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Common parietal activation in musical mental transformations across pitch and time

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A B S T R A C T

We previously observed that mental manipulation of the pitch level or temporal organization of melodies results in functional activation in the human intraparietal sulcus (IPS), a region also associated with visuospatial transformation and numerical calculation. Two outstanding questions about these musical transformations are whether pitch and time depend on separate or common processing in IPS, and whether IPS recruitment in melodic tasks varies depending upon the degree of transformation required (as it does in mental rotation). In the present study we sought to answer these questions by applying functional magnetic resonance imaging while musicians performed closely matched mental transposition (pitch transformation) and melody reversal (temporal transformation) tasks. A voxel-wise conjunction analysis showed that in individual subjects, both tasks activated overlapping regions in bilateral IPS, suggesting that a common neural substrate subserves both types of mental transformation. Varying the magnitude of mental pitch transposition resulted in variation of IPS BOLD signal in correlation with the musical key-distance of the transposition, but not with the pitch distance, indicating that the cognitive metric relevant for this type of operation is an abstract one, well described by music-theoretic concepts. These findings support a general role for the IPS in systematically transforming auditory stimulus representations in a nonspatial context.

Introduction

Every day, we experience many stimuli originating in different sensory contexts. In order to synthesize these inputs for coordinated perception and action, they often must be transformed in a way that shifts (or discards) absolute values, while preserving the relevant internal/intrinsic organization of the information. For example, visuospatial mental transformations, including mental rotation, depend on a network including the posterior parietal cortex (PPC) (reviewed in Jeannerod et al., 1995; Zacks, 2008), an area of multimodal association cortex that receives visual, auditory and tactile information, and is connected with frontal working memory areas and motor planning centers (Frey et al., 2008; Lewis and Van Essen, 2000).

People can also manipulate auditory information, such as when imagining a spoken sentence in different voices, or a tune played with different instruments. Musicians can execute complex auditory mental manipulations, such as transposing a tune to a different key or imagining a piece after undergoing musical variations. Although auditory information is sent to the PPC (Lewis and Van Essen, 2000), little is known about the region's role in transforming auditory representations, especially outside of a spatial context. In two independent recent studies, we found that that two types of musical mental transformation, temporal reversal and pitch transposition, each recruit PPC (Foster and Zatorre, 2010a; Zatorre et al., 2010), despite being neither visual nor spatial. These results suggested that a common neural substrate in the intraparietal sulcus (IPS) may subserve systematic transformations of auditory information.

However, merely observing similar activity is not sufficient to infer common functionality. Our prior work did not use comparable stimuli nor test the same participants, thus precluding direct comparison. Here, we applied functional MRI while musicians performed matched versions of the two melodic transformation tasks (in which the melodic materials were identical and only the transformation differed). The BOLD signal of each individual was examined to determine whether there was a spatial conjunction between activation on the two tasks. We predicted that a common region of IPS would be recruited for temporal and pitch transformation.

A second critical aspect here is to test whether IPS activity is specifically linked to mental transformation or manipulation, and not to other aspects of the task, such as working memory. Key evidence that the IPS is involved in transforming stimulus information during visual mental rotation is that its activity scales as a function of extent of rotation (Gogos et al., 2010). Thus, we predicted that the degree of musical transposition would be associated with higher IPS activity.

Finally, examination of how IPS activation changes with the degree of transposition allows us also to determine the underlying cognitive metric upon which the transformation is effected. Musical transposition may be thought of in terms of either pitch distance or key distance. The pitch distance refers simply to the number of semitones by which notes

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are shifted. Key distance reflects the harmonic "closeness" of the origin and destination keys (Krumhansl, 2004). Because key distance more closely reflects how changes of key are conceived in music theory, we predicted that key distance, rather than pitch distance, would better explain any transposition level-dependent IPS BOLD signal.

Methods

Subjects

We recruited 12 healthy, right-handed musicians (8 male; age 20–37, mean 25 years old). A detailed self-reported history of musical training and other musical experience was obtained from each subject, including estimates of practice hours per week for each year or phase of the participant's musical activities. This information was used to calculate a cumulative measure of hours of musical practice for each subject. Individuals had a minimum of 7 years of training (mean 15 years) and cumulative hours of practice ranged from 6600 to 30,000 (mean 17,000 h). All participants gave their informed consent. Ethical approval was granted by the Montreal Neurological Institute Ethics Review Board.

Stimuli

Stimuli in the tasks consisted of 5-note diatonic melodies with pitches between C4 and E7. The melodies were played with a piano tone sampled from a Steinway Model-C grand piano (http://www.pianosounds.com/) and rendered from MIDI files using TiMidity++ software (http://timidity.sourceforge.net/). All tones were 320 ms in duration, equivalent to eighth notes at a tempo of 93.75 beats per minute. Stimuli were presented binaurally via MRI-compatible headphones (MR Confon, Magdeburg, Germany).

