to motor learning?

Review of the Literature

Neural Adaptations to Motor Learning and Skill-Based Training:

Many papers have successfully shed light on the various adaptations that take place on a neural level when undergoing skill based training. The research has expanded on the various neurochemical, structural and functional changes that occur throughout the nervous system. This review provides an insight into some changes that follow different types of motor learning in different contexts using novel data acquisition techniques. In a research paper by Baptista and colleagues (2014), the authors set out to outline the role of changes in functional connectivity and gamma-aminobutyric acid (GABA) levels during long-term motor skill learning. They recruited 44 active participants and a control group of N=20 who completed no training. The active participants were further divided into two sub-groups, one undergoing high intensity 30 minute training sessions, and the other low intensity 15 minute training sessions. These sessions were completed 5 days/week for 6 weeks, and the motor task in question was a 3-ball cascade juggling task. All participants underwent fMRI for resting state functional connectivity measures and MR spectroscopy for GABA level monitoring in M1 to measure local inhibitory tone as well as resting state connectivity. Interestingly the researchers found differences in adaptations between the two groups, with the low intensity group showing increased functional connectivity and decreases in GABA. On the other hand, the high-intensity group showed a decrease in functional connectivity with no significant changes in GABA levels. All changes in functional connectivity were related to improved performance, whereas learning related changes in functional connectivity are also related to changes in GABA. This evidence suggests that learning related changes occur in relation to resting state network connectivity, and are in part a reflection of GABAergic plastic processes as outlined by Baptista and colleagues (2014).

Mehrkanoon et al., (2015) found that significant restructuring takes place relating to acute motor learning adaptations, namely within the cortico-cerebellar network. They identified these patterns using EEG following a dynamic force task, which could function as a potential marker for acute neural adaptations to motor learning. Some studies find no neural changes despite performance improvements in acute settings. Bakker and colleagues (2021) found that a single 30 minute specific balance training session significantly improved task performance, but found no significant change at a neural level following measures of intracortical facilitation, short-interval intracortical inhibition and long-interval intracortical inhibition using TMS. Interestingly, the authors also found that the improvements in performance were non-transferable to other similar skills and seemed specific to the trained movement (Bakker et al., 2021). Jensen et al., (2005) found significant increases in corticospinal excitability using TMS following 4 weeks of skill based training, suggesting its importance as a neuromuscular adaptation to motor learning. The authors found that as a comparison group, strength based training elicited different neural adaptations, again suggesting training specificity is key for skill based motor learning.

Poldrack and colleagues (2005) attempted to outline the neural correlates to motor skill automaticity. The authors outline that following several days of behavioral training 3 hours/day, there were significant differences in neural activity following fMRI sessions PRE and POST training. Namely, the researchers observed decreased activity in the right middle frontal gyrus, right caudate body and bilateral ventral premotor areas. These findings suggest a decrease in cognitive load when the task becomes automatized within a subject, and a refinement in neural activity related to task performance. Poldrack et al., (2005) also outline the role of the supplementary motor area as well as the putamen/ globus pallidus regions for sequence related motor learning.

Lin et al., (2018) found some practical implications for the type of practice in order to optimize skill acquisition. Through a comparison of fMRI data between two groups undergoing distinct practice types; repetitive practice and interleaved practice, the researchers identified the effects of the contextual interferences during interleaved practice on neural activity in different brain regions. The authors found that resting connectivity was increased for the group performing interleaved practice, with differences after the first day in the amygdala, hippocampus, thalamus, putamen, premotor cortex and cerebellum which were related to improved skill acquisition (Lin et al., 2018). These findings can help to understand the types of training needed to elicit certain neural patterns of activation. Practice with contextual interference can be beneficial during the consolidation phase of motor skill learning, and can be especially important in the context of skill transfer across multiple dynamic motor tasks.

Short- vs Long- Term Neural Adaptations to Motor Learning:

This section attempts to outline the timeline of neural adaptations related to motor skill acquisition and retention from short-term stages, through to long-term skill retention. Tallent and colleagues (2021) conducted a review which outlined the adaptations linked to the peripheral nervous system and neural adaptations across different timelines of exposure to motor skill training defined as; acute - 1 session, Short-term - 2 to 30 sessions, and long-term - 3+ years. The first adaptations linked to a novel motor task are associated with an improvement in synaptic efficacy (Coxon et al., 2014). In the shift from early to late stages of adaptations more structural plasticity occurs with an increase in M1 movement representations and synaptogenesis (Kleim et al., 2014). Literature also suggests both increased (Krings et al., 2000), and decreased (Bangert and Schlaug., 2006) cortical movement representations following motor skill training, this discrepancy is partially explained by an increase in efficiency which would reduce the apparent representations especially following long-term training. However, one limitation brought forward in this article was that long-term motor skill learning studies often employ cross sectional methods of analysis, which limits the inferences one can make regarding the longitudinal process of learning.

