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Research report

Reorganization of the thalamocortical network in musicians

Shoji Tanaka [a,*], Eiji Kirino [b,c]

[a] Department of Information and Communication Sciences, Sophia University, Tokyo 102-0081, Japan
[b] Department of Psychiatry, Juntendo University School of Medicine, Tokyo 113-8431, Japan
[c] Juntendo Shizuoka Hospital, Shizuoka 410-2211, Japan

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ABSTRACT

The cortico-thalamocortical network is relevant to music performance in that the network can regulate sensitivity to afferent input or sound, mediate the integration of multimodal information required for the performance, and play a role in skilled performance control. We, therefore, predicted that this network would be reorganized via musical training-induced neuroplasticity. To test this hypothesis, we analyzed resting-state functional connectivity of the thalamocortical network in musicians (n = 35) and nonmusicians (n = 35). The seed-to-voxel functional connectivity analysis of the left thalamus seed showed enhanced connectivity voxels in the precuneus/posterior cingulate cortex (PCC) in musicians compared with nonmusicians. Region of interest (ROI)-to-ROI functional connectivity analysis showed that the auditory areas were also more strongly connected with the left thalamus in musicians. Discriminant analysis using the ROI-to-ROI functional connectivity data of the precuneus/PCC and auditory areas as predictors yielded an 87% correct discrimination of musicians from nonmusicians. Therefore, we can conclude that, as a consequence of long-term musical training, musicians have a characteristically organized thalamocortical network. The precuneus and PCC are principal nodes of the default mode network and play a pivotal role in the manipulation of mental imagery. We propose that the reorganized thalamocortical network in musicians contributes not only to higher sensitivity to sound but also to the integration of mental imagery with sound, which are both presumed to be important for better music performance.

1. Introduction

1.1. The thalamocortical network

The thalamocortical network is critically involved in a vast majority of brain functions, such as cognition, language, music, and behavior (De Witte et al., 2011). The thalamus sends afferent fibers to and receives efferent fibers from many cortical areas, including not only primary sensory cortices but also motor and association cortical areas (Sherman and Guillery, 2011; Ward, 2013). In the interaction between the thalamus and the cortex, however, different interacting schemes emerge from the distinct architecture of the thalamocortical network (Guillery and Sherman, 2002; Sherman and Guillery, 2011; Sherman, 2016). One of the roles of the thalamocortical network is to relay peripheral sensory signals to the primary sensory cortex (McCormick and Bal, 1994). This is mediated by the first-order thalamic relay, terminating in layer 4 of the cortex (Guillery and Sherman, 2002; Sherman and Guillery, 2011; Sherman, 2016). The thalamocortical network has also been suggested to mediate higher-order relay (Guillery and Sherman, 2002; Sherman and Guillery, 2011; Sherman, 2016). The glutamatergic neurons in layer 5 of the cortex send axons to the thalamus. The signal is then sent back to the cortex by the higher-order thalamic relay. This cortico-thalamocortical pathway is suggested to play a role in ongoing cortical functioning and in monitoring of motor output via efference copy (Sherman and Guillery, 2011; Sherman, 2016). The corticothalamocortical pathway is thus considered to mediate dynamic cortico-cortical association through communication between different cortical areas via the thalamus.

Interestingly, studies have suggested that the corticothalamocortical network also mediates higher functions such as language processing and memory retrieval (Crosson, 2013; Llano, 2013; Pergola et al., 2013; Bohsali et al., 2015). A recent diffusion-weighted magnetic resonance imaging (MRI) study demonstrated structural connections between Broca's area and the thalamus (Bohsali et al., 2015). The authors argued that this thalamocortical network "may serve to selectively recruit cortical regions storing multimodal features of lexical items and to bind them together during lexical-semantic processing" (p. 80) (Bohsali et al., 2015). This study further suggested information transfer and modulation

* Corresponding author.
E-mail address: tanaka-s@sophia.ac.jp (S. Tanaka).

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between Brodmann areas 44 and 45, subregions of Broca's area. The corticothalamocortical network is also involved in memory functions. Lesions in the thalamus cause amnesia, diencephalic amnesia, and accompanying severe anterograde episodic memory impairments (Kopelman, 2015). Diencephalic amnesia is characterized by impairments in memory of temporal sequence, whereas medial temporal lobe amnesia is characterized by impairments in spatial memory (Kopelman, 2015). Memory impairments caused by thalamic lesions are not restricted to episodic memory. Semantic retrieval is also disrupted by lesions in the thalamus, particularly in the left medial thalamus (Pergola et al., 2013). The dynamics of the corticothalamocortical circuit have been studied computationally, demonstrating the capability of this circuit to manipulate spatial working memory representation (Miyashita et al., 2003; Tabuchi and Tanaka, 2003).

