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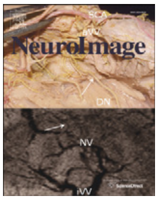

Morphological brain plasticity induced by musical expertise is accompanied by modulation of functional connectivity at rest

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ABSTRACT

The aim of this study was to explore whether musical practice-related gray matter increases in brain regions are accompanied by modifications in their resting-state functional connectivity. 16 young musically experienced adults and 17 matched nonmusicians underwent an anatomical magnetic resonance imaging (MRI) and a resting-state functional MRI (rsfMRI). A whole-brain two-sample *t* test run on the T1-weighted structural images revealed four clusters exhibiting significant increases in gray matter (GM) volume in the musician group, located within the right posterior and middle cingulate gyrus, left superior temporal gyrus and right inferior orbitofrontal gyrus. Each cluster was used as a seed region to generate and compare whole-brain resting-state functional connectivity maps. The two clusters within the cingulate gyrus exhibited greater connectivity for musicians with the right prefrontal cortex and left temporal pole, which play a role in autobiographical and semantic memory, respectively. The cluster in the left superior temporal gyrus displayed enhanced connectivity with several language-related areas (e.g., left premotor cortex, bilateral supramarginal gyri). Finally, the cluster in the right inferior frontal gyrus displayed more synchronous activity at rest with claustrum, areas thought to play a role in binding sensory and motor information. We interpreted these findings as the consequence of repeated collaborative use in general networks supporting some of the memory, perceptual-motor and emotional features of musical practice.

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Introduction

Musical practice as a model for studying brain plasticity

Musical expertise has become a useful model for investigating practice-related brain plasticity in humans (Dawson, 2011; Fauvel et al., 2013). Performing music is a complex behavior, which relies on immediate and accurate associations between motor sequences and auditory events. Neuroimaging studies have shown that musical training leads to structural plasticity within auditory and motor areas (Münte et al., 2002), as well as a reinforced functional coupling of these regions during musical tasks (Bangert et al., 2006; Haueisen and Knösche, 2001). Moreover, repeated musical practice improves not only perception and action, but also general cognitive processes such as memory (short- and long-term), executive functions and attention (Pantev and Herholz, 2011). The reason is that, in addition to engaging specific brain areas, the cognitive processes applied to musical material involve broad networks that are used to process other kinds of stimuli as well (Bialystok and DePape, 2009; Gaab and Schlaug, 2003). This is especially true for experienced musicians, who have to master increasingly difficult pieces of music (Pallesen et al., 2010). Finally, brain plasticity related to musical practice has also been observed in several white-matter (WM) tracts such as the corpus callosum (Bengtsson et al., 2005; Öztürk et al., 2002; Schlaug et al., 1995), the corticospinal tract (Bengtsson et al., 2005; Imfeld et al., 2009) and the arcuate fasciculus (Bengtsson et al., 2005).

Thus, musical practice seems to be both a multimodal and a multiprocess activity that involves large parts of the brain.

Learning-related modulation of resting-state functional connectivity

Researchers have recently discovered that during wakeful rest, the brain exhibits spontaneous activity, believed to be related to neuronal firing rather than to simple physiological noise (heart rate and breathing; Van den Heuvel and Hulshoff Pol, 2010). With the use of resting-state functional connectivity, it seems that the pattern of correlations between the blood-oxygen-level dependent (BOLD) time series of several distinct brain areas points to the existence of a network of organization

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(Damoiseaux et al., 2006) similar to those known to be engaged during the performance of sensorimotor and cognitive tasks (Van den Heuvel and Hulshoff Pol, 2010) and dependent upon the brain's anatomical connectivity (Van den Heuvel et al., 2009). Additionally, some authors have suggested that recent experiences and learning episodes can modulate subsequent patterns of resting-state functional connectivity both within and between the networks they recruited. For example, Lewis et al. (2009) found that sensory areas activated during an intensive training session for a very demanding visual task subsequently exhibited increased resting-state functional connectivity within parietal and frontal regions known to be involved in the control of spatial attention. Also using a visual learning paradigm, Urner et al. (2013) highlighted both short- and long-lasting learning-related changes in resting-state functional connectivity between the hippocampus and striatum. Regarding the motor domain, Vahdat et al. (2011) found that motor training reinforces resting-state functional connectivity within both a motor and a somatosensory network, while Albert et al. (2009) reported modulations in resting-state functional connectivity in the wake of new complex motor learning, but not after simple, familiar motor activities. This argues in favor of a learning consolidation function of resting-state brain activity. These findings have been replicated with studies featuring more cognitive tasks and with an emphasis on behavioral performances. Veroude et al. (2010) showed Dutch participants a weather report in Mandarin Chinese and assessed their resting-state functional connectivity both before and after an incidental auditory recognition task. When they divided the sample into high and low learners, they found that the high learners displayed not only greater post-task reorganization of resting-state functional connectivity between the regions involved in phonological shape storage (the auditory forms representation of words), but also stronger pre-task resting-state functional connectivity between the regions that sustain phonological rehearsal. These results pointed to both pre-existing and learning-induced differences between the two groups. Finally, a piece of evidence in favor of a memory consolidation role of task-related modulation of resting-state functional connectivity comes from a study by Tambini et al. (2010). They observed enhanced resting-state functional connectivity between the hippocampus and a portion of the lateral occipital lobe following incidental episodic encoding requiring highly associative memory processes for later recall (objects and faces), but not after episodic encoding with relatively low levels of subsequent associative memory (scenes and faces). Interestingly, the coefficient of correlation between the time series of the hippocampus and lateral occipital lobe during the post-encoding resting session was predictive of retrieval performances, thus powerfully demonstrating the importance of task-related modulation of resting-state functional connectivity for learning.

