

Activation of premotor vocal areas during musical discrimination

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Accepted 22 August 2006

Available online 5 October 2006

Abstract

Two same/different discrimination tasks were performed by amateur-musician subjects in this functional magnetic resonance imaging study: Melody Discrimination and Harmony Discrimination. Both tasks led to activations not only in classic working memory areas—such as the cingulate gyrus and dorsolateral prefrontal cortex—but in a series of premotor areas involved in vocal-motor planning and production, namely the somatotopic mouth region of the primary and lateral premotor cortices, Broca's area, the supplementary motor area, and the anterior insula. A perceptual control task involving passive listening alone to monophonic melodies led to activations exclusively in temporal-lobe auditory areas. These results show that, compared to passive listening tasks, discrimination tasks elicit activation in vocal-motor planning areas.

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Keywords: Music; Discrimination; Premotor; Vocalization; fMRI; Perception; Melody; Harmony

1. Introduction

An important requirement of species-specific communication systems in general—and acoustic communication systems in particular—is the need to match perceptual and production capacities. This is the classic problem of “parity” for the evolution of any kind of signaling system (Liberman & Whalen, 2000). Senders and receivers must share a common set of signals in order for communication to be efficient. Hence, production and perception capacities must co-evolve to an important degree. In the domain of speech, this has led to a proposal of a motor theory of perception (Liberman & Mattingly, 1985), in which the perception of speech is heavily tied in with the motor gestures involved in syllable production and co-articulation. This idea has also been applied to birdsong with the demonstration that neurons of the hypoglossal nerve, which innervate

the vocal apparatus, are active when a bird perceives song (Williams & Nottebohm, 1985).

Work in mammalian neurobiology has taken a different but related tack to the problem of parity, especially as it relates to perceptual processes. Experiments with Rhesus monkeys have led to the identification of neurons in premotor cortical areas that fire not only when an animal performs an object-directed action but when it observes the same action performed by another organism (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). This has led to the suggestion that processes like attention, discrimination and higher-level cognition involve a strong linkage between perceptual and production processes, and in fact rely on premotor circuits for their instantiation (Blakemore & Frith, 2005; Iacoboni, 2000; Rizzolatti & Craighero, 2004). This is compatible with theories from human psychology that posit that perception and action share a common representational domain (Prinz, 1997; Varela, Thompson, & Rosch, 1991), a viewpoint that stands in opposition to many computational perspectives that focus on perception as dissociated from action. The “shared representation” perspective sets itself apart not only from computational work in artificial intelligence but also from much work in neuroscience

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that focuses on generalized “attentional networks” distinct from premotor circuits.

Studies of discrimination processing for both speech and music have repeatedly shown that discrimination tasks activate premotor areas in addition to classical working memory areas. Perhaps the earliest neuroimaging evidence for the importance of premotor areas to acoustic discrimination was that of Zatorre, Evans, Meyer, and Gjedde (1992), who observed activation in Broca’s area during phonetic discrimination of syllables, as well as activation of the right frontal operculum (Brodmann area 45) during pitch discrimination using syllable carriers. Neither area was active during passive listening to syllables. Zatorre et al. interpreted these results in terms of a motor theory of discrimination (see also Zatorre, Halpern, Perry, Meyer, & Evans, 1996).

It is significant that the premotor areas activated in acoustic studies such as Zatorre et al.’s (1992) are those involved in *vocal* planning. This would suggest that discrimination processing for acoustic stimuli activates a process akin to—or perhaps identical to—sub-vocalization. Studies of musical imagery, which explicitly stimulate the process of covert vocalization in subjects, have clearly shown activations in premotor vocal areas, such as the supplementary motor area and lateral premotor cortex (Halpern & Zatorre, 1999). In the current study, we examined discrimination abilities as they relate to the melodic and harmonic dimensions of music, and analyzed the results in light of a companion study of vocalization using the same subjects (Brown, Parsons, Martinez, Hodges, & Fox, 2004). By looking at subjects’ brain activations for music-discrimination tasks in comparison to their activations for singing, we hoped to evaluate not only a general premotor theory of discrimination but, more specifically, a vocal-motor theory. Based on previous literature for musical discrimination (e.g., Gaab, Gaser, Zaehle, Jancke, & Schlaug, 2003) and musical imagery (Halpern & Zatorre, 1999), we predicted that activations during musical discrimination in our subjects would overlap, or at least be proximate to, those areas activated during singing.

2. Materials and methods

2.1. Subjects

Five male and six female neurologically-healthy amateur musicians, with a mean age of 24.6 years (range 19–46 years), participated in the study after giving informed consent (Institutional Review Board of the University of Texas Health Science Center). Each individual was right-handed, as confirmed by the Edinburgh Handedness Inventory (Oldfield, 1971). All subjects were university students, most in their first or second years as music education majors, with a mean of 5.0 years of formal music instruction in voice or instrument. Subjects began music instruction at a mean age of 12.3 years, having had an involvement in musical production (e.g., school bands, church choirs) for an

average of 12.3 years prior to the study. None of them had absolute pitch, as based on self-report. Their musical specializations included voice, flute, clarinet, trumpet, trombone, bass, guitar, piano, drums, and percussion. After having completed our study of the two discrimination tasks, we invited the subjects to be scanned a second time to do a passive listening task. Six of the original eleven subjects (three males and three females, mean age 23.5 years) consented to be scanned for a second time.

