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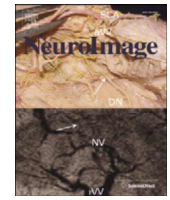

Activations of human auditory cortex to phonemic and nonphonemic vowels during discrimination and memory tasks

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ABSTRACT

We used fMRI to investigate activations within human auditory cortex (AC) to vowels during vowel discrimination, vowel (categorical n-back) memory, and visual tasks. Based on our previous studies, we hypothesized that the vowel discrimination task would be associated with increased activations in the anterior superior temporal gyrus (STG), while the vowel memory task would enhance activations in the posterior STG and inferior parietal lobule (IPL). In particular, we tested the hypothesis that activations in the IPL during vowel memory tasks are associated with categorical processing. Namely, activations due to categorical processing should be higher during tasks performed on nonphonemic (hard to categorize) than on phonemic (easy to categorize) vowels.

As expected, we found distinct activation patterns during vowel discrimination and vowel memory tasks. Further, these task-dependent activations were different during tasks performed on phonemic or nonphonemic vowels. However, activations in the IPL associated with the vowel memory task were not stronger during nonphonemic than phonemic vowel blocks. Together these results demonstrate that activations in human AC to vowels depend on both the requirements of the behavioral task and the phonemic status of the vowels.

Introduction

Human auditory cortex (AC) is believed to have an important role in processing speech-related information (Benson et al., 2001; Binder et al., 2000; Chang et al., 2010; Dehaene-Lambertz et al., 2005; Friederici, 2011; Hickok, 2009; Jäncke et al., 2002; Liebenthal et al., 2005; Obleser et al., 2006; Raizada and Poldrack, 2007; Rauschecker and Scott, 2009; Scott and Johnsrude, 2003; Weinberger, 2011; Woods et al., 2011). It is generally assumed that primary regions in and near Heschl's gyrus (HG) process physical features of sounds whereas regions in the anterior and posterior superior temporal gyrus/sulcus (STG/STS) are important for more speech-specific analysis. In addition to physical and speech-specific features of sounds, AC activations are also strongly affected by the characteristics of the tasks performed during the presentation of speech and nonspeech sounds (Angenstein et al., 2012; Harinen et al., in press; Hickok and Poeppel, 2000, 2007; Hickok and Saberi, 2012; Husain et al., 2006; Leung and Alain, 2011; Liebenthal et al., 2005; Petkov et al., 2004). However, the effects of different listening tasks on AC activations have not been studied systematically.

In a recent fMRI study, we compared AC activations to similar spatially varying sounds during spatial discrimination and spatial memory tasks (Rinne et al., 2012). During a memory task, subjects were required to indicate when a sound belonged to the same spatial category (left, middle or right) as the one presented 1–3 trials (depending on the difficulty level) before. During a discrimination task, subjects indicated when two halves of a sound had the same spatial location. We found that activations in the anterior AC increased during spatial discrimination but not during spatial memory, while activations in the posterior superior temporal gyrus (STG) and inferior parietal lobule (IPL) increased during spatial memory but not during spatial discrimination. These task-dependent activation patterns were almost identical to those observed in our previous study comparing AC activations during pitch discrimination and pitch memory tasks with spatially fixed stimuli (Rinne et al., 2009).

In the present study we investigated AC activations during discrimination and memory tasks performed on phonemic or nonphonemic vowels. We hypothesized that, as several previous studies have reported results suggesting that speech is processed in specialized systems in the AC (e.g., Binder et al., 2000; Chang et al., 2010; Desai et al., 2008; Hickok and Poeppel, 2007; Jäncke et al., 2002; Liebenthal et al., 2005; Obleser et al., 2006; Rauschecker and Scott, 2009; Scott and Johnsrude, 2003), activation patterns during vowel tasks could differ from those observed in our previous studies using pitch and spatial tasks. In particular, the present study tested the possibility that the activations in the posterior STG and IPL associated with the pitch and spatial memory tasks of our previous studies are due to categorical processing required in these tasks. Previous studies have shown that

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activations in these areas increase during tasks requiring categorical processing, during adverse listening conditions, and during demanding tasks (Alain et al., 2010; Chang et al., 2010; Dehaene-Lambertz et al., 2005; Desai et al., 2008; Husain et al., 2006; Leung and Alain, 2011; Obleser et al., 2007; Raizada and Poldrack, 2007; Rinne et al., 2009, 2012; Sabri et al., 2008; Sharp et al., 2010; Turkeltaub and Coslett, 2010). Thus, we hypothesized that activations in the posterior STG and IPL associated with categorical processing should be higher during vowel memory tasks performed on nonphonemic (hard to categorize) than on phonemic (easy to categorize) vowels.

Our subjects were concurrently presented with auditory (vowels) and visual (Gabor gratings) stimulus streams in 15 s blocks alternating with 8 s breaks with no stimuli. The auditory stream consisted of within-category vowel pairs (two 200 ms vowels separated by a 100 ms gap; pair onset-to-onset interval 900–1100 ms) from three phonemic (Finnish phonemes /u/, /a/ and /i/) or nonphonemic categories in all conditions. Each category contained 9 different vowels (Fig. 1a). In the visual task (b), subjects were required to detect Gabor orientation changes and to ignore the task-irrelevant phonemic or nonphonemic vowels. In discrimination tasks (c), subjects were required to indicate when the first and the second parts of the vowel pair were the same. In n-back memory tasks (d), subjects indicated when the vowel pair belonged to the same vowel category as the one presented 1, 2 or 3 trials (depending on the difficulty level; 3-back memory task was performed only on phonemic vowel pairs) before. Both discrimination and memory tasks were performed either on phonemic or nonphonemic vowel pairs in separate blocks. We expected that activations to vowels presented during the visual task (i.e., in the absence of an auditory task) would reveal stimulus dependent processing of vowels and that distinct task-dependent activation patterns would be observed during auditory tasks performed on either phonemic or nonphonemic vowels.

