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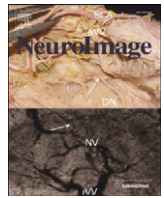
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## Common parietal activation in musical mental transformations across pitch and time

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### ABSTRACT

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.

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### 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 subservise 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  $\pm 4$  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

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

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.

### 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

**Table 1**

Correspondence of pitch distance and key distance values for the transposition levels that were tested. A pitch distance of 0 represents no transposition; this case was tested by the control task. A pitch distance of 12 denotes an octave transposition, which is equivalent to 0 change in key distance. Key distance is computed based on empirical perceptual data from Krumhansl (1990).

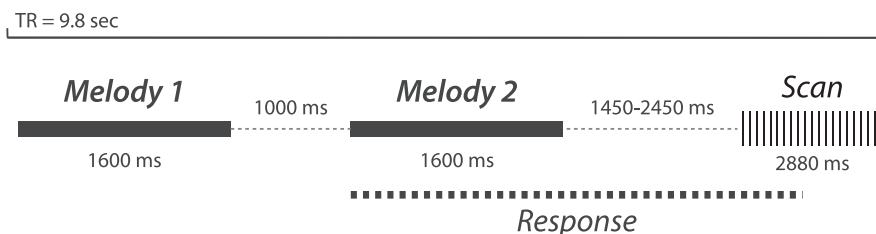
Pitch distance	Key distance
0	0.000
1	1.500
3	1.105
6	1.683
7	0.409
12	0.000

three task conditions, such that they only differed in terms of the transformation applied to the second melody in each stimulus pair. In the earlier version of the reversal task (Zatorre et al., 2010), the melodies were familiar tunes, and were also longer (5–8 notes); in the present reversal task all melodies were novel and 5 notes in duration. In addition, the baseline condition in the previous study consisted of randomly ordered notes from the false reversal pattern, whereas in the current study the baseline condition for both tasks was a same/different melody judgment. In the earlier version of the transposition task (Foster and Zatorre, 2010a), melodies varied between 7 and 10 notes, and the transposition interval was fixed at 4 semitones; in the present experiment all melodies were 5 notes, and the transposition varied across 5 different intervals.

#### fMRI protocol

The subjects underwent functional imaging in a 3 Tesla Siemens Magnetom Trio TIM with a 12-channel head coil. A 1 mm × 1 mm × 1 mm high resolution T1 anatomical was acquired before the two functional runs. For functional magnetic resonance imaging (fMRI), an echo-planar imaging (EPI) T2\*-weighted protocol with a voxel size of 3 mm × 3 mm × 3 mm was used to measure blood oxygenation level dependent (BOLD) signal. We used a sparse sampling (TR = 9.8 s) paradigm to minimize any BOLD effect or auditory masking due to MRI scanning noise (Belin et al., 1999; Hall et al., 1999). Correction for B<sub>1</sub> receive field intensity variation was applied using the scanner's "prescan normalize" feature. Motion correction of the EPI series was performed in the scanner using a combination of prospective acquisition correction (PACE) and offline post-processing.

A diagram of the stimulus and scan timing is found in Fig. 2. The inter-stimulus interval was 1 s. Our intent was to image brain activity associated with the process of transforming the second melody to compare with the first. The timing of stimuli in our experiment ensured that each fMRI scan was most sensitive to the BOLD response during the second melody, assuming a delay to the hemodynamic response function (HRF) peak of about 4 s (Belin et al., 1999). The interval between the stimuli and the scan was jittered by +/- 500 ms to optimize our ability to capture the peak of the hemodynamic response.



**Fig. 2.** Timeline of events during each fMRI trial. The target auditory pattern is followed by a comparison pattern that is an exact transformation (or in the control condition, identical melody), or an altered transformation of the target, and listeners make an exact/altered judgment. Participants are instructed to respond as soon as they hear an alteration, or immediately following the second melody if they hear no alteration.

#### Behavioral analysis

Subjects' accuracy in detecting altered melodies was assessed by signal detection theory, using *A*, a corrected version by Zhang and Mueller (2005) of the *A'* and *A''* non-parametric accuracy measures. We chose to use a signal detection method so that the index would not be affected by response bias. We chose a non-parametric index because some subjects' hit rate on the control task was 1.0, a situation in which the parametric *d'* index is undefined. The *A* index improves on the *A'* method by correctly calculating the average of the minimum and maximum proper receiver operating characteristic (ROC) curves that pass through a point defined by a given hit and false-alarm rate (Zhang and Mueller, 2005). With the present data, we found that the *A* index resulted in values very close to the *A'* method (mean absolute difference of 0.01, Pearson correlation coefficient of 0.999).