2.2. Tasks

Subjects performed two forced-choice, same/different discrimination tasks with their eyes closed. For both tasks, half of the samples were the same and half were different during each epoch of task. (1) *Melody Discrimination*. Subjects heard pairs of short, novel, one-line melodies, and had to determine if the two melodies were either identical (“same”) or if they differed by one *note* anywhere in the melody (“different”). Each epoch of the fMRI lasted 60 s, separated by 60 s of rest. During each minute of task, subjects heard six stimulus pairs, with an inter-stimulus interval of 1 s, during which time the response was registered. Each melody was 4–5 s in duration. The time difference between repetitions of the melodies was 0.5 s. Subjects indicated a response of same or different through the use of button press with two fingers of the right hand. (2) *Harmony Discrimination*. Subjects heard pairs of short, novel, harmonized melodies, and they had to determine if the two were either identical (“same”) or if they differed by one *chord* anywhere in the sequence (“different”). The melodic lines of the samples were always invariant across pairs. The modifications made to create “different” samples sometimes involved changing notes within an existing chord (e.g., converting a major chord to a minor chord by lowering the third degree of the chord by a semitone, as shown in the lower right sample in Fig. 1b). On other occasions, changes in chord class could be used (e.g., converting a G major chord to a D minor chord). Each epoch of the fMRI lasted 60 s, separated by 60 s of rest. During each minute of task, subjects heard six stimulus pairs, with an inter-stimulus interval of 1 s, during which time the response was registered. Each harmonized melody was 4–5 s in duration. For both tasks, the stimuli varied with regard to key, tempo, meter, note number and melodic contour. Consecutive samples were never in the same key. Every attempt was made to have consecutive samples differ in musical properties, so that subjects would not habituate to the musical features of the stimuli. For “different” samples, the placement of the different note or chord was not done in any systematic way, except that it never occurred on the first or last note/chord of a sample. The goal was simply to make the placement of the different note/chord as unpredictable as possible.

In order to control for the motor activations involved in button press, subjects performed a “control task” between task epochs. During this control task, subjects pressed a button each time they heard a piano tone of 147 Hz, which

was presented at random times during the 60 s. The number of tones matched the number of stimulus pairs in the discrimination tasks (namely 6).

During a second round of fMRI testing, six participating subjects performed a *Melody Listening* task. Subjects listened passively to a series of 5-s monophonic melodies (different from those used in the discrimination tasks) played in succession with a 1-s inter-stimulus interval. Sixty seconds of music listening were alternated with 60 s of rest. No response was required. The eyes were kept closed throughout the scan. From the standpoint of acoustic load, the Melody Listening task was nearly identical to the Melody Discrimination task in that subjects heard strings of monophonic melodies which were separated by short gaps.

2.3. Stimuli

All stimuli for the musical tasks (both discrimination and passive listening) were presented to both ears as piano tones, and were generated using Finale 2001 (Coda Music Technology) and digitized for presentation in the scanner using CoolEdit (Syntrillium Software). The majority of samples were composed for the study. Three of the Melody Discrimination samples and five of the Harmony Discrimination samples were adapted from fragments of little-known classical works.

2.4. Imaging procedure

During the fMRI session, subjects lay supine in the scanning instrument, with the head immobilized by a closely fitted thermal-plastic facial mask with openings for the eyes, ears, nose, and mouth. Auditory stimuli were presented through MR-compatible headphones. During scanning, subjects were told to close their eyes and to be as motionless as possible with the exception of movement of

the fingers of the right hand for button press during the discrimination tasks. Each task was acquired using a blocked design: 60 s of control task (or “rest” in the case of the passive listening task) was alternated with 60 s of task for a total of 6 min.

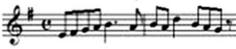
MRI images were acquired on an Elscint Gyrex 2T whole-body scanner (Elscint Ltd., Haifa, Israel), operating at 1.9T. Functional images were acquired using a 16-slice gradient-echo echoplanar imaging sequence. Each slice had an in-plane resolution of 3.2×3.2 mm, with 7 mm slice thickness, a 128×72 voxel matrix. The TR was 2 s. Following correction for intra-scan head motion, a statistical parametric image (SPI) was generated for each task for each subject using cross-correlation as implemented in SEE-IT (Xiong, Gao, Lancaster, & Fox, 1995, 1996). An individual subject’s SPI was registered to the Talairach standard using in-house “convex hull spatial normalization” software (Lancaster et al., 1999, 1995). Average functional z -maps were resliced to a 2 mm^3 voxel space and smoothed with a Gaussian filter (FWHM = 6 mm) prior to both intensity ($z > 3.08$, $p < .001$) and extent (cluster > 8 native space voxels) thresholding using “clustered pixels analysis” (Xiong et al., 1995, Xiong, Gao, Lancaster, & Fox, 1996). Local extrema were identified with a 3-D search algorithm (Mintun, Fox, & Raichle, 1989) using a $3 \times 3 \times 3$ voxel search cube (2 mm^3 voxel). Structural MRI scans were acquired with an in-plane resolution of 1×1 mm with a 1.5 mm slice thickness.