Task conditions

During the functional MRI scans, subjects performed three same–different auditory melodic discrimination conditions: Reversed melodies, Transposed melodies and Control melodies (see example stimuli in Fig. 1). A temporal reversal of a melody is known in music theory as a "retrograde" version and is a device sometimes used in musical composition (Randel and Apel, 1986). Transposition of melodies is commonly used to accommodate a singer's vocal range or the concert tuning of an instrument. In musical composition, melodies may be transposed in an exact or altered form in order to create modulations, harmonies and call-response patterns (Dowling and Harwood, 1986; Randel and Apel, 1986).

Both transformation conditions required a comparison between a sample and a transformed target. Subjects had already practiced these tasks in our laboratory and achieved a minimum performance criterion of 65% on each task. The conditions were presented in randomized 10-trial blocks totaling 40 trials each for the Reversed and Control conditions, and 80 trials for the Transposed condition. Individual trials consisted of two melody presentations. Subjects judged whether the second melody was an exact transformation of the first melody, then indicated their response with the left or right button of a computer mouse. Subjects were instructed to make their response as soon as they heard an alteration, or at the end of the second melody if they heard no alteration. They received no feedback about their responses. On half the trials, the pitch of a single note was changed by up to +/− 4 semitones (median of 1 semitone). The change preserved the melodic contour (the order of upward and downward pitch movement in a melody without regard to magnitude).

Control

No transformation was made to the melodies, so that this was a basic same/different discrimination. The position of the changed note in the altered melodies varied among the last four notes of the second sequence. This condition also served as the 0-level for our parametric analyses of transposition key-distance and pitch-distance.

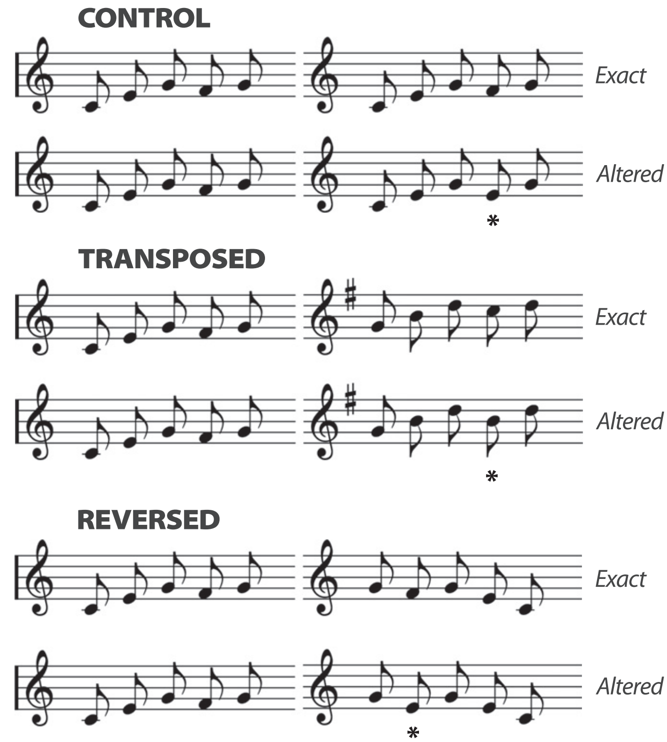

Fig. 1. Examples of task stimuli and pattern alteration in the control, transposed and reversed melody conditions. Asterisks indicate pattern alterations.

Reversed

The notes of the second melody were reversed in time, so that the final note became the first. The position of the changed note in the altered melodies (inexact reversals) varied among the last four notes of the reversed sequence; i.e. the first note of the reversal was always identical to the last note of the target, to avoid comparison of just these two tones in immediate memory.

Transposed

The notes of the second melody were uniformly shifted higher in pitch by 1, 3, 6, 7 or 12 semitones. The position of the changed note in the altered melodies (inexact transpositions) varied between the last two notes of the transposed sequence.

These pitch-distance intervals in the transposition condition corresponded with the key-distance values shown in Table 1. The key-distance index is based on a behavioral key proximity metric developed by Krumhansl (1990). Krumhansl's subjects rated how well different probe pitches completed an "incomplete" musical scale sequence. Put together, these measures formed a profile of the stability of pitches within a given key context. Krumhansl's measure of interkey distance is then arrived at by calculating the correlation of these pitch rating profiles between pairs of keys. This empirical determination of interkey relationships closely replicates the "circle of fifths," a concept used in music theory to represent the harmonic closeness of keys (Krumhansl, 1990). To convert Krumhansl's correlations into a distance metric more easily applicable to our data, we applied a transformation of $KD = (1 - KPC)$, where KD represents our key-distance index and KPC is Krumhansl's key profile correlation for a given pair of keys.

These task conditions have origins in earlier studies in our laboratory, and certain task parameters were changed in the current experiment so that the conditions would be more closely matched. Changing these parameters permitted us to use identical melodic materials between the