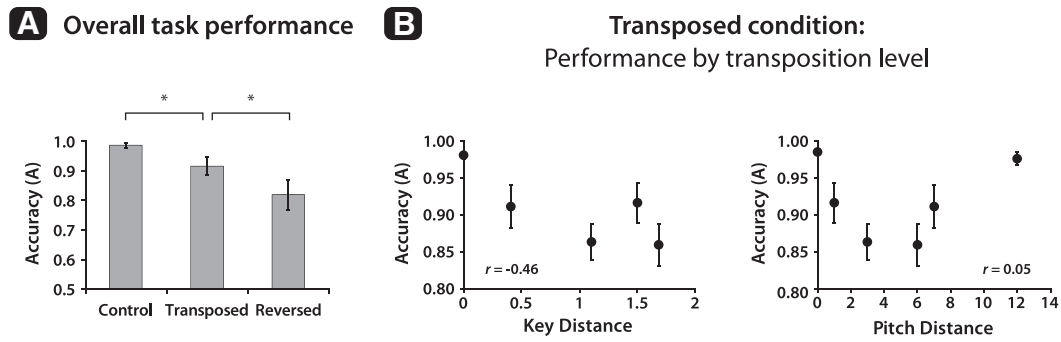
#### fMRI analyses

BOLD signal images were smoothed using a Gaussian kernel (5-mm full width half-maximum). These data were statistically analyzed using *fmrstat*, a suite of Matlab functions that employ the general linear model to analyze functional imaging data (Worsley et al., 2002). Each subject run was fit to a linear model that accounted for stimulus conditions set up in a design matrix corresponding to each acquisition, temporal drift and temporally correlated errors. This yielded the effects, standard deviations and *t* statistics for each run and for each contrast. Task-related BOLD contrasts were performed using only images from trials in which the subject made a correct response, to allow comparison across tasks that differed in overall performance level. Before group statistical maps for each contrast of interest were generated, in-house software was used to non-linearly transform each subject's anatomical and functional images into standardized MNI/ICBM stereotaxic coordinate space, using the non-linearly transformed, symmetric MNI/ICBM 152 template (Collins et al., 1994; Mazziotta et al., 2001; Talairach and Tournoux, 1988).

Statistical thresholds for whole-brain analyses were calculated based on random field theory (Worsley et al., 1996) using the *stat\_threshold* program from the *fmrstat* suite; random field theory corrects for multiple comparisons by taking into account correlations among nearby voxels due to spatial smoothness in the data (e.g., from the Gaussian blurring kernel). For individual within-subject analyses, a whole-brain corrected *P* < 0.05 threshold of *t* > 4.97 was used; for group contrasts, this threshold was *t* > 5.42.

For effects predicted in the IPS region identified in our previous studies (Foster and Zatorre, 2010a; Zatorre et al., 2010), we applied an uncorrected threshold of *P* < 0.005; for within-subject analyses, this corresponded to a threshold of *t* > 2.61 (140 degrees of freedom), and for group analyses, this corresponded to *t* > 2.63 (100 degrees of freedom).

Conjunctions within the IPS region were performed by taking the voxel-wise minimum *t* value across conjoined analyses. The conjunction results were then tested against the "conjunction null hypothesis",



**Fig. 3.** Behavioral performance on the control, transposed, and reversed melody conditions. Accuracy was calculated using A, a non-parametric signal detection index (Zhang and Mueller, 2005). Error bars represent standard error of the mean. (A) Mean performance across subjects on each task. Asterisks mark significant differences at  $P < 0.01$ . (B) Transposition level-dependent accuracy across subjects. Accuracy was calculated at each transposition level, and is plotted separately vs. the key-distance index (left) and pitch distance (right). The data point for 0 key distance in the left plot includes data from both the 0 and 12 pitch distances (refer to Table 1 for the relationship between key distance and pitch distance). The Pearson correlation between distance and accuracy is indicated on each plot.

which entailed using the same critical  $t$ -value determined for single analyses (as above) to determine whether there was significant neural activity across all the conjoined conditions (Nichols et al., 2005).

