

Speech-specific auditory processing: where is it?

Cathy Price¹, Guillaume Thierry² and Tim Griffiths³

¹Wellcome Department of Imaging Neuroscience, Institute of Neurology, London, WC1N 3BG, UK

²School of Psychology, University of Wales, Bangor, UK

³Newcastle University Medical School, Newcastle upon Tyne, UK

Are speech-specific processes localized in dedicated cortical regions or do they emerge from developmental plasticity in the connections among non-dedicated regions? Here we claim that all the brain regions activated by the processing of auditory speech can be re-classified according to whether they respond to non-verbal environmental sounds, pitch changes, unfamiliar melodies, or conceptual processes. We therefore argue that speech-specific processing emerges from differential demands on auditory and conceptual processes that are shared by speech and non-speech stimuli. This has implications for domain- vs. process-specific cognitive models, and for the relative importance of segregation and integration in functional anatomy.

Introduction

An increasingly popular trend in cognitive neuroscience is to label macro-anatomical brain structures with functional labels that correspond to those generated by classical behavioural paradigms. For example, in the domain of reading, an area in the left occipito-temporal sulcus has been labelled the visual word form area (VWFA) [1]. These labels generate the impression that there are brain structures dedicated to the cognitive functions they describe. Moreover, this controversial approach allows the same brain areas to have multiple functional labels that depend on the investigators' field of interest. For example, the visual word form area [1] has also been labelled the 'lateral occipital tactile-visual area' [2].

The alternative, but more difficult approach, is to identify functional labels that describe the process driving activation. This requires a two-way line of investigation: in addition to the conventional delineation of brain areas that respond to a pre-specified function, we also need to identify the functions that activate a pre-specified brain area. In this article, we adopt this alternative approach by considering the non-verbal stimuli and tasks that activate auditory speech processing areas. The speech processing areas we consider have been defined on the basis of group studies. In other words, we are focusing on functional anatomy that is consistent over populations rather than unique to any one individual (see Box 1). Our claim is that, contrary to popular belief, the human brain has not

developed macro-anatomical brain structures that are dedicated to speech processing. Instead, we argue that speech-specific processing emerges at the level of functional connectivity among distributed brain regions, each of which participates in processes that are engaged by both speech and non-speech tasks.

Left hemisphere auditory processing of speech

Auditory processing of meaningful speech involves several auditory and linguistic processes that include, at least, (i) on-line analysis of the spectrotemporal structure of the acoustic stimulus; (ii) recognition of phonetic cues and features; (iii) syntactic analysis; and (iv) access to and retrieval of semantic information. Functional neuroimaging

Box 1. Characterizing neuronal populations with haemodynamic functional imaging

In this article, we have defined activation as being in the same area if the peak coordinates of each effect are less than 6 mm apart in all three (x, y, and z) directions. By focusing on peak activations only, we have excluded edge effects from spatially proximate areas. We have shown that, even in this context, non-speech activation overlaps with speech activation. Within the macro-anatomical areas that we refer to, speech and non-speech processing can either rely on (1) the same neuronal populations, or (2) different, functionally independent, neuronal populations that are in close spatial proximity. Standard haemodynamic functional imaging techniques cannot distinguish these possibilities: in individual subject analyses, the accuracy with which an activation is located is typically 4–6mm in PET and 3–6mm in fMRI (depending on the voxel size) but, at the group level, localization is less accurate because of individual differences in functional anatomy. Spatial smoothing will also limit the resolution of two spatially proximate activations. Therefore, if there are micro-anatomical regions with differential sensitivity to speech and non-speech, their resolution with fMRI will require single subject analyses without spatial normalization and smoothing [49–51].

Neuronal adaptation techniques in fMRI [52,53] can also be informative. The assumption is that, if the response to stimulus Y is less when it is preceded by stimulus X, then stimulus X must be 'adapting' the same neuronal population that responds to stimulus Y. In other words, if there are different neuronal populations for speech and non-speech stimuli, then activation for speech might be less when it is preceded by speech than when it is preceded by non-speech, even if the neuronal populations for speech and non-speech are spatially overlapping (i.e. located in the same area).

