

available at www.sciencedirect.comwww.elsevier.com/locate/brainres**BRAIN
RESEARCH****Research Report****A network for audio–motor coordination in skilled pianists and non-musicians**

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ABSTRACT

Playing a musical instrument requires efficient auditory and motor processing. Fast feed forward and feedback connections that link the acoustic target to the corresponding motor programs need to be established during years of practice. The aim of our study is to provide a detailed description of cortical structures that participate in this audio–motor coordination network in professional pianists and non-musicians. In order to map these interacting areas using functional magnetic resonance imaging (fMRI), we considered cortical areas that are concurrently activated during silent piano performance and motionless listening to piano sound. Furthermore we investigated to what extent interactions between the auditory and the motor modality happen involuntarily. We observed a network of predominantly secondary and higher order areas belonging to the auditory and motor modality. The extent of activity was clearly increased by imagination of the absent modality. However, this network did neither comprise primary auditory nor primary motor areas in any condition. Activity in the lateral dorsal premotor cortex (PMd) and the pre-supplementary motor cortex (preSMA) was significantly increased for pianists. Our data imply an intermodal transformation network of auditory and motor areas which is subject to a certain degree of plasticity by means of intensive training.

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1. Introduction

From several points of view, high-level music performance is an interesting topic to study the neural underpinnings of action and perception and to address the question to what extent the human cerebral cortex is modified structurally and functionally due to training. First of all, playing a musical ins-

trument poses great demands on the human motor system. Complex movement coordination is required at tremendous speed and accuracy. In addition, musicians are arguably challenged by no other profession in their expertise in the auditory domain. Music performance requires detection of minimal changes in pitch and rhythm to ensure a perfect artistic outcome. Thus, highly skilled musicians are an ideal

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Abbreviations: CMA, cingulate motor area; HG, Heschl's gyrus; IFG, inferior frontal gyrus; M1, primary motor cortex; NL, nucleus lentiformis; PM(d), (dorsal) premotor cortex; PM(v), (ventral) premotor cortex; PP, planum polare; PT, planum temporale; SII, secondary somatosensory cortex; (pre)SMA, (pre)supplementary motor area; STG, superior temporal gyrus; STS, superior temporal sulcus; ROI, region of interest

model to investigate the function and plasticity of the auditory and the motor cortex (Munte et al., 2002; Schlaug, 2001). The combination of proficiency in the auditory and the motor modality, however, makes musicians particularly interesting for the studying of interaction and coordination between both modalities. The information flow between sensory processing and motor planning areas is crucial in music performance (Janata and Grafton, 2003). Fast feedforward and feedback connections are required to coordinate auditory input and motor output (Bangert and Altenmüller, 2003). Furthermore, these connections depend on cortical processing circuits which are capable of transforming auditory information into a code that is appropriate for use by the motor system and vice versa.

An impressive amount of data about visuo-motor transformation processes in humans and monkeys has been published (Caminiti et al., 1991; Ellermann et al., 1998; Grefkes et al., 2004; Rizzolatti et al., 1996), reviewed by Burnod et al. (1999). A preeminent structure consistently appearing in these studies is the premotor cortex. However, little is known about comparable audio-motor transformation centers so far (Hickok and Poeppel, 2000; Hickok et al., 2003). In the context of vocal performance, Hickok et al. (2003) carried out an interesting analysis to examine an audio-motor network. fMRI data were recorded during a passive listening task and during an active auditory rehearsal task in order to reveal cortical areas involved in perception and production of speech and singing. Only brain areas being active in both tasks were considered to be audio-motor integration areas. Hickok et al. (2003) identified bilateral premotor cortex (PM), bilateral inferior frontal gyrus (IFG) and an area in the posterior part of the Sylvian fissure in the left hemisphere as belonging to the above-mentioned audio-motor network. Apart from that, the left superior temporal sulcus (STS) supported the speech task while the music task recruited the contralateral STS.