## Results

### Behavioral

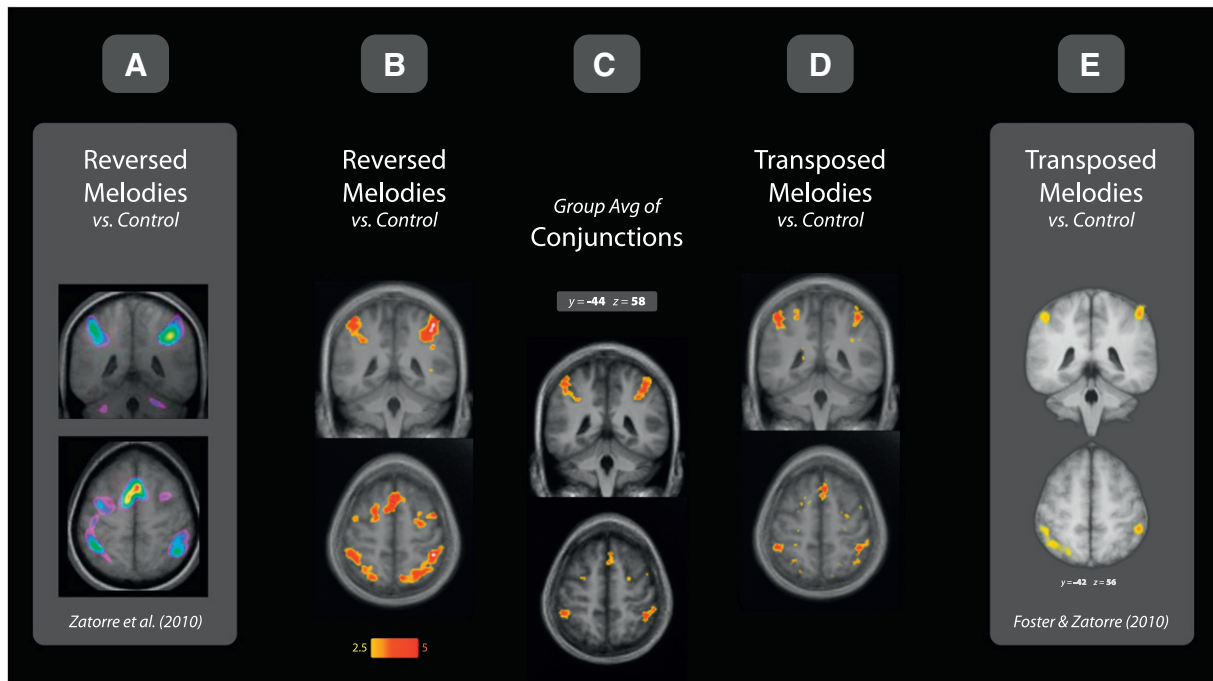
Subject performance varied significantly among the conditions (Fig. 3A,  $P < 0.001$ ,  $F(2,22) = 30.95$ , ANOVA). The differences in overall performance presumably reflect different levels of difficulty depending on the nature of the mental transformation required in each task. Performance on the Transposed condition varied significantly depending on the transposition level ( $P < 0.001$ ,  $F(5,55) = 7.31$ , ANOVA). Fig. 3B shows subject accuracy on each transposition level, plotted separately

based on the pitch distance and key distance of the transposition. Across subjects, key distance was significantly correlated with discrimination accuracy, whereas there was no correlation between pitch distance and accuracy (key distance, Pearson  $r = -0.46$ ,  $P < 0.0001$ ; pitch distance,  $r = 0.05$ ,  $P = 0.66$ ).

### Task-related BOLD signal

Contrasting the Reversed condition with the Control task revealed significant bilateral clusters of BOLD signal increase in the predicted area of anterior IPS (Fig. 4B; Table 2). Other clusters of significant increase were found in the supplementary motor area. No other areas met the significance threshold at the whole-brain level.

For the Transposed task, contrasting with the Control task revealed significant bilateral clusters of BOLD signal increase in the predicted



**Fig. 4.** BOLD activity related to mental melody transformation. (A) and (E) show results previously obtained for mental reversal (panel A; from Zatorre et al., 2010) and mental transposition (panel E; from Foster and Zatorre, 2010a). (B) and (D) show BOLD signal increases from the present study in IPS for melody judgments when mental reversal or mental pitch transposition are required. The baseline condition in both cases is a matched melody judgment that does not require any mental transformation. Panel (C) shows the average of 10 individual per-subject conjunctions between the reversal and transposition conditions. These conjunctions were calculated as the voxel-wise minimum  $t$  value between the reversed-minus-control and transposed-minus-control contrasts in each subject.

**Table 2**

Coordinates of the most significant peak BOLD increases in the Reversed condition (top), Transposed condition (middle), and the average of subject conjunctions between Reversed and Transposed (bottom). All coordinates are listed as mm in MNI (ICBM-152) space. Significance: (\*\*) indicates  $P < 0.0001$  (uncorrected) in a priori regions (intraparietal sulcus), and (\*\*\*) indicates  $P < 0.05$  (corrected) anywhere in the brain. When peaks were closer than 15 mm only the most significant peak is reported.