In summary, asserting that different functions activate the same area depends crucially on the precision with which activation is located. For PET and fMRI, spatial precision can be improved by examining data at the individual subject level and adopting experimental designs that use neuronal adaptation techniques to segregate functional populations.

Corresponding author: Price, C. (c.price@fil.ion.ucl.ac.uk).

Available online 5 April 2005

allows us to test whether these processes are linked to specific brain regions, and if so, what the response properties of these regions are. Many functional imaging studies have demonstrated that auditory speech processing activates extensive regions in the vicinity of the left superior temporal sulcus, even when attempts are made to control for non-linguistic processing [3–15]. These speech-selective activations can be classified in terms of areas that are (i) activated by speech more than all other stimuli/tasks; or (ii) equally activated by speech and non-speech tasks. For example, Thierry *et al.* [12] compared auditory processing of speech and environmental sound sequences matched for duration, rhythm, content and interpretability. A set of areas was identified as commonly activated by the perception and comprehension of both stimulus types, irrespective of task difficulty, including the left inferior frontal and posterior temporal areas that are traditionally associated with language-specific functions. In addition, Thierry *et al.* [12] identified areas that were more activated by speech than by environmental sounds – but what does this mean? Do these regions process only speech; or do they take part in non-linguistic processes that are more strongly engaged by speech than other stimuli? If the latter is true, then understanding the non-linguistic processes that activate ‘speech’ areas would give us insight into how speech processing emerges at the functional level.

To substantiate our claims, we take a set of candidate speech areas and determine the non-linguistic processes that activate them. Our regions of interest are those that were activated by speech more than environmental sound perception and comprehension in the study by Thierry *et al.* [12] (Figure 1a). All other speech areas, such as the left posterior temporo-parietal cortex, were excluded because they were measured as being equally activated by speech and environmental sounds. Therefore, within the resolution of our imaging technique (see Box 1), these shared areas cannot be dedicated to speech.

We consider five discrete areas of activation (labeled A to E in Figure 1). At the very least, we would expect these areas to include activation related to the analysis of phonetic features involved in speech but not environmental sound processing. Previous studies have demonstrated that anterior superior temporal responses (areas A and E in Figure 1) are greater for intelligible than unintelligible speech, whereas the most posterior area (area B) responds to both intelligible and unintelligible speech samples [3]. Scott and colleagues have therefore associated the posterior aspect of the superior temporal sulcus with analysis of the phonetic cues and features linked to the temporal ordering of acoustic events; and the left anterior superior temporal areas with ‘intelligibility’ (word form recognition and beyond) [3].

In the following sections, we discuss a series of published experiments showing that each of the speech areas identified in Figure 1 also responds to either environmental sound, melody, pitch or conceptual-level processes. Although the results of these studies are consistent with the conclusions of Scott and colleagues, they also highlight the non-verbal acoustic and conceptual