Taken together, the aforementioned studies have given rise to the idea that, even in the absence of external stimuli or demands, the brain is constantly sharing information, consolidating recent learning, and maintaining associated the activity of brain areas that are likely to be used together in the future (Fox and Raichle, 2007).

Expertise-related modulation of resting-state functional connectivity

Several studies have specifically investigated the effects of long-term expertise on the architecture of resting-state functional connectivity. One of them took Chinese chess masters as model of experts (Duan et al., 2012), and another choose professional or student musicians (Luo et al., 2012). In accordance with these different types of expertise, Duan et al. (2012) focused on cognitive resting networks, whereas Luo et al. (2012) looked at perceptual and motor networks. The boardgame experts in the first study (Duan et al., 2012) displayed a particular pattern of the default mode network (DMN; a set of areas more active at rest than during task performance, thought to sustain spontaneous mind wandering, and mainly comprising the posterior cingulate cortex and prefrontal cortex, as well as temporal and parietal areas Damoiseaux et al., 2006) that included the caudate nucleus. This structure is not classically viewed as belonging to the DMN, but is involved in motivation and decision-making processes, and was found to be strongly engaged in the expert players during a chess task. For their part, the expert musicians (Luo et al., 2012) exhibited stronger resting-state time-series correlations among the perceptual and motor networks, probably related to the regular multimodal activity described earlier. These rsfMRI studies of long-term expertise suggest that changes in resting-state functional connectivity can be observed in individuals owning an expertise.

Morphometric difference-based resting-state functional connectivity

One method of investigating the brain's organization at rest is to look for the overall pattern of connectivity between the BOLD signal time courses of one specific area (classically called *seed area*) and those of the rest of the brain. This area is chosen because it has been shown to be of relevance for the population and/or cognitive process being studied. Several works have already combined structural MRI and rsfMRI by choosing the structurally affected areas for subsequent resting-state functional connectivity analysis. This has been done in the framework of several pathologies: heroin dependence (Yuan et al., 2010), antipsychotic-naive first-episode schizophrenia (Lui et al., 2009), idiopathic generalized epilepsy (Wang et al., 2012), social anxiety disorder (Liao et al., 2011); and expertise: professional badminton players (Di et al., 2012) and *baduk* (go) players (Jung et al., 2013). In the case of expertise studies, because rsfMRI does not require the performance of any particular task, functional connectivity changes may reflect a cumulative effect of experience over time (Lewis et al., 2009), and can therefore be used as complementary to task-related fMRI for highlighting practice-related functional brain changes in dismissing the potential confounds due to differences in behavioral performances.

Aims of the present study

In sum, musical practice shapes the brain both structurally and functionally, with practice-related enhancement of GM possibly related to the dendritic growth required for building or strengthening synaptic projections (Anderson, 2011; Draganski and May, 2008). There is sometimes an overlap between expertise-related structural and functional plasticity (Groussard et al., 2010b; Ilg et al., 2008). Furthermore, resting-state functional connectivity between regions could either reflect their anatomical connectivity (WM fiber tracts), their amount of concomitant activation during active states, or recent learning consolidation. We therefore reasoned that musical practice-related structural plasticity could be accompanied by the modulation of resting-state functional connectivity. Accordingly, we generated resting-state functional connectivity maps from brain areas that displayed greater GM volume in a sample of experienced musicians than in a group of nonmusician counterparts, and ran a second between-group comparison to highlight areas that had significantly increased resting-state functional connectivity with the structurally modified regions in the musician group. Furthermore, we conducted a supplementary analysis to investigate the relationship between our structural and functional results.

Material and methods

Participants

Thirty-three young volunteers (13 men, mean age ± *SD*: 24.35 ± 3.39 years, mean educational level ± *SD*: 15 ± 1.56 years of schooling) with no history of neurological or psychiatric disease took part in this study (Table 1). Sixteen were students who currently played a musical instrument (violin, cello, guitar, flute, recorder, trumpet, clarinet, or piano) in their spare time at least several times a week, and had been doing so for a mean duration (±*SD*) of 16.13 (±4.29) years at the time of the study. They were recruited from the local conservatory or other classical music schools where they have learned music theory for at

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