Analysis	Region	x	y	z	T	Sig.
Reversed > Control	Intraparietal sulcus	38	-78	38	4.72	**
	Intraparietal sulcus	-38	-78	36	4.13	**
	Intraparietal sulcus	24	-66	50	4.70	**
	Intraparietal sulcus	-30	-52	44	4.68	**
	Intraparietal sulcus	-44	-46	56	4.36	**
	Intraparietal sulcus	44	-42	52	5.48	***
Pre-supplementary motor area	-4	20	56	5.71	***	
Transposed > Control	Intraparietal sulcus	-32	-58	50	4.29	**
	Intraparietal sulcus	-50	-44	58	4.38	**
	Intraparietal sulcus	42	-44	58	3.95	**
Conjunction (Rev > Ctrl, Transp > Ctrl)	Intraparietal sulcus	-30	-58	50	4.56	**
	Intraparietal sulcus	44	-46	56	4.56	**
	Pre-supplementary motor area	0	30	42	5.05	**

area of anterior IPS (Fig. 4D; Table 2 lists the most highly significant peaks that were more than 15 mm apart). No clusters were significant in non-predicted brain areas.

In order to test whether regions of IPS are activated in common between the mental Reversal and Transposition, we first selected those subjects who had significant IPS activation in both of the mental transformation conditions (contrasting with the Control task). The 10 subjects meeting this criterion were then included in a per-subject conjunction analysis between the task contrasts. (The aim of the individual conjunction analyses was to exclude the possibility that each person has spatially distinct areas of activity in the two tasks, that when averaged across subjects then appear to overlap.) Nine of the 10 subjects yielded a significant conjunction in IPS (Fig. 5). We then performed a group average across all

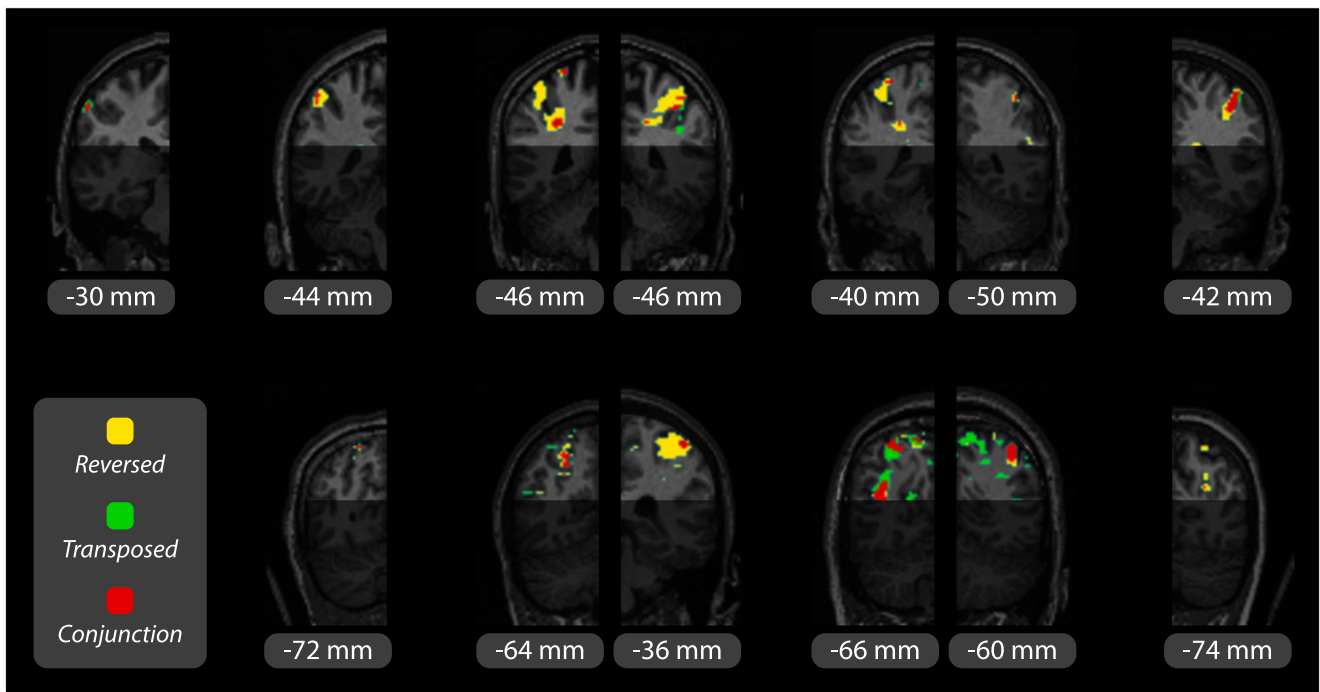
of the individual conjunction analyses to determine if the conjunction results were spatially consistent across individuals. This analysis revealed significant effects in bilateral IPS (Fig. 4C; Table 2). Outside the IPS, the most consistent activations in both conditions were found in pre-SMA (significant in the Reversed condition; Table 2) and in bilateral inferior frontal sulcus adjacent to BA 44/45 (not significant). Shading is used in Figs. 5 and 6 to indicate that only effects within the IPS can be interpreted at the a priori statistical threshold.