3. Results

Fig. 1 presents typical stimuli for both of the Melody Discrimination and Harmony Discrimination tasks. Behavioral performance was as follows: subjects scored 76.3% correct ($SD = 3.4\%$) on the Melody Discrimination task, and 67.7% correct ($SD = 2.5\%$) on the Harmony Discrimination

a Melody Discrimination

Same  

Different  

b Harmony Discrimination

Same  

Different  

Fig. 1. Representative stimuli for the two discrimination tasks performed in this study: (a) Melody Discrimination (the stimulus pairs are either identical or differ by one *note*), and (b) Harmony Discrimination (the stimulus pairs are either identical or differ by one *chord*). For each task, representative “same” and “different” stimulus pairs are presented. For the “different” samples in the two tasks, an asterisk marks the point of difference in the second sample compared to the first.

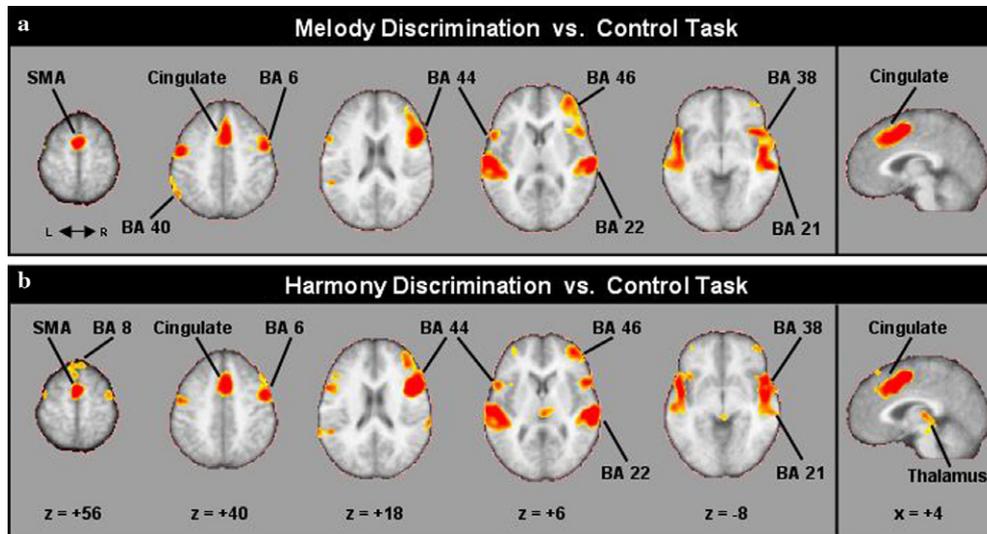


Fig. 2. Axial views of BOLD-signal increases during the (a) Melody Discrimination, and (b) Harmony Discrimination tasks, as contrasted with a control task for button press (see Section 2). The Talairach coordinates of the major activations (contrasted to the control task) are presented in Tables 1 and 2, respectively, for the two tasks. The averaged activations for 11 subjects are shown registered onto an averaged brain in all the figures. The right side of the figure is the right side of the brain in all the figures. Note that the same set of five axial slice-levels is shown in Figures 2, 3 and 4, with an additional sagittal section shown uniquely in Fig. 2. Note also that bilateral activations are labeled on only one side of the brain. The label SMA stands for supplementary motor area. The intensity threshold in Figures 2, 3 and 4 is $z > 3.08$, $p < .001$ (one-tailed).

task. Both scores were significantly above chance level. One factor that could have contributed to the relatively low-level performance on these tasks is that the stimuli were quite long (as many as 16 notes), and that the “different” note could occur anywhere in the stimulus fragment. Inquiries between the fMRI scans and debriefing of the subjects after the scanning session indicated that scanner noise did not impede the ability to perceive the stimulus material. The poorer performance of the subjects on the harmony task compared to the Melody task most likely related to the greater complexity of the stimuli of the former task, involving chord progressions in addition to melodies.

The imaging results for the Melody Discrimination task are presented in Fig. 2a and Table 1. Auditory activations reflecting the presentation and processing of the musical stimulus-material were seen in a large stretch of the posterior part of the superior and middle temporal gyri bilaterally (BA 22 and 21) as well as in the anterior part of the temporal lobe, also known as the planum polare (BA 38/22). Next, strong activations were seen in parts of the premotor cortex close to or overlapping with areas involved in vocalization, including the supplementary motor area (SMA; medial BA 6), the mouth area of the primary/premotor cortex bilaterally (BA 4/6), dorsal Broca’s area (superior BA 44) of the right hemisphere, the frontal operculum (inferior BA 44) bilaterally, and the right anterior insula. Activations were also seen in a lengthy anteroposterior stretch of the right cingulate gyrus, in the right dorsolateral prefrontal cortex (BA 46), and in the inferior parietal lobule (BA 40). No activations were detected in the thalamus, basal ganglia, or brain stem. However, an activation unique to this task

was seen in the quadrangular lobule (lobule VI) of the left posterior cerebellum.

