The parietal opercular auditory-sensorimotor network in musicians: A resting-state fMRI study

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ABSTRACT

Auditory-sensorimotor coupling is critical for musical performance, during which auditory and somatosensory feedback signals are used to ensure desired outputs. Previous studies reported opercular activation in subjects performing or listening to music. A functional connectivity analysis suggested the parietal operculum (PO) as a connector hub that links auditory, somatosensory, and motor cortical areas. We therefore examined whether this PO network differs between musicians and non-musicians. We analyzed resting-state PO functional connectivity with Heschl's gyrus (HG), the planum temporale (PT), the precentral gyrus (preCG), and the postcentral gyrus (postCG) in 35 musicians and 35 non-musicians. In musicians, the left PO exhibited increased functional connectivity with the ipsilateral HG, PT, preCG, and postCG, whereas the right PO exhibited enhanced functional connectivity with the contralateral HG, preCG, and postCG and the ipsilateral postCG. Direct functional connectivity between an auditory area (the HG or PT) and a sensorimotor area (the preCG or postCG) did not significantly differ between the groups. The PO's functional connectivity with auditory and sensorimotor areas is enhanced in musicians relative to non-musicians. We propose that the PO network facilitates musical performance by mediating multimodal integration for modulating auditory-sensorimotor control.

1. Introduction

Auditory-sensorimotor coupling is critical for musical performance, during which auditory and somatosensory feedback signals are used to ensure desired motor outputs. Previous studies have revealed that listening to music evokes activity in the sensorimotor cortex. One study that utilized magnetoencephalography (MEG) revealed that listening to piano music evoked neuronal activity in the contralateral motor cortex in well-trained pianists (Haueisen & Knösche, 2001). In musicians, this enhanced auditory-motor coupling seems to be associated with involuntary movements of body parts (e.g., fingers for pianists) triggered by listening to a piece of music performed by a well-trained musician (Haueisen & Knösche, 2001). Similarly, a functional magnetic resonance imaging (fMRI) study revealed that activity in auditory and sensorimotor cortical areas during a passive listening task was stronger in musicians than in non-musicians (Bangert et al., 2006). The activation of the sensorimotor cortex is believed to reflect simulation or mirror-neuron-like activity representing hand movements that occur while playing the piano. In fact, mirror-neuron-like activity has been observed even in non-musicians listening to a piece of piano music that

they had recently been trained to play (Lahav, Saltzman, & Schlaug, 2007). Furthermore, resting-state fMRI studies have indicated that compared to non-musicians, musicians exhibit stronger functional connectivity between the primary auditory cortex and primary motor cortex (Luo et al., 2012), stronger right-side functional connectivity between the auditory cortex and ventral premotor cortex (PMC), and reduced trans-hemispheric connectivity between hand-controlling motor areas (Palomar-García, Zatorre, Ventura-Campos, Bueichekú, & Ávila, 2017). These findings suggest that musicians have a selectively enhanced network involved in auditory-sensorimotor integration. The network responsible for the integration of auditory/somatosensory information and motor commands is thought to include auditory areas such as Heschl's gyrus (HG) and the planum temporale (PT), as well as sensorimotor regions such as the precentral gyrus (preCG) and postcentral gyrus (postCG). However, the functional connectivity of this network has yet to be compared between musicians and non-musicians.

A stepwise functional connectivity analysis of the visual, auditory, and somatosensory cortices with resting-state fMRI data obtained from healthy young adults revealed convergent connections between these cortices and several brain regions (Sepulcre, Sabuncu, Yeo,

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Liu, & Johnson, 2012). Furthermore, this analysis suggested that functional hubs may be located in the opercular/insular regions and that the parietal operculum (PO) is a connector hub that links auditory, somatosensory, and motor areas (Sepulcre et al., 2012). This connectivity is consistent with that observed in previous functional and anatomical studies of the PO (Eickhoff et al., 2010). Researchers have argued that this network might also mediate a more direct link between auditory inputs and motor outputs during language processing, thereby bypassing Wernicke's and Broca's areas (Sepulcre, 2015). Integration of auditory, motor, and somatosensory information is critical for musical performance, during which auditory and somatosensory feedback are used to ensure desired motor outputs (Zatorre, Chen, & Penhune, 2007). Given the largely overlapping activation of brain regions involved in language and music (Brown, Martinez, & Parsons, 2006; Koelsch et al., 2002; Musso et al., 2015), the PO's role as a connector hub may not be restricted to language processing. The PO may also mediate the integration of auditory and sensorimotor processing during musical performance.

