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ORIGINAL ARTICLE

Reorganization of large-scale cognitive networks during automation of imagination of a complex sequential movement

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Summary We investigated the functional reconfiguration of the cerebral networks involved in imagination of sequential movements of the left foot, both performed at regular and fast speed after mental imagery training. Thirty-five volunteers were scanned with a 3 T MRI while they imagined a sequence of ankle movements (dorsiflexion, plantar flexion, varus and valgus) before and after mental practice. Subjects were distributed in two groups: the first group executed regular movements whereas the second group made fast movements. We applied the general linear model (GLM) and model-free, exploratory tensorial independent component analytic (TICA) approaches to identify plastic post-training effects on brain activation. GLM showed that post-training imagination of movement was accompanied by a dual effect: a specific recruitment of a medial prefronto-cingulo-parietal circuit reminiscent of the default-mode network, with the left putamen, and a decreased activity of a lateral fronto-parietal network. Training-related subcortical changes only consisted in an increased activity in the left striatum. Unexpectedly, no difference was observed in the cerebellum. TICA also revealed involvement of the left executive network, and of the dorsal control executive network but no significant differences were found between pre- and post-training phases. Therefore, repetitive motor mental imagery induced specific putamen (motor rehearsal) recruitment that one previously observed during learning of overt movements, and, simultaneously, a specific shift of activity from the dorsolateral prefrontal cortex (attention, working memory) to the medial posterior parietal and cingulate cortices (mental imagery and memory rehearsal). Our data complement and confirm the notion that differential and coupled recruitment of cognitive networks can constitute a neural marker of training effects.

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Introduction

Recent techniques based on fMRI have led to a better understanding of the organization of brain circuitry and are reshaping our view of brain connectivity [1]. Brain circuitry is more dynamic than expected and the elucidation of the changes in cerebral activation occurring during motor training has numerous applications not only to increase our understanding of physiological activations in the brain, but also to propose novel methods of neurorehabilitation. It is established that motor training modulates activity in a long-range sensorimotor circuit, including the dorsal premotor, supplementary motor (SMA), somatosensory and superior parietal cortices, and in the thalamus, striatum and cerebellum [2—4]. Striato-cerebellar activation appears to be task-, complexity- and time-dependent [5]. The cerebellum is preferentially recruited by complex movements and sensorimotor tasks. During the learning process, a progressive increased activation of the dentate nucleus is observed from the early phase of training to the late one, in parallel with a decreased activation of the cerebellar cortex [6]. Afterwards, the transition from short-term to long-term learning is accompanied by a switch from the cerebellar system to the striatal system (posterior lentiform nucleus) and from the cerebellar anterior lobe to the posterior lobe. Therefore, cortical plastic changes could mainly be guided first by a cerebello-cortical loop in charge of on-line, sensory feedback- or internal model-based control and correction of the performance, and second by a neostriato-cortical loop when the motor skill is fully automated. Learning is classically subdivided into three consecutive phases: en coding, consolidation and retrieval of motor memory with specific, task- and practice-related timescales [5]. If encoding strongly engages sensorimotor system, consolidation differentially recruits, for instance, premotor areas, such as SMA, for off-line, post-practice stabilization of motor memory. Furthermore, this consolidation process depends on the structure of practice, such as repetitive blocked-ordered practice versus random-ordered one.

However, neuroplastic modifications do not only concern sensorimotor structures but also cognitive brain areas. Indeed, training can cause a decreased activation in dorsal attentional and executive fronto-parietal circuits and a simultaneous increased activation in the default-mode network [7]. This shift of activity between neocortical networks fits with the ''scaffolding framework'' hypothesis postulating that executive networks transiently supervise sensorimotor system to optimize novel task performance [8].

Overt motor performance can be significantly improved by purely mental training based upon mental imagery (MI). MI is defined as the mental simulation of a movement without overt actual execution, and is subserved by a network passing through the prefrontal, cingulate, premotor and parietal cortices, and neostriatum and neocerebellum [9,10]. Mental practice may also have an active influence upon cognitive networks functionally ''scaffolding'' sensorimotor system during early phases of motor skill acquisition. In a previous study [2], we investigated the brain and cerebellar areas involved in the control of speed during an overt and covert execution of a complex foot motor sequence. We found that the cerebellar anterior vermis is involved in the regulation of movement velocity whereas cerebellar hemispherical activation deals with patterning and sequencing of submovements. In the present experiment, we wondered:

- whether training with mental practice of these movements at regular and fast velocity would first improve the overt and covert motor performance;
- would entail specific plastic changes of brain networks underlying these performances.

To this aim, we studied the functional reconfiguration of neural networks (neuroplasticity) activated during execution and imagination of the same sequential left foot movements performed at regular and high speed after training by mental imagery. Our goals were to clarify:

- which training-related changes occurs in terms of motor and cognitive brain activation;
- to increase our understanding of the repercussions of post-training velocity-related changes of brain networks.

In order to assess both training-related changes and post-training velocity-related modifications, we applied GLM analysis to estimate post-training effects and, complementarily, multivariate approach to better characterize subnetwork activation. We have selected the left foot of right-footed subjects to increase the task-complexity and to allow for identification of brain areas in charge of executive control of non-automated movements. So far, only a few studies have been devoted to complex sequential foot movements and in particular to the impact of imagination/execution at different speed on brain activity, despite the importance of daily motor activities, such as locomotion, sport and dance.

Methods

Participants

Thirty-five healthy subjects volunteers (18 women, 17 men; mean age: 23 years, SD: 2.99) without history of neurological disease participated in this study. They all were right-handed and right-footed. The protocol was approved by the ULB-Erasme Ethics Committee and all subjects gave their written informed consent before participating. Three subjects were excluded; one subject stopped the experiment before the end of the fMRI and unexpected lesions were discovered for two subjects.

Procedure

The general experimental design is illustrated in Fig. 1. The motor task performed by each subject before and after training consisted of repetitive left ankle movements of dorsiflexion (D), plantarflexion (P), varus (Vr) and valgus (Vl). These movements were executed at maximal amplitude and made in a predetermined order: D-P-Vr-Vl-P-D. Subjects were divided in two groups: one group ($n = 16$) performed foot movements at regular velocity, whereas the second group ($n = 16$) executed fast foot movements. All subjects underwent a training consisting in five times a week of