The results for Harmony Discrimination are presented in Fig. 2b and Table 2. Not only was the activation profile quite similar to that for Melody Discrimination but a similar pattern of laterality was seen, including right-hemisphere dominance for activations in the cingulate gyrus, dorsal Broca’s area, frontal operculum, and dorsolateral prefrontal cortex. Subcortical activations were seen in the midline thalamus and the midbrain that were not seen in the Melody Discrimination task. A composite image comparing the Harmony Discrimination and Melody Discrimination tasks (Fig. 3) shows the high degree of overlap between these two tasks. Residual signal was found in the superior frontal gyrus (BA 8) and midline thalamus for the harmony task and inferior parietal lobule (BA 40) for the melody task. Direct subtraction of the brain activation due to Melody Discrimination from that due to Harmony Discrimination resulted in no cortical signal outside of BA 8 (data not shown). Overall, the profile of activation for Harmony Discrimination strongly overlapped that for Melody Discrimination, both in terms of brain regions and laterality.

Regarding our hypothesis that acoustic discrimination would activate areas involved in vocalization, we compared the motor coordinates for the Melody Discrimination task with those for an overt Melody Repetition task from Brown, Parsons, et al. (2004), in which same subjects had to sing back melodies they heard. When subjects in that study sang tonal monophonic melodies, the principal precentral gyrus activations were located at $-48, -8, 40$ (BA 4) and $54, -6, 40$ (BA 6). For the Melody Discrimination task with the same subjects (Table 1), significant foci of activation were seen at a nearly identical location in the left

Table 1
Stereotaxic coordinates and *z*-score values for activations in the Melody Discrimination task contrasted with the button-pressing control task

Melody Discrimination				
Region	<i>x</i>	<i>y</i>	<i>z</i>	<i>z</i> -score
<i>Frontal</i>				
<i>Right</i>				
Premotor cortex (6)	50	0	34	9.17
Dorsal Broca's area (45)	48	14	20	7.00
Dorsolateral prefrontal cortex (46/10)	36	48	8	5.46
Dorsolateral prefrontal cortex (46)	40	34	20	4.97
Frontal operculum (45)	44	30	12	4.58
<i>Left</i>				
Primary motor cortex (4)	−48	−8	38	7.50
Frontal operculum (44)	−54	8	10	4.90
<i>Temporal</i>				
<i>Right</i>				
Middle temporal gyrus (21)	50	−20	−2	7.48
Superior temporal gyrus (22)	62	−20	4	6.87
Middle temporal gyrus (21)	58	−28	−2	6.70
Superior temporal gyrus (22)	60	−30	6	6.10
<i>Left</i>				
Superior temporal gyrus (22)	−58	−22	2	8.71
Superior temporal gyrus (22)	−52	−40	10	6.18
Superior temporal sulcus	−54	−10	0	6.07
Middle temporal gyrus (21)	−48	0	−8	6.06
Planum polare (22/38)	−50	6	−4	5.96
Superior temporal gyrus (22)	−64	−32	10	5.25
<i>Parietal</i>				
<i>Left</i>				
Inferior parietal lobule (40)	−52	−58	40	4.36
<i>Other</i>				
<i>Right</i>				
Cingulate gyrus (32)	4	2	48	9.18
Anterior insula	48	12	−2	5.85
<i>Posterior Cerebellum</i>				
<i>Left</i>				
Quadrangular lobule (VI)	−30	−60	−26	4.39

Brain atlas coordinates in Tables 1–3 are in millimeters along the left-right (*x*), anterior-posterior (*y*), and superior-inferior (*z*) axes. In parentheses after each brain region is the Brodmann area, except in the case of the cerebellum, in which the anatomical labels of Schmahmann et al. (2000) are used. The intensity threshold is $z > 4.00$, $p < .00003$ (one-tailed).

hemisphere (−48, −8, 38) and at a more anterior location in the right hemisphere (50, 0, 34). Likewise, frontal operculum (BA 44) activations for singing were seen at −48, 6, 10 and for discrimination at −54, 8, 10. These results suggest that acoustic discrimination tasks activate not just “premotor” areas in general but vocal-motor areas in particular.

Finally, as we were intrigued by the very strong activations in premotor areas during these discrimination tasks, we invited our subjects back for a second round of scanning, this time to perform passive listening to monophonic melodies in which no discrimination of any kind was required (Melody Listening). Six of the original 11 subjects participated. As shown in Fig. 4 and Table 3, the task led to activations that included superior temporal regions

but not the premotor or prefrontal areas activated by the discrimination tasks. Thus, a striking difference was seen between passive and active tasks: passive tasks activated almost exclusively temporal-lobe auditory association areas whereas discrimination tasks activated, in addition to those areas, many regions involved in vocal-motor planning and production. This is suggestive of a key role of vocal premotor areas in discrimination processing for music. Importantly, we ruled out any effect of cohort by re-analyzing the two discrimination tasks for the subgroup of 6 that participated in the second study. The results were qualitatively identical to the full group, showing the same pattern of premotor activations (premotor cortex, supplementary motor area, and Broca's area) as the group of 11 (data not shown).

4. Discussion

An advantage of this study was that we had run a companion PET study with the same subjects (Brown, Parsons, et al., 2004), and hence were able to identify vocal-motor areas directly in these subjects. We were therefore able to interpret the results of these fMRI discrimination tasks in light of the PET vocal tasks performed by the same individuals; in that study, subjects performed imitative repetitions of monotone sequences or simple melodic sequences, or they generated harmonizations along with another melodic line. The major finding of the current study is that discrimination, compared to passive perception, activates a network of vocal-motor planning areas, suggesting that discrimination is mediated by sensorimotor processing even when no motor response occurs. We now discuss the brain areas activated during passive listening and active discrimination.