*BOLD signal related to transposition magnitude*

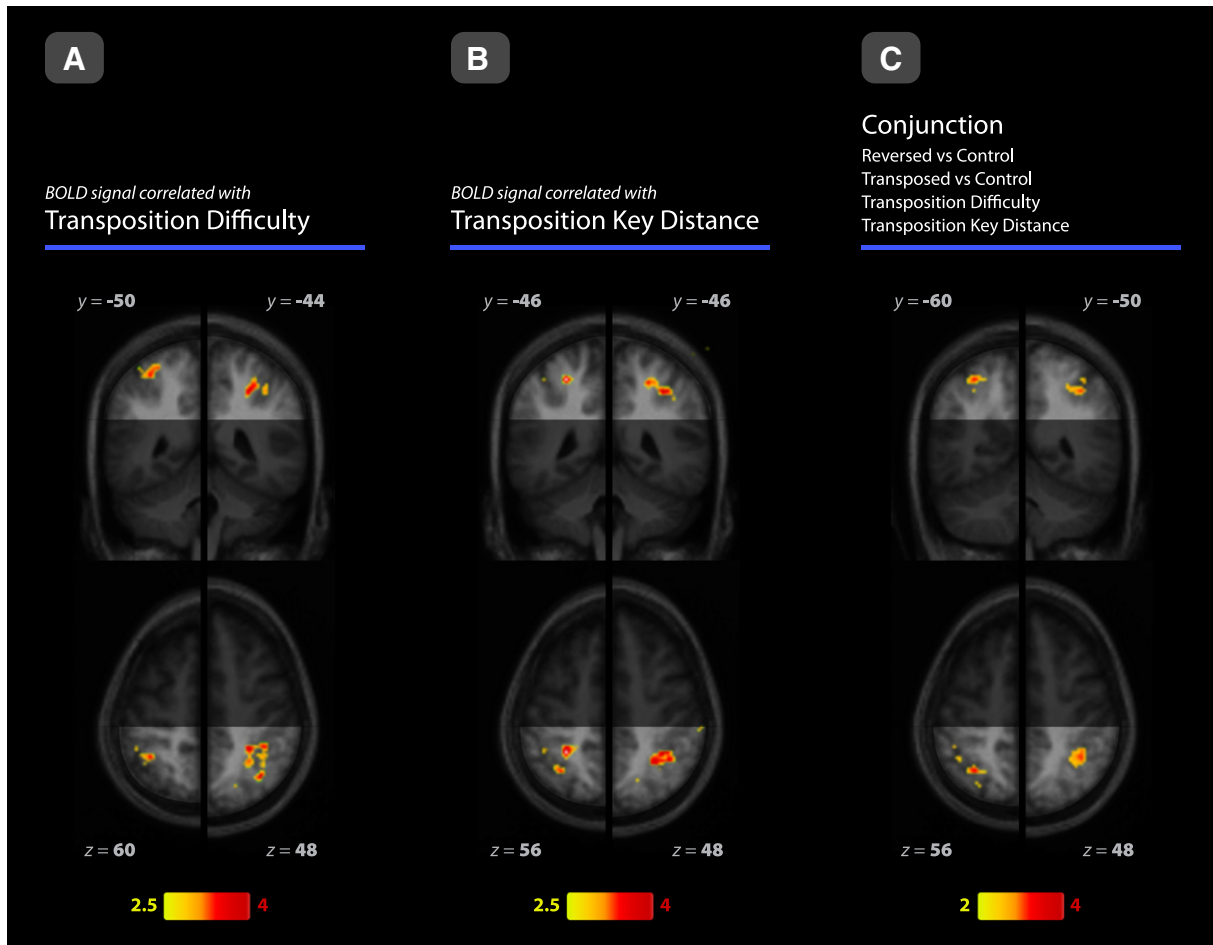
In a previous study, we found that activation of the right IPS positively correlated with individual performance on the Transposed task on a subject-by-subject basis (Foster and Zatorre, 2010a). In the current experiment we wanted to test whether IPS recruitment varies with the level of melodic transposition within subjects. We examined this question in two ways: first, by testing for BOLD signal covariation with the empirically determined difficulty of five different melodic transposition levels; and second, by examining BOLD signal correspondence with two musically relevant parameters of transposition: pitch distance and key distance.

In order to find difficulty-related effects, we took the overall accuracy at each transposition level (pooling trials across all subjects) and performed a BOLD correlation analysis in all 12 subjects to test whether greater difficulty (calculated via  $1 - accuracy$ ) on the task is associated with greater activation in the IPS. Only BOLD values from correct trials were used; this was essential to ensure that any detected effects represented correct mental transformation across all difficulty levels. We found several significant peaks in the BOLD-difficulty correlation in bilateral IPS (Fig. 6A; Table 3).