1.2. The thalamocortical network for music

Involvement of the precuneus and posterior cingulate cortex (PCC) in musical processing has been suggested (Spada et al., 2014; Raglio et al., 2015; Tanaka and Kirino, 2016a). These brain regions process mental imagery (Cavanna and Trimble, 2006; Gardini et al., 2009), which requires the integration of multimodal information. The integration of multimodal information appears to be critical for music performance. A recent EEG study employing an auditory oddball task with congruent/incongruent visual stimuli demonstrated that musicians evoked larger mismatch negativity and P300 event-related potentials than nonmusicians, which is suggestive of more efficient audiovisual integration in musicians (Nichols and Grahn, 2016). Different dimensions of musical information, such as rhythm and melody, are processed in different cortical and subcortical regions (Bengtsson and Ullén, 2006). In addition to corticocortical association networks, therefore, the corticothalamocortical network would also mediate the integration of different kinds of information (Sherman and Guillery, 2011). Recently, Musacchia and colleagues (Musacchia et al., 2014) reviewed the literature to investigate the mechanism underlying the integration of separately represented musical tonal and rhythmic information, as the thalamocortical network conveys these two types of information separately to the cortex. Based on the "core" and "matrix" model of the thalamocortical network (Jones, 1998, 2001), they proposed that acoustic information forms a driver input to layer 4 of the auditory cortex while rhythmic information forms a modulatory input to the supragranular layers. Thus, rhythm modulates the neuronal dynamics of the auditory cortex through the corticothalamocortical network.

1.3. The network for skill learning

Skilled motor control is a critical feature of music performance, in which the cortico-striato-pallido-thalamocortical (CSPTC) network plays a central role (Graybiel, 2005). In the CSPTC network, the basal ganglia, receiving converging cortical efferents, provide input to the thalamus, which sends afferents to cortical areas through the thalamocortical network (Alexander et al., 1986; Goldberg et al., 2013). There are several CSPTC networks working in parallel, each of which corresponds to a different function (Alexander et al., 1986). For example, the CSPTC network with the putamen as the striatal node is responsible for skill learning and motor control (Graybiel, 2005). A recent functional MRI (fMRI) study investigating the corticostriatal network found that musicians have a more selective CSPTC network with a smaller degree of connectivity, compared with nonmusicians (Tanaka and Kirino, 2016b). To the best of our knowledge, the reorganization of the CSPTC network in musicians has never been reported elsewhere. However, this result does not necessarily mean that skill is not important in music performance. Rather, this result suggests that the selective network is a consequence of network reorganization optimized for music performance. This finding is consistent with previous anatomical MRI studies showing a smaller volume of the striatum in musicians as well as in ballet dancers (Hänggi et al., 2010; James et al., 2014; Sato et al., 2015).

1.4. Hypothesis

The corticothalamocortical network is relevant to music performance in that the network can regulate sensitivity to afferent input or sound, mediate the integration of multimodal information relevant to performance, and play a role in skilled performance control as a part of the CSPTC circuit. Therefore, we predicted that this network would be reorganized as a consequence of long-term musical training. To test this hypothesis, we examined the resting-state functional connectivity of the thalamocortical network in musicians and nonmusicians.

2. Results

2.1. Voxel functional connectivity

We analyzed seed-to-voxel functional connectivity of the thalamus. The functional connectivity of the left thalamus showed greater group differences than that of the right thalamus. Figs. 1 and 2 show the functional connectivity maps of the left thalamus. The group comparison showed that a region extending across the precuneus and PCC had significantly stronger connectivity with the left thalamus in musicians compared with that in nonmusicians [$T(1,68) \geq 3.21$, $k = 854$, $p = 0.000043$, family-wise error (FWE) corrected]. There was no region whose connectivity with the left thalamus was weaker in musicians than in nonmusicians. For the right thalamus, there was no region showing a significant between-group difference in functional connectivity with the right thalamus.

2.2. Network organization

ROI-to-ROI functional connectivity analysis provided the connectivity matrix of the thalamus with the remaining 130 ROIs. First, we compared the connectivity between musicians and nonmusicians. The ROIs showing larger group differences in the functional connectivity with the left thalamus are listed in Table 1. Then, the 130 connections were subjected to hierarchical cluster analysis; from this, we extracted groups of functional connections that can be considered to work cooperatively (Fig. 3). The clusters in musicians included: (i) the precuneus/PCC, hippocampus, and parahippocampal cortex; (ii) the auditory and opercular/insular regions; (iii) the anterior cingulate cortex (ACC), putamen, pallidum, frontal operculum (FO), inferior frontal gyrus (IFG), and anterior supramarginal gyrus (aSMG); (iv) the caudate nucleus, paracingulate gyrus, amygdala, nucleus accumbens, superior frontal gyrus (SFG), and frontal pole (FP); (v) cerebellar regions; and (vi) visual areas. The first and second clusters differed between musicians and nonmusicians. In musicians, the first cluster was merged with the temporal pole (TP), inferior temporal gyrus (ITG), temporal fusiform cortex (TFusC), and amygdala. The second cluster in nonmusicians did not include the planum temporale (PT) or central operculum (CO).

2.3. Discriminant analysis

A quadratic discriminant analysis was performed using estimated functional connectivity data as the predictors of member-