4.1. Passive listening

Listening passively to monophonic melodies (Fig. 4) led almost exclusively to activations throughout the planum temporale bilaterally, encompassing the posterior part of the superior temporal gyrus (BA 22) and superior temporal sulcus. A host of imaging studies that have focused on passive listening to music or speech—rather than active discrimination—have indeed shown activations that are restricted for the most part to temporal cortical areas (Hickok & Poeppel, 2000; Menon et al., 2002; Patterson, Uppenkamp, Johnsrude, & Griffiths, 2002; Petersen, Fox, Posner, Mintun, & Raichle, 1988; Scott, Catrin Blank, Rosen, & Wise, 2000; Wise et al., 1991; Zatorre, Evans, & Meyer, 1994; see also Belin, Zatorre, Lafaille, Ahad, & Pike (2000) for passive listening to a variety of vocal sounds). There is thus a strong precedent in the literature for arguing that passive listening to music or speech (i.e., in the absence of some kind of active cognitive processing like discrimination, recognition, generation, etc.) principally activates primary and secondary auditory areas.

Table 2
Stereotaxic coordinates and *z*-score values for activations in the Melody Discrimination task contrasted with the button-pressing control task

Harmony Discrimination				
Region	<i>x</i>	<i>y</i>	<i>z</i>	<i>z</i> -score
<i>Frontal</i>				
Right				
Premotor cortex (6)	50	0	34	9.91
Supplementary motor cortex (6)	2	−2	52	9.39
Dorsal Broca's area (45)	48	14	18	8.48
Dorsal Broca's area (44/6)	44	6	18	8.23
Prefrontal cortex (46/10)	36	48	10	7.15
Dorsolateral prefrontal cortex (46)	40	36	20	5.87
Dorsolateral prefrontal cortex (46)	44	44	2	4.99
Primary motor cortex (4)	48	−8	50	4.94
Dorsolateral prefrontal cortex (46)	46	36	14	4.38
Premotor cortex (6)	40	−8	54	4.18
Left				
Primary motor cortex (4)	−44	−8	36	6.10
Frontal operculum (44)	−50	8	14	5.36
Premotor cortex (6)	−44	2	30	5.23
Premotor cortex (6)	−42	4	26	5.16
Dorsal Broca's area (45)	−44	22	22	4.72
Supplementary motor cortex (6)	−2	18	56	4.09
Dorsolateral prefrontal cortex (10)	−34	50	2	4.02
<i>Temporal</i>				
Right				
Superior temporal gyrus (22)	60	−20	4	7.86
Superior temporal gyrus (22)	60	−32	6	7.65
Planum polare (38/22)	52	10	−6	6.14
Left				
Superior temporal gyrus (22)	−54	−22	4	7.61
Planum polare (22)	−50	4	−4	6.78
Superior temporal sulcus	−50	−10	−2	6.15
Superior temporal gyrus (22)	−64	−32	10	5.90
Superior temporal gyrus (22)	−64	−40	14	5.86
Superior temporal gyrus (22)	−50	−42	12	5.67
<i>Other</i>				
Right				
Cingulate gyrus (32)	4	10	42	8.44
Thalamus	4	−24	6	4.72
Left				
Anterior insula	−36	12	0	4.95

The intensity threshold is $z > 4.00$, $p < .00003$ (one-tailed).

4.2. Action-based discrimination

In contrast to these results for passive listening, active discrimination tasks for music led to a series of brain areas becoming activated (in addition to the auditory association areas activated in the listening task) that corresponded mostly to parts of the vocal premotor circuit of the brain. Most of these same areas were activated in vocal production tasks for music or language (Brown, Martinez, & Parsons, 2006; Brown, Parsons, et al., 2004), hence demonstrating a strong connection between discrimination processing and vocal production. Previous studies that have compared passive and active music listening (e.g., Zatorre et al., 1994) have provided similar results to our own regarding the recruitment

of premotor circuits during active but not passive processing. In addition, similar lines of argument can be applied to musical imagery, during which important components of the vocal premotor circuit have been shown to be active. Halpern and Zatorre (1999) observed a large number of frontal lobe motor-planning areas become activated during imagery of melodic continuations and repetitions, including BA 47, dorsal BA 44, the frontal operculum (bilateral BA 45), the SMA, and lateral premotor cortex. Of these areas, only the SMA was acknowledged by these authors as being specifically involved in “motor planning associated with a subvocal singing or humming strategy during the [imagery] generation process” (p. 703). However, we hypothesize that the premotor activations seen by ourselves, Halpern and Zatorre (1999), and many others reflect an important underlying connection between discrimination, mental imagery, and vocal-motor production through the control of sensorimotor—and more specifically *audiovocal*—circuits.

Based on discussions in the literature, we would like to propose a theory of discrimination predicated on the recruitment of two different types of brain areas whose roles may be different but interrelated, namely (1) domain-specific vocal-motor planning areas that may be specialized for template matching processes involved in sensorimotor integration (mainly BA 4/6 and BA 44/45); and (2) domain-general discrimination areas involved in working memory, attention, and error detection (mainly BA 24/32 and BA 46). It is hypothesized that activation in this latter group of areas might be reflective of differences in processing mode between the active and passive conditions with regard to attentional engagement, task difficulty, the necessity or not for error detection, and other general aspects of mental set. These two sets of areas will now be described in sequence.