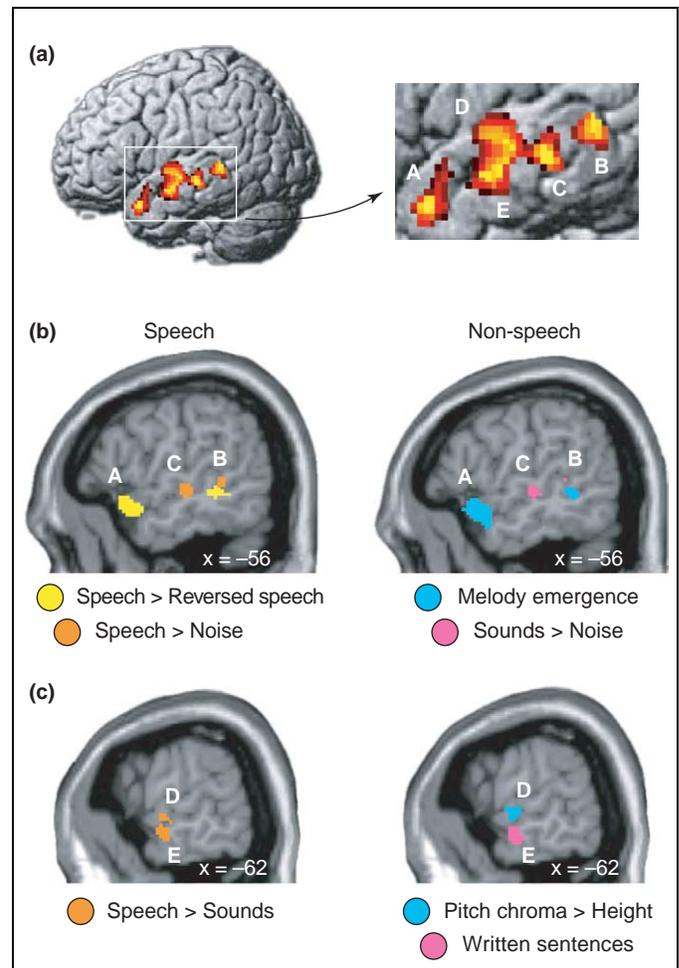


Figure 1. Left hemisphere speech areas. (a) Our five regions of interest (A, B, C, D and E) identified on the basis of activation for semantic decisions on speech relative to environmental sounds [12] (following re-analysis of the data with 6 mm smoothing). (b) Peak activation (56 mm left, according to [54]) for speech compared with reversed speech (yellow) [24]; speech compared with noise (orange) [12]; melody emergence (blue) [23]; and environmental sounds compared with noise (pink) [12]. (c) Peak activation (62 mm left according to [54]) for speech compared with environmental sounds (orange) [12]; pitch chroma compared with pitch height (blue) [27]; and written sentences compared with randomized words (pink) [29]. To isolate the highest point of activation only, different thresholds are used for each comparison (range: $t=3.1$; $p<0.001$ uncorrected, to $t=4.7$, $p<0.05$ corrected for multiple comparisons across the entire brain). Details of the loci of these activations are listed in Table 1.

mechanisms that underlie speech perception and comprehension.

Environmental sound processing

We start by considering whether the areas that are activated by speech more than environmental sounds were also activated by environmental sounds relative to meaningless stimuli. This can be addressed in the study published by Thierry *et al.* [12], which included sequences of environmental sounds, spoken words, meaningless scrambled environmental sounds and meaningless scrambled speech. Activation peaks for speech and environmental sounds relative to their scrambled counterparts, in the areas activated by speech relative to environmental sounds (A–E) are listed in Table 1. As can be seen, in areas A¹, B¹, C, and D, peak activation for environmental sounds relative to scrambled sounds was within 6 mm of activation for speech relative to scrambled

Table 1. Location of speech and non-speech activation peaks illustrated in Figure 1

Activation	Speech Sentences	Speech Sentences	Speech Words	Sounds Meaningful	Written Sentences	Music Melody	Pitch Chroma
Baseline	Sounds	Noise	Reversed sp.	Noise	Words	Emergence	Height
Region							
A ¹	-46 14 -22	-46 14 -24		-50 18 -24			
A ²	-56 10 -14	-56 10 -16	-50 8 -16			-56 10 -12	
B ¹	-58 -38 2	-56 -40 2		-58 -38 6		-60 -36 0	
B ²			-54 -42 -4			-58 -42 -2	
C	-56 -24 -6	-58 -22 -4		-54 -22 -2			
D	-58 -12 2	-62 -8 -2		-62 -8 0			-58 -2 -2
E	-62 -6 -10	-64 -6 -8			-66 -10 -12		

Three dimension coordinates (x y z) of peak activation according to Talairach and Tournoux [54] for comparisons reported in Figure 1, using the same colour scheme. Sounds=meaningful sequences of environmental sounds; Reversed sp.=auditory speech after digital reversal.

speech. Only one of our candidate speech areas (E), located anteriorly in the left middle temporal gyrus, was activated by speech but not environmental sounds. Given the nature of the task (conceptual decisions), activation in areas elicited both by speech and environmental sounds (A–D) could be related to auditory or conceptual processes that are common to speech and environmental sounds, even though they are more involved in the processing of speech.

