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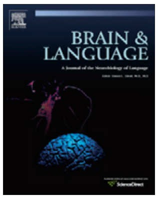

Short Communication

Increased activation in superior temporal gyri as a function of increment in phonetic features

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ABSTRACT

A common assumption is that phonetic sounds initiate unique processing in the superior temporal gyri and sulci (STG/STS). The anatomical areas subserving these processes are also implicated in the processing of non-phonetic stimuli such as music instrument sounds. The differential processing of phonetic and non-phonetic sounds was investigated in this study by applying a "sound-morphing" paradigm, where the presence of phonetic features were parametrically varied, creating a step-wise transition from a non-phonetic sound into a phonetic sound. The stimuli were presented in an event-related fMRI design. The fMRI-BOLD data were analysed using parametric contrasts. The results showed a higher sensitivity for sounds containing phonetic features compared to non-phonetic sounds in the middle part of STG, and in the anterior part of the planum temporale (PT) bilaterally. Although the same areas were involved in the processing of non-phonetic sounds, a difference in activation was evident in the STG, with an increase in activation related to increment of phonetic features in the sounds. The results indicate a stimulus-driven, bottom-up process that utilizes general auditory resources in the secondary auditory cortex, depending on specific phonetic features in the sounds.

1. Introduction

Superior temporal regions, including the primary auditory cortex (PAC) are important for the initial processing of speech sounds such as words, pseudowords, and consonant–vowel syllables (CV) (e.g. Belin, Zatorre, Lafaille, Ahad, & Pike, 2000; Binder et al., 2000; Fecteau, Armony, Joanette, & Belin, 2004; Hugdahl, Thomsen, Ersland, Rimol, & Niemi, 2003; Liebenthal, Binder, Spitzer, Possing, & Medler, 2005; Meyer, Zysset, von Cramon, & Alter, 2005; Specht, Osnes, & Hugdahl, 2009; Specht & Reul, 2003). However, sub-syllabic phonetic sounds such as consonants or vowels are also processed in superior temporal lobe areas (Obleser et al., 2006; Rimol, Specht, Weis, Savoy, & Hugdahl, 2005; Uppenkamp, Johnsrude, Norris, Marslen-Wilson, & Patterson, 2006). Phonetic sounds are processed differentially dependent on voicing, where more rapidly changing speech cues e.g. voiced speech sounds show a greater leftward asymmetry in planum temporale compared to voiceless speech sounds (Griffiths & Warren, 2002; Jancke, Wustenberg, Scheich, & Heinze, 2002).

Whalen et al. (2006) and Benson et al. (2001) view reports of phonetic processing outside PAC as an indication of specialized and domain-specific processes. They argue that only phonetic information is passed on from PAC to specialized areas in the STG for completion of the acoustic analysis, whereas the acoustic analysis of non-phonetic information is completed in PAC. However, non-speech sounds such as noise, tones, and animal sounds also activate areas outside of PAC as shown in several brain imaging studies (e.g. Overath, Kumar, von Kriegstein, & Griffiths, 2008; Rimol et al., 2005; Specht & Reul, 2003; Zaehle, Geiser, Alter, Jancke, & Meyer, 2008). Price, Thierry, and Griffiths (2005) questions on the basis of such reports, the idea that macro-anatomical structures are dedicated to specific speech related processes. They pose an alternative view where the observed brain activation reflects differential demands imposed on a general perceptual system associated with phonetic sounds compared to non-phonetic sounds. In their view, a phonetic sound requires more from a general rather than a different perceptual process, making the underlining mechanism process-specific rather than domain-specific (Price et al., 2005).

The fact that both phonetic and non-phonetic sounds engage the same anatomical locations is not a direct evidence of one common perceptual process. Different processes can still be allocated to the same brain area. An indication of two distinctly different processes could be that phonetic stimuli initiate a qualitatively different activation response than non-phonetic stimuli. Such a

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process could, for example, require a certain level or threshold of phonetic information before specific phonetic processes could emerge. An alternative possibility could be e.g. a linear, logarithmic, or quadratic relationship between the presence of phonetic features in the stimulus to be processed and neuronal activation within a given anatomical area. In this case, processing of phonetic and non-phonetic stimuli would involve an overlapping neuronal pool, where processing of phonetic stimuli puts a higher demand on the same process' resources, as suggested by Price et al. (2005).

The answers to such questions are difficult to infer using only linear activation contrasts from two or more sound categories, e.g. between a phonetic sound and a non-phonetic sound, or silence. A parametric design can reveal neural correlates to gradual or incremental changes within a stimulus category such as a gradual increase in phonetic features. With this design it is possible to test whether area-specific brain activation is linear, quadratic or following an otherwise specific pattern of relationship between increments in stimulus properties and brain activation in specific areas (Aguirre, 2002; Friston, 2003; Wood, Nuerk, Sturm, & Willmes, 2008).