4.2.1. SMA

We observed broad and extensive activations along the mesial portion of the brain, encompassing mainly the dorsal part of the cingulate gyrus (discussed below) but also the SMA (medial BA 6). The SMA is well known to be involved in motor planning and coordination, both for overt vocalization (Brown, Ingham, Ingham, Laird, & Fox, 2005; Brown, Parsons, et al., 2004; Perry et al., 1999; Turkeltaub, Eden, Jones, & Zeffiro, 2002) and covert vocalization (Halpern & Zatorre, 1999; Wise et al., 1991). The part of the SMA that we saw activated in our discrimination tasks is quite close to that observed in our study of vocalization, although the peak activity was slightly ventral. So, activation here may represent a process of subvocalization, as pointed to by work on musical imagery (Halpern & Zatorre, 1999). As mentioned above, Halpern and Zatorre (1999) suggested that, of the motor planning areas that they saw activated in their study of imagery, the SMA was the one that they most closely associated with the generative aspect of image formation, making appeal to a notion of covert vocalization. The SMA seems to be a point of key overlap between vocal production, discrimination and mental imagery for music.

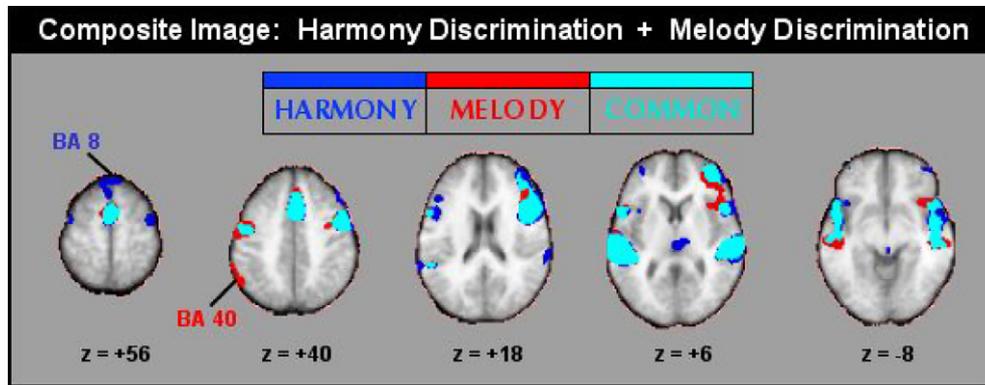


Fig. 3. Composite image analysis, demonstrating the overlap between the Harmony Discrimination and Melody Discrimination tasks. Harmony Discrimination activations are presented in blue, Melody Discrimination activations in red, and common activations in cyan. For this figure, Brodmann labels are color-coded to highlight activations that are unique to the harmony task (blue) or melody task (red). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

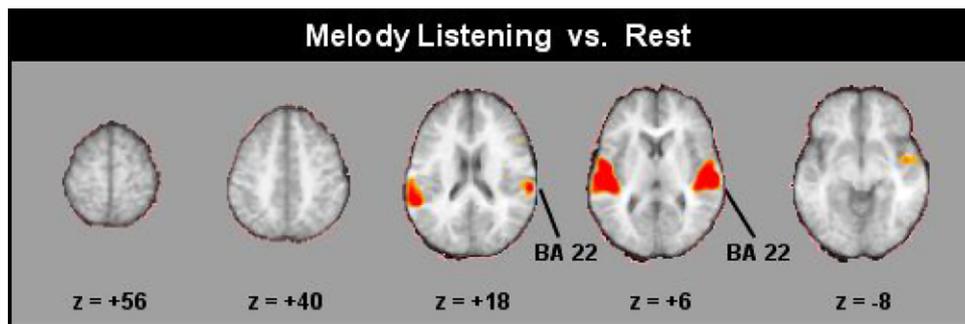


Fig. 4. Axial views of BOLD-signal increases during the passive Melody Listening task. The Talairach coordinates of the major activations (contrasted to Rest) for the task are presented in Table 3. The intensity threshold for this figure is $z > 3.08$, $p < .001$ (one-tailed).

Table 3
Stereotaxic coordinates and z -score values for activations in the Melody Listening task contrasted with rest

Melody Listening				
Region	x	y	z	z -score
<i>Temporal</i>				
<i>Right</i>				
Superior temporal gyrus (22)	56	-22	6	8.50
Superior temporal sulcus	48	-8	-2	7.91
<i>Left</i>				
Superior temporal sulcus	-48	-12	2	7.56
Superior temporal gyrus (22)	-48	-22	8	7.24
Superior temporal gyrus (22)	-56	-24	8	7.16
Primary auditory cortex (42)	-50	-32	12	6.96
Superior temporal gyrus (22)	-54	-42	18	5.79

The intensity threshold is $z > 4.00$, $p < .00003$ (one-tailed).