The functions of the operculum remain unclear because the operculum has not been investigated as intensively as other cortical and subcortical areas have. The operculum is located in the cerebral cortex adjacent to the Sylvian fissure and crosses the frontal, temporal, and parietal cortices (Chen et al., 1995). Recent studies suggest that the central operculum and insula, which are interconnected and appear to work cooperatively, are involved in music-related emotional processing (Gebauer, Skewes, Westphael, Heaton, & Vuust, 2014). These results are consistent with those of a previous study that reported that a patient with a central opercular/insular lesion did not emotionally respond to music (Griffiths, Warren, Dean, & Howard, 2004). Rhythm perceptions activate the precentral operculum and ventral premotor cortex (PMC) in a manner dependent on preferred rhythms and tempos (Kornysheva, von Cramon, Jacobsen, & Schubotz, 2010). A recent meta-analysis of studies using auditory stimuli, including music, further revealed coactivation of the Rolandic or pericentral operculum and the PMC (Neumann, Lotze, & Eickhoff, 2016). This opercular region is activated during both singing and speaking, though it is more strongly activated during the former (Özdemir, Norton, & Schlaug, 2006). The PO comprises the parietal ventral and secondary somatosensory areas and is mainly associated with higher-order somatosensory processing (Eickhoff et al., 2010). Its involvement in music was suggested in previous studies that reported PO activation in subjects performing or listening to music. For example, fMRI studies revealed that the PO is activated in opera singers during actual and imagined singing of an Italian aria (Kleber, Birbaumer, Veit, Trevorrow, & Lotze, 2007) and in untrained participants listening to pleasant music (Koelsch, Fritz, Cramon, Müller, & Friederici, 2006). Another fMRI study reported activation of the PO and supplementary motor area in subjects playing a plastic keyboard, which suggests that the PO provides a link between the somatosensory cortex and other modality-specific cortices, particularly the auditory cortex (Baumann et al., 2007). Collectively, these findings suggest that the PO plays an important role in musical performance.

We hypothesized that musicians and non-musicians differ in PO connectivity with auditory and sensorimotor cortical areas. To test this hypothesis, we analyzed resting-state PO functional connectivity with the HG, PT, preCG, and postCG in 35 musicians and 35 non-musicians.

2. Materials and methods

2.1. Ethical issues

Our study procedures were approved by the ethics committees of Sophia University and Juntendo University. All participants provided written informed consent prior to participation.

2.2. Participants

We recruited 70 university students majoring in either music (n = 35; ages: 18–27 years; mean age: 21.7 years) or in non-musical disciplines (n = 35; ages: 18–27 years; mean age: 21.0 years). All participants were healthy, right-handed Japanese women with no histories of neurological or neuropsychiatric disorders. We recruited only women because most Japanese university music students are woman, and the resultant difficulty in recruiting male music students could have introduced gender bias. The music students had begun their musical training at 3–5 years of age and had continued practicing music through to the initiation of this study. These students specialized in classical music for various instruments, including the piano, violin, cello, and clarinet. The non-musicians' majors were diverse and included literature, philosophy, psychology, economics, science, and engineering. All participants completed the imaging experiment.

2.3. Image acquisition

We acquired whole-brain images with an Achieva 3.0-tesla MRI scanner (Philips, Amsterdam, the Netherlands) with a 32-channel head coil. For anatomical reference, we collected high-resolution T1∗-weighted images from the participants with a three-dimensional magnetization-prepared rapid acquisition gradient echo sequence (repetition time [TR] = 15 ms, echo time [TE] = 3.3 ms, flip angle = 10°, 180 sagittal slices, voxel size = 1 mm × 1 mm × 1 mm). The image acquisition time was 3 min 31 s.

We collected blood oxygen level-dependent fMRI data while the participants rested with their eyes closed. We used a T2∗-weighted gradient-echo-planar imaging sequence (TE = 30 ms, TR = 2000 ms, field of view = 240 mm × 240 mm, matrix = 64 × 64, flip angle = 90°, 33 axial slices, voxel size = 3.75 mm × 3.75 mm × 4.00 mm). Each session consisted of 200 scans. The image acquisition time was 6 min 40 s.

2.4. Preprocessing

The imaging data were preprocessed with the CONN toolbox, version 16.b (Whitfield-Gabrieli & Nieto-Castanon, 2012), for MATLAB R2016b (MathWorks, Natick, MA). The fMRI data were co-registered to each participant's T1 image. The first four volumes were discarded, and the remaining 196 were preprocessed. Slice timings were corrected according to slice orders. The fMRI data were realigned and subsequently normalized to the standard Montreal Neurological Institute template as implemented in Statistical Parametric Mapping software (Wellcome Trust Centre for Neuroimaging, London, United Kingdom; http://www.fil.ion.ucl.ac.uk/spm/). Head movement artifacts were removed with the Artifact Detection Tools scrubbing procedure (McGovern Institute for Brain Research, Cambridge, MA; www.nitrc.org/projects/artifact_detect/). Signal contributions from white matter, cerebrospinal fluid, and six micro head movement parameters were regressed out of the data. The fMRI data were bandpass-filtered at 0.008–0.09 Hz. All functional images were spatially smoothed using a Gaussian filter kernel (full width at half maximum = 8 mm) for seed-to-voxel connectivity analysis but not for region of interest (ROI)-to-ROI connectivity analysis.

2.5. Analyses

We constructed a model of the auditory-sensorimotor network comprising the HG, PT, preCG, and postCG for between-group comparisons of functional connectivity. We performed ROI-to-ROI analysis on this model with the CONN toolbox. We calculated Pearson's correlation coefficients between the activation time course of the PO and those of the HG, PT, preCG, and postCG. The boundaries of these ROIs were defined in the CONN toolbox based on the Harvard-Oxford Atlas (Bohland, Bokil, Allen, & Mitra, 2009). Positive and negative