Available online at www.sciencedirect.com

ScienceDirect

Brain and Cognition 63 (2007) 59–69

Brain and Cognition

www.elsevier.com/locate/b&c

Activation of premotor vocal areas during musical discrimination

Steven Brown *, Michael J. Martinez

Research Imaging Center, University of Texas Health Science Center at San Antonio, USA

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.

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

---

* Corresponding author. Present address: Department of Psychology, Simon Fraser University, Robert C. Brown Hall, 8888 University Drive, Burnaby, BC, Canada V5A 1S6. Fax: +1 604 291 3427.

E-mail address: s_brown@sfu.ca (S. Brown).

0278-2626/$ - see front matter © 2006 Elsevier Inc. All rights reserved.
doi:10.1016/j.bandc.2006.08.006

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