4.2.2. Primary/premotor cortex

Both discrimination tasks led to strong activations in the precentral gyrus, straddling the border of BA's 4 and 6. Zatorre et al. (1994) too observed activation in this exact region during the two pitch-discrimination tasks that they performed but not during passive music listening. These activations in BA 4/6 overlap those we observed in the primary motor cortex (BA 4) during overt vocalization for speech and song (Brown et al., 2006, 2004), and thus almost

certainly represent the junction of the primary mouth area and the somatotopic mouth area of the premotor cortex. Hence, we suggest that the premotor areas activated strongly in this study of musical discrimination are in fact areas involved in vocal planning. The "vocality" of these activations provides provocative support for an hypothesis of action-based discrimination involving audiovisual integration. Further support for this notion comes from the musical imagery study of Halpern and Zatorre (1999) in which the tasks were explicitly designed to induce subvocalization in subjects. In their covert melody-repetition task, in which subjects heard melodies and had to mentally imagine them again, the BA 6 coordinates in the left hemisphere were at $[-46, -7, 39]$; our left-hemisphere activation for the melody discrimination task was as $[-48, -8, 38]$. For their covert melody-continuation task, their BA 6 coordinates in the left hemisphere were at $[-48, -6, 41]$ and in the right hemisphere at $[51, -1, 47]$; our coordinates were at $[-48, -8, 38]$ in the left hemisphere and $[50, 0, 34]$ in the right. Likewise, Gaab et al. (2003), in a similar study to this one in which subjects had to compare the last or second to last note of a melody to its first note, found bilateral activations in the premotor cortex: their left hemisphere activation was at $[-41, -7, 45]$ compared to our melody-discrimination coordinate of $[-48, -8, 38]$. Again, this location is essentially the somatotopic mouth area of the primary motor

cortex or quite proximate to it. Overall, these results suggest that even though our subjects had no time at all for explicit subvocalization, primary and premotor vocal areas involved in this process were activated.

4.2.3. Broca's area

Broca's area encompasses Brodmann areas 44 and 45 of the inferior frontal gyrus. It has been implicated historically in phonetic encoding and speech articulation, but also language syntax (Dapretto & Bookheimer, 1999; Heim, Opitz, & Friederici, 2003; Indefrey et al., 2001), non-linguistic tongue movements (He et al., 2003), tone discrimination (Müller, Kleinhans, & Courchesne, 2001), and sign language (Horwitz et al., 2003; Petitto et al., 2000), among others. In the current study, we saw activations in what we would like to think of as *two* divisions of Broca's area, a dorsal division centered around z of 20 (what we will call "dorsal Broca's area") and a ventral one occupying what is known as the frontal operculum, with a peak coordinate at around z of 10. In our previous studies of singing, we saw bilateral BA 44 activations exclusively in the opercular part of Broca's area. Again, it is important to point out that the frontal operculum activations seen with these discrimination tasks match very closely those seen in our studies of vocalization for speech and song. We argued previously that activations in the frontal operculum may have been related to a process of "template matching" in creating imitations of melodic sequences (Brown, Parsons, et al., 2004). Template matching would also seem to be an important process in performing same/different discriminations, as subjects have to make on-line comparisons between the second presentation of the stimulus and the first presentation so as to make a judgment about similarity or difference. Hence, the strong activations seen in the dorsal part of BA 44/45 in the current study but not in our studies of vocalization may reflect the greater resources required for the discrimination tasks compared to the vocal repetition tasks of the previous study.

The importance of the frontal operculum for active processing for music is well-supported in the literature dealing with musical discrimination, including discrimination of pitch (Binder et al., 1997; Gaab et al., 2003; Griffiths, Johnsrude, Dean, & Green, 1999; Zatorre & Binder, 2000; Zatorre et al., 1994; Zatorre et al., 1992), chords (Maess, Koelsch, Gunter, & Friederici, 2001), durations (Griffiths et al., 1999), rhythms (Parsons, 2003), time intervals (Rao, Mayer, & Harrington, 2001), sound intensities (Belin et al., 1998), chords, keys and timbres (Koelsch et al., 2002), and in error detection for melody and harmony during score reading (Parsons, 2003). In virtually all of these studies, only the opercular part of Broca's area, and not the dorsal region, is activated. Given that studies of vocal production show that the opercular part of Broca's area is the region most closely associated with vocal production, this adds support to our "vocal planning" hypothesis of musical discrimination.

To summarize the discussion thus far, we see that the activations in the SMA, lateral premotor cortex and Broca's area during discrimination processing correspond with identical or closely-localized activations during overt vocalization tasks for speech and song, thereby arguing that one important component of the circuit for discrimination consists of motor planning areas involved in vocalization. This suggests that discrimination, like mental imagery, involves an important element of sensorimotor integration and action-based processing. We now move on to look at domain-general working memory areas involved in discrimination, namely the anterior cingulate cortex and the dorsolateral prefrontal cortex.