Doyon and colleagues (2008) developed a model following a review of the literature mapping the different neuroplastic adaptations to motor skill learning longitudinally. A figure adapted from the model is shown below depicting the neuroplastic adaptations across the stages of motor learning according to Doyon et al., (2008).

Figure 1:

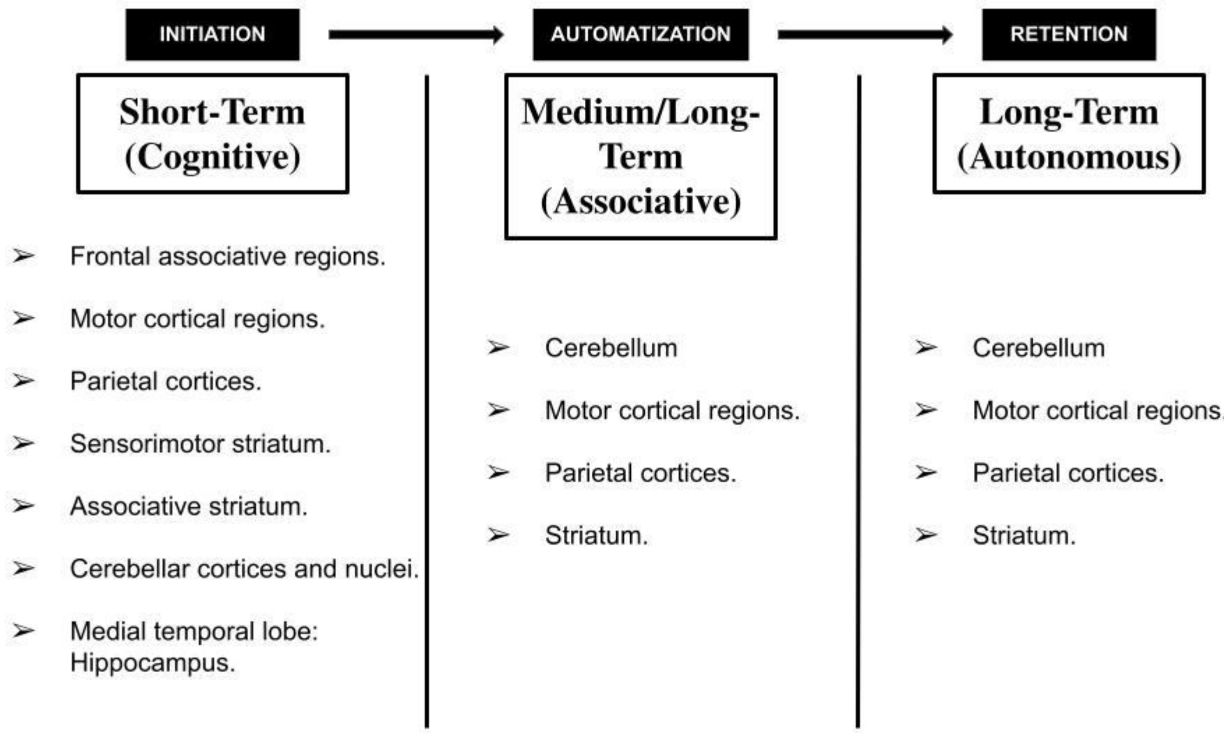

Figure 1 depicts the upregulated cerebral plasticity across the stages of motor learning from short to long-term (Doyon et al., 2008). The representation of the adaptations is superimposed on Fitt's model of motor learning following the cognitive, associative and autonomous stages (Fitts and Posner 1967). Notice the nature of adaptations seems to stabilize from medium to long-term.

Ma et al., (2011) attempted to shed some light on the resting state cortical adaptations associated with motor learning at different stages. 10 right handed participants were asked to practice a motor learning task, namely a sequential finger movement pattern, for 15 minutes each day while video recording their practice sessions. The participants also underwent fMRI sessions during week 0, week 2 and week 4 of training to assess their resting functional connectivity. The authors interestingly identified patterns in neural adaptations related to training duration. During the first 2 weeks there were significant increases in strength for the resting state functional connectivity in the right postcentral gyrus and bilateral supramarginal gyri. These increases in functional connectivity were significantly related to improved performance. The only further change in functional connectivity in weeks 2 to 4 was a sustained increase in the left supramarginal gyrus. This study also included participants which appropriately had no professional experience with musical instruments, however sports participation could have also been screened for. One potential limitation for this article was the absence of data collected for brain regions such as the basal ganglia, the thalamus and the cerebellum, as well as having a limited sample size (Ma et al., 2011).