The applied tasks (e.g. passive listening, lexical decision, etc.) and the corresponding load on general cognitive processes is another important aspect when we infer on stimulus-driven processes. The given task influences the magnitude and extension of activation even in primary sensory areas (Jancke, Mirzazade, & Shah, 1999). In fact, cognitive instructions facilitate phonetic and phonological processing even in the absence of speech signals (Dehaene-Lambertz et al., 2005; Dufor, Serniclaes, Sprenger-Charolles, & Demonet, 2007).

To investigate the processing of phonetic features we applied a stimulus design, based on the previously described "sound-morphing" technique (Specht, Rimol, Reul, & Hugdahl, 2005; Specht et al., 2009). In the current study, we varied the presence of a phonetic sound, the vowel /a/ or /o/, within a non-phonetic sound, a flute sound. We interpolated the vowel spectrum linearly into the flute spectrum, resulting in a transition from flute to vowel sound consisting of seven distinct steps. Step 1 was a sound consisting of mainly flute sound features, and vowel sound features increased over the subsequent steps, steps 2–7. Non-phonetic control sounds were created in a similar manner, resulting in a step-wise transition from flute into either an oboe or trumpet sound. We did not inform the participants about the presence of phonetic features in some of the sounds since the expectation of hearing phonetic sounds could trigger phonetic related processing (cfr. Dufor et al., 2007). The participants performed a task that was unrelated to the stimuli properties, in order to keep the attention constant during the data acquisition (Jancke et al., 1999).

We expected particular neuronal sensitivity for phonetic features in the superior temporal gyrus (STG) and planum temporale (PT), which are areas implicated in the processing of phonetic stimuli (Boatman, 2004; Demonet, Thierry, & Cardebat, 2005; Hickok & Poeppel, 2007; Scott & Wise, 2004). We further expected to see a graded increase of activation in these areas related to the relative presence of phonetic features in the stimulus sound.

2. Results

2.1. Whole brain analysis

Parametric analysis of the sounds with phonetic features revealed increasing activity over the seven manipulation steps bilaterally in the posterior part of the temporal lobe comprising STG (BA 22) and anterior parts of PT (BA 21) adjacent to Heschl's gyrus (see Table 1 and Fig. 1). The increase in activity was particularly evident in STG as compared to PT. The parametric analysis for non-phonetic sounds revealed no such significant increase in activation when correcting for FDR at cluster level. There was no significant activation when comparing the phonetic and non-phonetic stimulus categories over the seven manipulation steps when correcting for FDR at cluster level.

2.2. Post-hoc analysis

All estimated models were significant for the sounds with phonetic features; (1) linear, adjusted R square = .625, $F(1,5) = 10.9$, $p < .021$; 2) logarithmic, adjusted R square = .836, $F(1,5) = 31.6$,

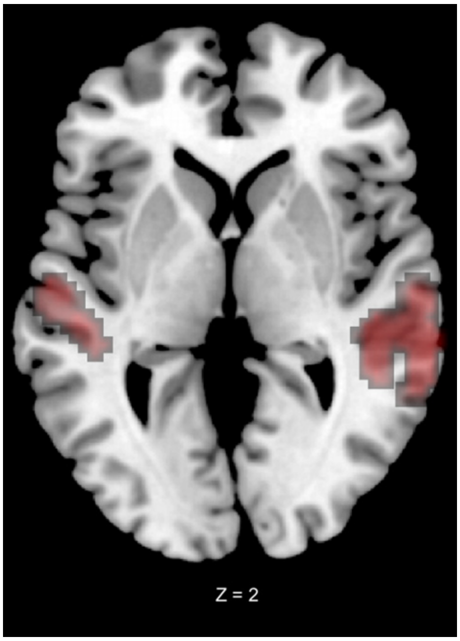

Fig. 1. Parametric t-test of phonetic sounds. Significant increase in bilateral activations comprising middle superior temporal gyrus and planum temporale. FDR corrected threshold of $P < .05$ at cluster level.

Table 1
Significant effects from a parametric analysis of sounds with phonetic features investigated with t statistics. The table describes the activations in terms of cluster size (voxel size $2 \times 2 \times 2$ mm), significance value, and localization (MNI space).

Statistical values				Coordinates			Anatomical location		
Cluster level		Peak-level		x	y	z	Hemisphere	Structure	Brodmann area
K_E	$^{p}FDR_{corr}$	T	P_{corr}						
296	**0.000**	**4.39**	**0.000**	**60**	**−15**	**−3**	**Right**	**STG**	**22**
		4.25	0.000	55	−33	0	Right	MTG	21
		3.94	0.000	48	−30	0	Right	STG/MTG	21
77	**0.035**	**3.79**	**0.000**	**−60**	**−12**	**6**	**Left**	**STG**	**22**
		3.77	0.000	−45	−33	3	Left	STG/MTG	21

Note: Contrasts were FDR corrected = .05 at cluster level. The primary maximum per cluster is set in bold. STG = superior temporal gyrus, MTG = middle temporal gyrus.