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Neural correlates of professional classical singing

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We evaluated cerebral activation maps of 43 subjects with respect to their classical singing skills. Professional opera singers, music conservatory vocal students, and medical students overtly sung parts of an Italian aria in a sparse sampling functional magnetic resonance (fMRI) experiment. Professional opera singers compared to medical students revealed increased activation in bilateral dorsolateral prefrontal cortex (DLPFC) and inferior parietal lobe (IPL, both pronounced in the right hemisphere), right primary somatosensory cortex (S1) in the somatotopic representation of the articulators, but also in the cerebellum and the thalamus. Vocal students compared to medical students revealed bilateral increased activation in the IPL, the DLPFC, and S1. Opera singers compared to vocal students showed increased activation in the left caudate nucleus, the left cerebellum, bilateral DLPFC, and the medial dorsal and ventrolateral thalamus. A subsequent regression analysis was performed with the amount of weekly singing practice and showed practice dependent activation of DLPFC, bilateral IPL (pronounced in the right hemisphere), and S1. A further regression analysis excluding the opera singers showed left lateralized activation in the same regions. We conclude that experienced singers developed a specialized network for enhanced somatosensory processing and performance monitoring as well as motor sequence attention.

Keywords: neuroimaging; classical singing; musicians; non-musicians; functional brain activation

Several neuroimaging studies have revealed experience dependent plasticity in the primary motor and somatosensory cortices, the cerebellum, the anterior corpus callosum, as well as the fiber tract organization in white matter of instrumental musicians (Bengtsson *et al.* 2005, Gaser and Schlaug 2003, Hutchinson *et al.* 2003). Functional differences were often characterized by reduced recruitment of premotor and supplementary motor areas and a more circumscribed, as well as enhanced activation, in areas related to motor execution (Lotze *et al.* 2003). Keyboard and string players are among the musicians most often studied, mainly because of the exceptional demands on their manual dexterity. Classical singing, however, has largely been neglected.

In contrast to instrumental playing, which involves largely fine motor control of peripheral muscle groups, singing and particularly singing of classical music requires more body-core centered motor and anatomic activity of vital bodily importance, representing a complex interplay of laryngeal, respiratory, and articulatory activity (Jurgens 2002).

Sensory feedback is especially crucial for vocal control. Lesions of the sensory superior laryngeal nerve result in hoarseness and a drop of fundamental frequency (Shiba *et al.* 1995) while information on the current air volume of the lungs is required for the generation of vocal motor patterns (Nakazawa *et al.* 1997). The inhibition of sensory information from the supralaryngeal tract results in impaired articulation (Prosek 1975). Furthermore, auditory feedback is necessary for pitch accuracy (Murbe *et al.* 2002).

In a first functional magnetic resonance imaging (fMRI) study that involved professional singing, we compared overt and imagined singing of an Italian aria (Kleber *et al.* 2007). Based on the results of this study, we aimed to identify neural activation patterns of overt singing performance related to the singers' level of proficiency. We proposed that areas involved in sensory feedback control and performance monitoring will show enhanced activation in experienced singers.

METHOD

Participants

A total of 43 right handed subjects without reported history of neurological or psychiatric disease participated. Ten professional opera singers (mean age=38.07 years, range=30-44 years; 7 female), 22 professional vocal students (mean age=25.22 years, range=20-30 years; 15 female), and 11 medical students (mean age=23.54 years, range=23-29 years). Medical students had no or very little amateur singing experience (i.e. 1-5 hours per week, mean=2.6 h). Vocal students reported an average of 9.77 years singing experience (range=4-23; based on their first professional singing lesson), and 18 hours singing practice per week (range=8-30). Opera singers reported 21.03 years of singing experience (range=14-28), and 27.6 hours singing practice per week (range=20-42).

Materials

The fMRI technique applied corresponds to the one previously reported for overt and imagined singing (Kleber *et al.* 2007). Whole head scans (66 volumes per block) were performed with a 1.5 Tesla whole body Scanner (Siemens Vision) using echo planar imaging (EPI; TE: 40 ms; TR: 10 s, TA: 3 s, 36 transversal slices of 3 mm thickness and 1 mm gap, matrix 64*64). A sparse sampling method avoided movement artifacts and allowed undisturbed monitoring of own voice during singing.