To test for a relationship between BOLD signal and both key- and pitch-distance, we performed a trial-wise parametric analysis of the Transposed task using data from all 12 subjects, in which both the key distance and pitch distance of the transposition interval were entered as separate parameters in the regression analysis. The zero-transposition level (i.e. the control condition) was included so that we could dissociate the key distance and pitch distance parameters (there was no correlation



**Fig. 5.** Individual subject BOLD activity showing overlap of effect between mental reversal and mental transposition of melodies within IPS. Of the 10 subjects who had significant activation on the two tasks, 9 showed a significant conjunction in IPS in one or both hemispheres. Where subjects had a significant conjunction in both hemispheres they are shown together, otherwise only the relevant hemisphere is shown. Shaded areas are non-IPS regions that fall outside of the analyses.



**Fig. 6.** Transposition level-related effects and overall conjunction of mental-transformation related BOLD activity in IPS. Shaded areas are non-IPS regions that fall outside of the analyses. (A) IPS BOLD signal correlation with transposition task difficulty (1–accuracy) across 5 levels of pitch transposition (see [Methods](#) for a description of the key-distance index). (B) IPS BOLD signal correlation with transposition key-distance for the same 5 levels of pitch transposition (see [Methods](#) for a description of the key-distance index). (C) 4-way conjunction between the mental reversal task contrast ([Fig. 4B](#)), mental transposition contrast ([Fig. 4D](#)), transposition difficulty correlation ([Fig. 6A](#)), and transposition key-distance correlation ([Fig. 6B](#)) analyses. The voxel-wise conjunction demonstrates that the transposition-level dependent effects overlap with the common area of IPS activation for mental reversal and transposition shown in [Fig. 4C](#).

between the two: Pearson's  $r = -0.30$ ,  $P = 0.56$ ,  $n = 6$ ). No effect of pitch distance was seen in the IPS. In contrast, for key distance, several peaks around  $t \sim -3$  were found in the right IPS at locations similar to those found in the transposition difficulty analysis ([Fig. 6B](#); [Table 3](#)).

Outside the IPS region, we found effects having similar T values in left middle temporal gyrus, right precentral gyrus, left inferior frontal sulcus and left supplementary area in the BOLD-difficulty analysis, and

**Table 3**

Coordinates of the most significant peak BOLD signal correlation with transposition difficulty (top), transposition key-distance (middle), and a 4-way conjunction between BOLD activation in the reversal task, activation in the transposition task, correlation with transposition difficulty, and transposition key-distance (bottom). All coordinates are listed as mm in MNI (ICBM-152) space. Significance: (\*) indicates  $P < 0.005$  (uncorrected) in a priori predicted regions (intraparietal sulcus) for the 4-way conjunction, and (\*\*) indicates  $P < 0.0001$  (uncorrected) in a priori regions (intraparietal sulcus). When peaks were closer than 15 mm only the most significant peak is reported.

Analysis	Region	x	y	z	t	Sig.
Correlation with transposition difficulty	Intraparietal sulcus	38	-62	46	3.95	**
Correlation with transposition key distance	Intraparietal sulcus	32	-60	42	3.89	**
Conjunction (Rev > Ctrl, Transp > Ctrl, Transp Difficulty, Transp Key)	Intraparietal sulcus	-32	-60	56	2.82	*
		40	-50	48	2.69	*

in left superior parietal lobe in the key distance analysis; however, only effects within the IPS can be interpreted at the a priori statistical threshold.

Given the similarity of IPS activation effects among all 4 of the above analyses, we performed a final conjunction of the task analyses across all subjects to determine whether transposition level-dependent activation overlaps with task-related activation on the reversed and transposed tasks. We found a significant conjunction among the 4 results in bilateral IPS ([Fig. 6C](#); [Table 3](#)).

## Discussion

Our goal was to determine whether mental reversal of melodic sequences, a manipulation of temporal order, engages similar parietal regions as mental transposition, a manipulation of pitch height. Comparing each condition to the same control task, we found activation in bilateral intraparietal sulcus (IPS) for both types of mental transformation ([Fig. 4](#)). A voxel-wise conjunction analysis found common foci for reversal and transposition within nine of the ten subjects who exhibited significant activation on both tasks ([Fig. 5](#)). The within-subject conjunction analyses confirmed that voxel-wise overlap in IPS activation between transformation tasks is not an artifact of subject averaging. BOLD signal variation across transposition trials was explained by the key-wise (musical) distance of the transposition interval, but not by the pitch-distance.