Materials and methods

Subjects

Subjects (N = 22, 13 women) were right-handed, 20–41 years of age (mean 24 years), had normal hearing (self-reported), normal or corrected-to-normal vision, and no history of psychiatric or neurological illnesses. An informed written consent was obtained from each subject before the experiment. The study protocol was approved by the Ethical Committee of the Hospital District of Helsinki and Uusimaa, Finland. All subjects were native Finnish speakers. Data from 6 subjects were rejected due to low performance in the demanding auditory tasks (mean d′ in auditory tasks <1.7).

Stimuli

Vowels (duration 200 ms including a linear 5 ms onset and offset ramp) were synthesized using the Praat software package (version 5.1.12, www.praat.org). The vowels formed three phonemic and three nonphonemic categories with nine vowels in each (Fig. 1a). The phonemic categories were defined based on typical Finnish /a/,

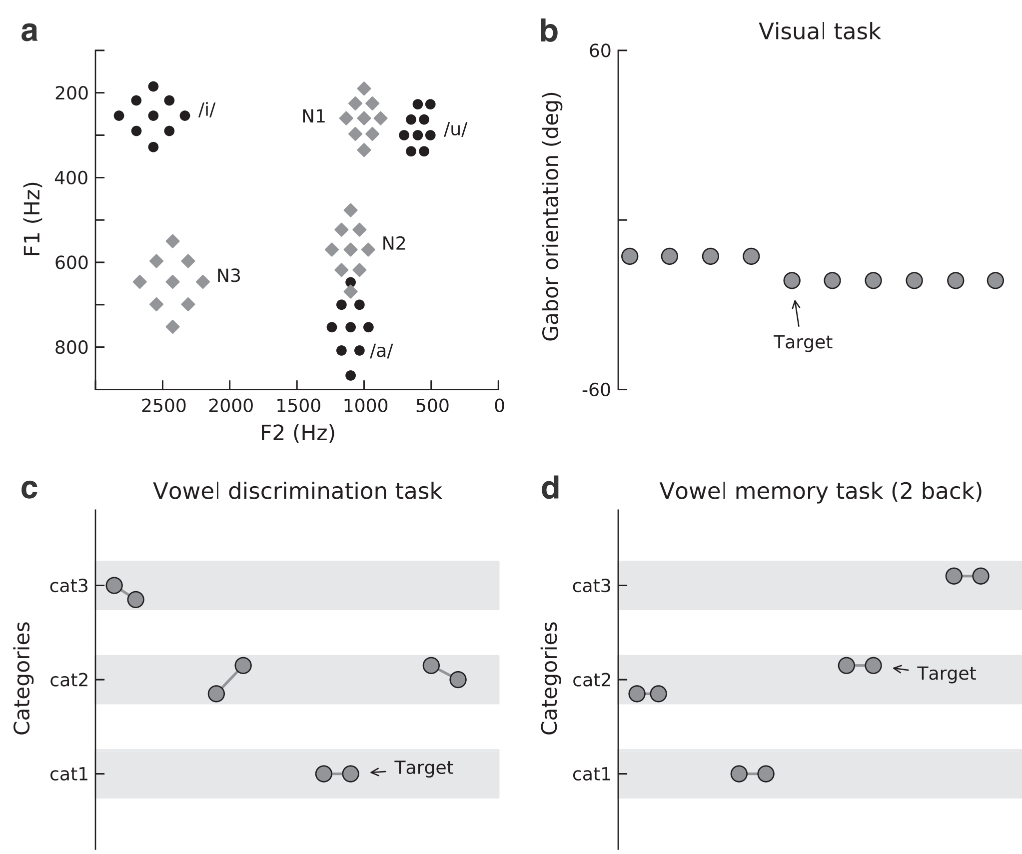

Fig. 1. In 15 s blocks (alternating with 8 s rest with no stimuli), subjects were presented with vowel pairs (two 200 ms vowels separated by a 100 ms gap, onset-to-onset interval 900–1100 ms) from three Finnish phonemic or three nonphonemic vowel categories and Gabor gratings (duration 100 ms, onset-to-onset interval 300–500 ms). (a) The phonemic categories were defined based on typical Finnish /i/, /u/ and /a/ phonemes. The nonphonemic categories (N1, N2 and N3) were organized in regions of F1–F2 space where no prototypical Finnish phonemes exist. Each category contained 9 different vowels. In the visual task (b), subjects were required to detect Gabor orientation changes. In the vowel discrimination task (c), they were required to indicate when the first and the second parts of the vowel pair were the same. In the n-back vowel memory task (d), subjects indicated when the vowel pair belonged to the same vowel category as the one, presented 1, 2 or 3 trials (depending on the difficulty level) before (2-back task is illustrated). In b–d, time scale on the horizontal axis is schematic.