Procedure

Subjects overtly sung six phrases from the Italian aria *Caro mio ben* (by Tommaso Giordani) in an fMRI scanner, performing each phrase separately after a visual cue. The aria's phrase structure fits naturally the sparse sampling technique employed. Subjects first rehearsed the task outside the scanner and then again within the scanner prior to the actual measurement. Successful task accomplishment was monitored via loud speakers.

RESULTS

Statistical maps (fixed effect) were calculated for each subject. First level contrast images of each subject were then used for group statistics calculated as random effects analysis at the second level. A one-way analysis of variance (ANOVA) with three groups (medical students, vocal students, and opera singers) was performed. Nonsphericity correction was applied to account for unequal variances due to the different group sizes. For the analysis of differential effects between groups a small volume correction was performed with apriori defined pre-selected regions of interest (ROI) based on previous results (Kleber *et al.* 2007). The statistical threshold was set as $p<0.001$ uncorrected. A second-level regression analysis explored individual differences in brain activity related to the amount of time spent with singing per week.

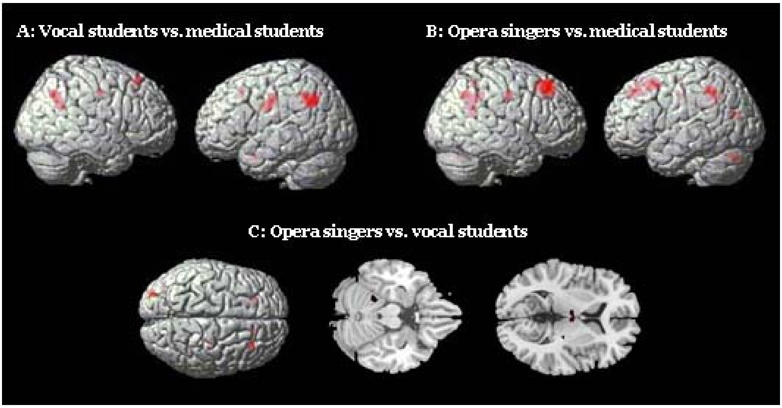

Figure 1. Examples of activation sites (p<0.001, uncorrected). (See full color version at www.performancescience.org.)

Vocal students versus medical students

Examples of activation sites are given in Figure 1a. We detected bilateral activation in the IPL (BA39/40, including the supramarginal and angular gyrus), the DLPFC (BA8/9), the bilateral primary somatosensory cortex (S1) in the somatotopic representation of the articulators, but also the left temporal pole. A subsequent regression analysis including only vocal and medical students was performed with the amount of hours spent with singing per week. Increased activation involved IPL bilaterally (BA39/40), the DLPFC (BA8/9), the left primary somatosensory cortex (S1) in the representation of the articulators, and the left temporal pole.

Opera singers versus medical students

Examples of activation sites are given in Figure 1b. We detected increased activation in the DLPFC (BA8/9, superior and middle frontal gyrus), the IPL bilaterally (BA 39/40), the primary somatosensory cortex (S1) bilaterally in the somatotopic representation of the articulators, the cerebellum (Larsell's lobule HVI and HVII), the occipital lobe (BA19), the left temporal pole and the thalamus (posterior ventral lateral nucleus).

Opera singers versus vocal students

Examples of activation sites are given in Figure 1c. We detected increased activation in the basal ganglia (left caudate nucleus), the left cerebellum

(Larsell's lobules IV/V, VII), the DLPFC (BA 8/9, middle and superior frontal gyrus), and the anterior thalami (medial dorsal and ventrolateral nuclei).

Regression analysis over all subjects: Weekly singing time

The time spent with singing per week was correlated with increased activation in the DLPFC with additional superior frontal medial cortex activation, IPL (most pronounced in the right angular and supramarginal gyrus), the right primary somatosensory cortex (S1) in the representation of the articulators, the left temporal pole, the occipital cortex (BA19), the basal ganglia, and the left thalamus (pulvinar nucleus).