### Convergence of results

Although both involve musical sequences, the two types of mental transformation are quite different. In transposition, the pitch of each tone is changed by a constant musical interval. In reversal, the pitches are not altered, but their order is changed. Given these differences, an alternative hypothesis, that the two operations might engage IPS but in spatially distinct subregions, would also have been reasonable. Electrophysiological studies of transformational operations (e.g., visuomotor planning or orientation judgment) in the macaque suggest that the IPS exhibits regional heterogeneity in input modality, cell tuning patterns, and task recruitment (Grefkes and Fink, 2005). Spatial distinctions within IPS have also been reported in human fMRI data as a function of task demands (Culham and Kanwisher, 2001). Given this, it is likely that some IPS recruitment is particular to either temporal (reversal) or pitch (transposition) transformation, whereas a subset of activity, as supported by the conjunction analysis, serves common aspects of the tasks. We would also note that with the present data we can only say that the two tasks recruit common IPS areas within the limits of resolution imposed by fMRI. Thus, the possibility that these tasks engage adjacent IPS areas cannot be discounted. However, the close spatial proximity across tasks most likely does reflect some common operation within the IPS.

As shown in Fig. 4, these findings correspond closely with our previous studies of mental melody reversal (Zatorre et al., 2010) and melodic transposition (Foster and Zatorre, 2010a). However, in those studies, the materials used were quite different in terms of melody duration, familiarity, and timbre; here the conditions were matched by using identical materials for both tasks. That the overall pattern of IPS activation remains the same under the different conditions in three studies supports the conclusion that a mental transformation operation is indeed reflected in increased IPS activation. In another previous study (Foster and Zatorre, 2010b) we found that proficiency on the transposed melody task is associated with greater cortical thickness and gray matter concentration in IPS. The location of this anatomical effect lies very close to the current functional findings. Taken together, the four data sets converge to indicate that functional and structural properties of the IPS are implicated in these auditory transformations.

### The role of the IPS in transforming information

The pattern of IPS activation during mental melody transformation is similar to activations reported for other types of mental transformation, such as visual mental rotation, quantitative calculation, and visually-guided manual tasks (e.g. Alivisatos and Petrides, 1997; Frey et al., 2005; Harris et al., 2000; Ischebeck et al., 2006; Kong et al., 2005). In neuroimaging studies of mental rotation, the IPS is consistently recruited (e.g. Alivisatos and Petrides, 1997; Gogos et al., 2010; Harris et al., 2000; Jordan et al., 2001), and lesions of PPC are also known to impair mental rotation ability (Ditunno and Mann, 1990; Mehta and Newcombe, 1991). Parametric variation of rotation angle results in greater IPS activation for larger angles (Gogos et al., 2010). The bilateral regions of IPS activation reported for mental rotation are close to areas activated during mental melody transformation, suggesting that transformation of melodic sequences, albeit not explicitly spatial, may engage the same or similar neural networks as those involved in visual transformations.

Dual-stream models of auditory and visual processing consider the PPC an important stage in the “dorsal stream,” connecting lower-level sensory regions with motor response regions (Goodale and Milner, 1992; Rauschecker and Tian, 2000). Several regions of IPS have been defined for visuomotor processes in the monkey based on functional roles in actions such as eye saccades, reaching and grasping (Cohen and Andersen, 2002; Culham and Kanwisher, 2001; Grefkes and Fink, 2005). In humans, the importance of IPS for visuomotor control has been demonstrated in paradigms such as joystick control of on-screen

objects, pantomimed grasping of objects, and pointing to objects in varying locations (Chaminade and Decety, 2002; Simon et al., 2002).

There is controversy, however, about whether the auditory dorsal stream is intrinsically spatial in nature (Belin and Zatorre, 2000; Rauschecker and Scott, 2009; Warren et al., 2005). A recent reformulation of the auditory dual-stream model (Rauschecker and Scott, 2009) incorporates the theory of internal models (Kawato, 1999) to account for both spatial and non-spatial roles for the dorsal stream. One implication of this view is that the dorsal stream may be better defined by the types of operations it performs upon information rather than the types of information represented per se (Belin and Zatorre, 2000). Our data help to clarify this theoretical question. We do not claim that there is a specialized area within IPS for musical manipulations per se. Rather, although some degree of regional specialization is evident within human IPS, the overlap in task-related activation indicates that common task demands, such as transformation, may be performed in a modality-independent manner. The PPC receives multiple sensory inputs (Frey et al., 2008; Schroeder and Foxe, 2002), so the IPS is well suited for general manipulations of represented information. Therefore, our findings are consistent with the view that the IPS has the capacity to systematically transform auditory, visual and tactile representations, even when the information is not explicitly spatial in nature.

The IPS also has an important role in mental calculation such as subtraction and multiplication (Delazer et al., 2003; Ischebeck et al., 2006; Kong et al., 2005). Similar to angle-dependent activation in mental rotation, calculations involving larger quantities result in greater activation of IPS (Stanesco-Cosson et al., 2000). Therefore one property of parietal transformation operations is that more difficult manipulations result in greater IPS activity. In accord with these findings, we observed that more difficult levels of transposition resulted in greater IPS recruitment (Fig. 6) in the present study; note that this effect was seen when analyzing only data from correct trials, indicating that the pattern reflects degree of mental transformation, rather than some non-specific effect of task success.