4.2.4. Anterior cingulate cortex

Both discrimination tasks showed broad activations throughout the dorsal extent of the anterior cingulate region, with a peak activation in the vicinity of the callosomarginal sulcus separating the cingulate gyrus from the supplementary motor area (see the sagittal slices in Fig. 2). The cingulate gyrus, and especially the anterior zone, has been classically associated with visual attention but has more recently been suggested to play a more specific role that might be nicely tied into theories of discrimination, namely "conflict monitoring" (Botvinick, Cohen, & Carter, 2004; Carter et al., 1998; MacDonald, Cohen, Stenger, & Carter, 2000). Conflict monitoring is in fact an ideal description of what discrimination processing for same/different tasks like ours entails, namely a search for differences or discrepancies. It is for this reason that we suggest that the anterior cingulate may play a role that is discrimination-specific and perhaps domain-general with the regard to the processing analyzed in this study. Activation in the anterior cingulate has been reported in several other studies of musical discrimination. In Zatorre et al.'s (1994) study of same/different discrimination for the first and late notes of melodies, there were two foci of activation in the anterior cingulate gyrus, one at $x = -1$ and one at $x = 5$. In Griffiths et al.'s (1999) study of pitch discrimination, there were three foci of activation in the anterior cingulate gyrus, two in the right hemisphere ($x = 8$ and $x = 10$), and one in the left hemisphere ($x = -8$). The fact that we did not observe anterior cingulate activations in previous studies when subjects performed melody repetitions, melody completions, or harmonizations suggests that the anterior cingulate is not involved in simple imitative or generative processing but rather in functions more related to discrimination and error detection. And the fact that activation of the anterior cingulate has not been seen in studies of musical target detection (e.g., Hugdahl et al., 1999; Satoh, Takeda, Nagata, Hatazawa, & Kuzuhara, 2001) may again suggest a more specific role of this area in error detection rather than basic attentional modulation.

4.2.5. Dorsolateral prefrontal cortex

Both discrimination tasks led to activations in the right prefrontal cortex near the junction of BA 46 and

BA 10. This region has been classically associated with working memory processes and the online storage of information during tasks. Such a function would seem to be a requirement for the kinds of same/different discrimination tasks performed in this study. Both tasks showed an exclusive activation in the right hemisphere, consistent with notions of hemispheric asymmetry in the dorsolateral prefrontal cortex that posit that the left prefrontal cortex is dominant for semantically-guided information production whereas the right homologue is dominant for monitoring and verification (Cabeza, Locantore, & Anderson, 2003). Seen from this perspective, the common right-hemisphere activation for the music tasks might be related to shared *processing* features (monitoring), again consistent with this area being important for domain-general, discrimination-related processes dependent upon working memory.

Many other studies of discrimination and target detection for music have observed activations here. Hugdahl et al. (1999) had subjects perform target recognition tasks for particular timbres of musical instruments (i.e., a pool of three instrument sounds and the detection of a given target in particular trials). In addition to seeing principal activations in BA 22 bilaterally, they observed an activation in right BA 46, which may have been involved in working memory for keeping the target in mind. Rao et al. (2001), in an event-related fMRI study, observed a late activation in right BA 46/10/9 for a task involving discrimination of time intervals between tones. Belin et al. (2002) detected right BA 10 activations in a Go/NoGo task that involved the discrimination of sound durations. Griffiths et al. (1999) saw two foci of activation in the right prefrontal cortex when subjects had to make discriminations based on the pitch or duration of six-element tone sequences. Studies that have seen bilateral activations in this region include Zatorre et al.'s (1994) first note/last note pitch discriminations with novel melodies and Tillmann, Janata, and Bharucha's (2003) pitch priming experiments. These results show that musical discrimination tasks that activate the prefrontal cortex have a strong tendency to activate the right hemisphere (and sometimes the left as well), in keeping with general theories of laterality based on stimulus features (Hellige, 1993) but perhaps also processing features (Cabeza et al., 2003).

In sum, we argue that discrimination processing involves a combination of domain-specific sensorimotor areas and domain-general areas involved in working memory and error detection. The former areas seem to be related to vocal planning, highlighting the overlap between discrimination and vocal production. This suggests that discrimination for music is mediated, or might in fact be equivalent to, covert audiovisual integration. Gaab et al. (2003), whose study of pitch discrimination in monophonic melodies most closely matches the task used in the current study, found bilateral activations in the premotor cortex directly abutting the primary mouth representation, just as we did.

4.3. Melody and harmony

In comparing the discrimination of note changes in monophonic melodies (the melody task) with the discrimination of chord changes in harmonized melodies (the harmony task), we found that the activations were highly similar, both in terms of functional brain areas and in terms of lateralization. There were no cortical areas except BA 8 activated by the harmony task that were not also activated by the melody task, although the harmony task uniquely activated parts of the thalamus and midbrain. The analysis of composite images for Melody Discrimination and Harmony Discrimination—as well as direct subtraction of the melody task from the harmony task—validated this point. This result is in strong agreement with our previous findings from a PET study using a completely different approach to the melody/harmony issue (Brown, Parsons, et al., 2004). In that study, we compared vocal repetition of monophonic melodies vs. vocal harmonization in synchrony with the melodic line of a chordal passage. We saw strongly overlapping activations for melody repetition and harmonization, with a greater degree of bilaterality in the harmonization condition than the melody condition. A synthesis of these two studies demonstrates not only a similarity between melody and harmony processing in the brain but a parallel similarity between the perception (i.e., discrimination) and production of music. This provides further validation for our original contention that harmony processing in the brain is contained within a basic melodic system (Brown, Parsons, et al., 2004) and is evolutionarily derived from a melody processing system (Brown, in press).

Acknowledgment

This work was supported by a grant from the Chevron-Texaco Foundation.

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