DISCUSSION

We proposed that increased auditory and proprioceptive processing for vocal control in expert singers would lead to enhanced and circumscribed functional activation of areas related to somatosensory and auditory processing. Our analyses did not show enhanced auditory activation related to singing proficiency. This could be explained by diminished activity in the superior temporal gyrus that is often found during self-perception of the own voice (Houde *et al.* 2002), i.e. the auditory cortex attenuates its sensitivity during singing production and modulates its activity as a function of the expected acoustic feedback, which may cover effects related to musical ability.

However, in accordance with our hypothesis singing experience revealed enhanced activation of primary somatosensory cortex in the somatotopic representation of the articulators (Lotze *et al.* 2000).

Sensory guided adjustments of the singer's articulators are used to modulate the resonance characteristics of the vocal apparatus, which eventually results in desired qualitative changes of the vocal sound in classical singing (Sundberg 1974). The primary somatosensory cortex (S1) is thought to be part of a feedback control system for somatosensory error detection and thus contributes to accurate feedforward motor commands in classical singing (Guenther *et al.* 2006). Somatosensory state cells in S1 are supposed to process the actual somatosensory state during sound production while somatosensory error cells in the IPL detect if this state matches the desired somatosensory goal that was previously learned throughout the development of singing skills (Guenther *et al.* 2006). Error processing during singing with pitch-shifted auditory feedback has also shown to involve the IPL (Zarate and Zatorre 2005). The IPL in general is thought to contribute to verbal working memory and probably reflects a store for phonological and non-verbal short-term information (Zatorre 2001). It has shown to be involved in vibrotactile frequency discrimination and tongue movements (Soros *et al.* 2007, Watanabe *et al.* 2004) and utilizes proprioceptive feedback from the articulators for the word formation process (Jurgens 2002). This is achieved by integrating sensory and motor signals in order to accomplish sensorimotor transformations necessary for motor planning and sensory guidance of movements (Fogassi and Luppino 2005). Motor sequences require also a constant redirection of motor attention, which is attributed to the supramarginal gyrus, a subdivision of the IPL (Rushworth *et al.* 2003) that was more active in vocal students and opera singers. The angular gyrus, also increasingly active in experienced singers, has been attributed to action awareness (Farrer *et al.* in press), which refers to the processing and comparison of action intentions and action consequences. This perceived discrepancy between movement intention and consequence also involved the DLPFC. Both areas were most active in professional opera singers. The DLPFC is thought to be essential for maintaining a "task set," i.e. a representation of task goals held in memory against which one can evaluate and monitor one's own performance (Fassbender *et al.* 2004). It is specifically involved in goal-directed selection and response generation (Mitchell *et al.* 2005) and implicated in the mental preparation of a forthcoming sequential action (Pochon *et al.* 2001).

Taken together, S1, IPL and the DLPFC seem to work in concert in a feedback control system for accurate fine tuning of feedforward motor commands with regards to the achievement of performance goals in classical singing. This involves also increased attentional abilities for maintaining and manipulating information that was previously processed in posterior sensory cortices (Johnson *et al.* 2007).

Additional activation was found in the cerebellum, basal ganglia, and the thalamus of the most experienced opera singers. The cerebellum is involved in the control of complex motor sequences (Braitenberg *et al.* 1997), probably based on a feedforward prediction of the timing and the use of sensory feedback information to modify and correct subsequent movements (Zatorre *et al.* 2007). Skilled instrumentalists typically exhibit decreased cerebellar activation, probably reflecting enhanced movement efficiency in musicians (Koeneke *et al.* 2004). However, this could also be attributed to the non-musical tasks employed. Thalamic activation was focused in the medial dorsal (projecting to the prefrontal cortex) and the ventrolateral thalamus, which projects to the motor cortex and receives its main input from the cerebellum. Thalamic lesions severely affect speech production (Jurgens 2002). Functional activation related to long-term learning, i.e. when the movements become automatic, has shown to activate increasingly the basal ganglia

(Floyer-Lea and Matthews 2005), which play an important role in motor behavior related to speech (Friederici 2006) but are also involved in learning and memory functions (Packard and Knowlton 2002).

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