IPS activation is often seen in attentionally demanding auditory tasks (e.g. Binder et al., 1997; Pugh et al., 1996), so it is important to distinguish more general difficulty- or attention-related effects vs. activation related to specific aspects of the task such as transformation. Although the control task in the present study does not permit us to make this distinction, we found in a previous study that IPS activation during mental transposition is not explained by a general effect of difficulty (Foster and Zatorre, 2010a). Briefly, several auditory pattern discrimination tasks were matched in structure and task instructions, differing only in whether participants had to discern an alteration in pitch, time or phoneme syllable. Additionally, only one of the tasks involved mental transformation (pitch transposition). BOLD signal in IPS was related to task performance in the pitch transposition condition only. When we looked at how BOLD signal varied within each subject based on task difficulty itself, BOLD signal was not greater in IPS for the task each subject individually found most difficult. Thus, rather than being related to a more general aspect of difficulty in such tasks, i.e. detecting alterations in sound patterns, these previous data suggest that IPS activation is linked to something specific about the transposition task. The present results provide further support for the interpretation that IPS activation during mental transposition reflects the difficulty of the mental transformation operation per se.

### The mental representation of transposition

Varying the transposition interval resulted in differences in performance accuracy (Fig. 3) as well BOLD signal level in bilateral IPS (Fig. 6). The covariation of IPS activation with transposition difficulty provides further evidence that recruitment of this region is directly related to mental transposition. Examining the relationship between IPS activation and transposition level can also help to understand



the frame of reference or cognitive metric upon which the mental transposition operates. The simplest model would be that mental transposition proceeds as a function of the pitch interval; this model predicts greater IPS recruitment for larger pitch distances. Considering that tonotopy is a ubiquitous feature of auditory functional organization, if pitch relationships followed this principle they would be organized in a monotonic fashion, such that pitch transformations would map onto brain activity according to the distance between the fundamental frequencies of the relevant tones. An alternative, more in keeping with music cognition (Dowling and Harwood, 1986) and music-theoretic models (Krumhansl, 2004), is that transposition depends on harmonic relationships between keys. According to this model (see Table 1), the cognitive “distance” between two melodies would depend on the number of shared tones in their underlying musical scales, a concept described in music theory by the so-called circle of fifths. Thus, melodies that are transposed, for example, by seven semitones (corresponding to the interval of a fifth) are considered closely related because they share many scale tones (e.g. the keys of C and G), whereas two melodies at a smaller distance, such as one semitone, are distantly related because they share few scale tones (e.g. the scales of C and C#). This key-distance model would predict greater IPS recruitment for transpositions between more harmonically dissimilar keys, the metric for which can be empirically derived from perceptual data (Krumhansl, 1990).

We did not observe any significant correlation of IPS BOLD signal with pitch distance; in contrast the key-distance parameter produced strong correlations in left and right IPS (Fig. 6B). Moreover, these peaks were in essentially the same locations as the transposition difficulty-related peaks (Fig. 6A). Therefore, mental transposition appears to rely upon key-centered coordinate frames, where transformation to more distant keys is more difficult because it is less harmonically related, and hence requires additional processing in IPS. This imaging result is consistent with behavioral performance on the transposition task, where accuracy across different transposition levels was more highly correlated with key distance than pitch distance (Fig. 3). These findings demonstrate that an abstract concept derived initially from music theory—key distance—has a physical instantiation in neural operations carried out within the IPS.

Whereas the relevant dimension for mental transposition seems to be key distance, in the reversal condition the transformation is upon time, i.e. the temporal order of notes. Hence our results show that the IPS is involved in manipulating melodic information based upon both temporal and more abstract, cognitively based frames of reference. The temporal dimension is present in auditory representations from early stages of processing; however, it is unknown where pitch sequences become transformed into key-centered representations. Processing of some higher-level auditory features occurs in regions adjacent to core auditory cortex, and this is believed to include contour extraction and local (note-wise) interval processing (Stewart et al., 2008; Zatorre, 1985). However, given the well-known role of PPC in visuomotor and visuospatial transformations across different reference frames, it seems more likely that the IPS is involved as part of an interactive network including feedforward and feedback loops to sensory cortical areas (Rauschecker and Scott, 2009).

## Conclusions

We show the specific involvement of IPS in transforming melodic information for both temporal and pitch-based transformations. This pattern of results bears a strong similarity to visuospatial transformation-related activation, both in terms of the anatomical location and the dependence of activation level upon transformation level. These findings therefore support an interpretation of dorsal stream processing in terms of the type of operations it performs rather than the nature of the information represented, and show that such operations can be performed over abstract cognitive frames of reference.

## Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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