Most of the previously published studies on instrumental music performance in professionals or amateurs focused either on music perception or instrument playing. Recent studies investigated brain activation on musical motor performance (Lotze et al., 2003; Meister et al., 2004). As expected, a wide range of primary, secondary (premotor cortex (PM), supplementary motor area (SMA)) and other motor and somatosensory areas (e.g., basal ganglia, cerebellum) were involved. Interestingly, Lotze et al. (2003) also demonstrated differences between amateurs and professionals in the primary and secondary auditory cortices. Although some studies had been set out to study combined auditory and motor control processes (Kristeva et al., 2003; Parsons et al., 2005), only very few of them focused on the interaction between both modalities. To our knowledge there is only one study which consequently addresses this issue (Bangert et al., 2001, 2003). In this study DC-EEG scalp maps recorded from piano novices during an audio-motor task become increasingly similar to the maps of professional pianists during the course of an audio-motor training. Haueisen and Knösche (2001) and Popescu et al. (2004) used a different approach to address audio-motor interaction. These two MEG studies observed activation in motor areas during pure auditory music stimulation in musicians (the former) or in non-musicians (the latter).

The results imply either direct or indirect connectivity between auditory and motor areas.

All the aforementioned studies investigating audio-motor interactions are based on electrophysiological recordings. The high temporal resolution of these methods is an advantage for the discovery of fast interactions between the modalities of interest. However, imaging technologies like PET or fMRI benefit from higher spatial resolution. Increased spatial resolution may be crucial to distinguish between primary and secondary sensory and motor structures. Furthermore, precise localization information helps to decide whether involuntary motor activity in musicians is indeed related to purposeful finger movement (focus of activity in hand areas) rather than unspecific motor activity which is not constrained to areas usually activated by finger movements (e.g., the urge of Jazz listeners to tap the rhythm of the music with their limbs). The tendency to react to music and rhythmic sound by tapping, drumming or even dancing is known from many cultures. However, to our knowledge there is no systematic neurophysiological study on involuntary motor activity induced by music which is not specific to a certain body part.

The value of studying music and in particular highly trained musicians as a model for cortical plasticity has been increasingly recognized in the last decade. Several anatomical and functional studies examined the effect of plastic changes due to intensive musical training. Increased grey matter volume for musicians was found in the anterior corpus callosum (Schlaug et al., 1995), the cerebellum (Hutchinson et al., 2003; Schlaug, 2001) and in primary and secondary somatosensory and motor areas (Gaser and Schlaug, 2003). All these brain regions play an important role in either fine motor control or bimanual information transfer, both vital processes for music performance. A seminal MEG study (Elbert et al., 1995) showed that fingers of the left hand of violinists show stronger representation by means of signal amplitude in the primary somatosensory cortex than those of a control group. The same method was used to reveal increased auditory cortical representations for musical timbre in violinists and trumpeters relative to non-musicians (Pantev et al., 2001). fMRI studies, however, showed rather a decrease of intensity of activation in motor areas in musicians vs. non-musicians. Further studies observed weaker activity in primary and secondary motor areas (primary motor area (M1), supplementary motor area (SMA), preSMA and cingulate motor area (CMA)) for pianists compared to non-musicians in either bimanual (Jancke et al., 2000b) or unimanual piano playing like tapping tasks (Hund-Georgiadis and von Cramon, 1999). Even the comparison of professional vs. amateur violinists during the performance of a Mozart concerto by Lotze et al. (2003) revealed mainly stronger activity in motor areas for the amateurs. The lower activity in cortical motor control areas has commonly been attributed to a diminished neural effort needed to perform a particular motor task. Finally, Stewart et al. (2003a,b, 2004) showed changes in activity of cortical areas in the parietal cortex after laymen learned to read and play music. The observed activity highlighted the involvement of a well known visuomotor transformation area in the translation of visually perceived musical notes into a motor program for key presses.

The functional imaging studies outlined in this section highlight the potential of music training to modify human

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