Attempting to examine the timeline of cortical adaptations to skill acquisition and retention, a review by Seidler (2011) outlined the neural correlates of motor learning across the early and late stages of skill acquisition. The findings suggest an engagement of the basal ganglia thalamocortical loops, medial cerebellum, anterior cingulate cortex, inferior frontal gyrus, as well as the visual and the parietal cortical areas during the early stages of motor learning (Seidler 2011). This activation pattern suggests an early phase of high attention and error correction, which fits the behavioral observations for an early stage. On the other hand, the late stages of motor learning engaged the parietal and cingulate motor cortical areas as well as the lateral cerebellum, which indicate information storage and motor refinement in the context of long-term learning. These also seem to relate to the activation patterns linked to skill transfer, or one's ability to use similar motor patterns in a slightly modified environmental context.

Practical Applications:

Following an outline of the various neural adaptations related to motor skill acquisition and retention, many practical applications can be found to enhance motor skill learning. One important factor across various studies seemed to be the specificity of the motor task one wishes to learn. The quality and volume of practice also seems to have positive effects on neural adaptation acquisition, suggesting more frequent practice of the movement with a potential inclusion of external motivating factors such as; performing the movement in front of a mirror, or recording it for reference and feedback, could help skill acquisition. Research has shown preliminary evidence in support of adjunct aerobic exercise as a facilitator for cortical adaptations linked with motor skill learning (Singh et al., 2015). This can be particularly useful to athletes competing in intense, yet skill dependent sports, as well as in clinical populations involved in neural rehabilitation. When performed a priori to motor skill learning, aerobic exercise can facilitate the induction of experience dependent plasticity (Mang et al., 2014, Singh et al., 2014). Another training element that may be modified to induce improvements in motor learning is the inclusion of variations and contextual inferences within the training sessions to improve the “transferability” of that novel skill, which can be useful in a variety of sports and their related movements (Lin et al., 2018). This is of particular interest for athletes who compete in dynamic, skill-movement oriented sports such as football or ice hockey, who might suffer from repetitive practice of the same exact movements when trying to adapt those skills to an infinitely variable context of environmental stimuli. That being said, repetitive movement training can still have profound adaptive benefits during the early stages of motor skill acquisition. In contrast however, sports such as darts, or even basketball, when isolating actions such as the free throw, can still benefit from repetitive practice at later stages of motor skill acquisition. This is due to those specific tasks always presenting the majority of the movement requirements exactly the same way, i.e. the same distance from the target, the same equipment, often practiced indoors away from potential weather perturbations, and with the same sequence of actions needed to complete the motor skill action. Many of the techniques used to monitor neural adaptations such as EEG, TMS and fMRI, if accessible, could also provide useful markers for neural adaptation progression throughout training programs. This could be done by periodically taking these measures from athletes or individuals who are currently working on developing a skill based motor task, similar to what is already done in the form of metabolic and biomechanical assessments to assess other physiological adaptations to training.

Conclusion:

In summary there are numerous neural adaptations that have been found to be related to motor skill acquisition. During the initial stages of motor learning one can expect many neuroplastic adaptations in the frontal associative regions, motor cortical regions, parietal cortices, sensorimotor striatum, associative striatum, cerebellar cortices and nuclei, medial temporal lobe: hippocampus (Doyon et al., 2008). Increased engagement of the basal ganglia thalamocortical loops, medial cerebellum, anterior cingulate cortex, inferior frontal gyrus, as well as the visual and the parietal cortical areas is also seen in the early stages of skill acquisition (Seidler 2011). When moving from the early stages to consolidation phases, an individual might find that these initial increases in activity, connectivity and neural representation decrease and it is presumed that this is caused by improved efficiency in the circuitry (Bangert and Schlaug., 2006, Baptista et al., 2014). Long-term neural adaptations involve a 'cementing' of the novel circuitry involving brain regions such as the cerebellum, motor cortical regions, striatum and parietal cortices (Doyon et al., 2008). Finally there seems to be a high degree of specificity regarding repetitive training related adaptations to motor skill learning, making it so that in dynamic environments it might be best to include interference into the training regime to allow for future skill transferability, especially in the later stages of skill consolidation and retention (Lin et al., 2018).

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