Music processing

In this section, we illustrate the spatial correspondence between music and speech activations [16–22] using data previously published by Griffiths *et al.* [23]. The stimuli were sequences of sounds at regular time intervals associated with pitch, where the temporal regularity and associated pitch value were systematically varied. Within sequences, the perceived pitch value was changed according to a pattern (an unfamiliar tonal melody), or remained constant (repetition of the same note). The effect of increasing the number of pitch changes in the melody relative to the constant pitch condition can be regarded as the emergence of melody. This was associated with activation in anterior and posterior regions of the superior temporal sulci [23] that also respond to hearing words compared with reversed words [24]. As both paradigms only required participants to attend to the auditory stimuli, activation is unlikely to reflect a verbal strategy. It might, however, relate to processes that are shared by both melody and speech processing. For instance, various authors have emphasized that both music and speech involve prosodic [25,26], syntactic [22], and even conceptual [21] processes. Alternatively, because melodies require sound information to be integrated over relatively long time frames (seconds rather than milliseconds), activation during analysis of the supra-segmental structure of the auditory stimulus (i.e. speech prosody and melody) might be an adequate explanation.

With respect to the different functions of the anterior and posterior temporal areas (A and B), the anterior region has been reported to respond to intelligible speech more than unintelligible speech whereas the posterior area has been associated with phonetic cues and features [3]. As neither of these processes is required in melody processing, we hypothesize that the anterior area (A) could be involved in integration of sound sequences that take place over a longer timescale than the posterior area (B).

Pitch dimensional processing

We now consider the response properties of area D, which was activated by speech and environmental sounds [12] but with no discrete peak during melodic processing [23]. Nevertheless, area D does appear to be activated in the study of Warren *et al.* [27] where the stimuli were harmonic complexes associated with pitch that could vary in the dimensions of either pitch height (high vs. low frequencies; an important feature for the discrimination of sources, such as male and female voices) or pitch chroma (the value or name of the note within a given octave; important for the production of pitch patterns over time, such as melodies or prosody in speech). Pitch chroma variation activated areas anterior to the primary auditory cortex whereas pitch height variation activated areas posterior to the primary auditory cortex. More specifically, activation for pitch chroma relative to pitch height overlapped with the ‘speech area’ that we labelled as D (Figure 1). Warren *et al.* [27] proposed that this area is involved in the ‘tracking of acoustic information’ (as opposed to the analysis of the sound source). Greater activation in area D for speech relative to environmental sound processing is consistent with such an explanation as speech is heavily reliant on the temporal ordering of acoustic changes.

Conceptual processing

Of the five areas activated by words relative to environmental sounds [12], only one, area E, failed to show activation in the environmental sound, pitch- or melody-processing paradigms. Activation within 6 mm of area E has previously been reported by Scott *et al.* [3] for normal speech relative to speech with an inverted spectral envelope. Area E is not specific to speech, however, because it is also engaged by conceptual processing of visual words or pictures [28–30]. For example, conceptual decisions on pictures of objects [28–30] activate an area located at (–64, –12, –14) and the same area is activated when written words are visually presented in a grammatical order compared with a random order [29] (see Figure 1 and Table 1).

In summary, areas that are more activated for speech than environmental sounds are also engaged by environmental sound, pitch, melody or non-auditory conceptual processing. In line with previous conclusions [3,9], the ventral middle temporal cortex (E) is more responsive to comprehension processes whereas the dorsal regions

(B, C and D) appear to be more involved in the processing of acoustic features.

Right hemisphere processing and laterality issues

Speech comprehension is classically associated with the left temporal lobe [31] but the right hemisphere also contributes to speech processing. Figure 2 illustrates that a right anterior temporal area (A) is activated by speech and melodies; right mid-temporal regions (C and E) are activated by speech and environmental sounds. In contrast to these areas, a right posterior temporal area (B) is activated by environmental sounds and melodies but not speech. Direct comparison of speech with environmental sound processing has established that the right posterior temporal area is activated by environmental sounds more than speech during semantic decisions [12]. Moreover, anterior and posterior right superior temporal regions are activated by tasks that tap voice relative to verbal content [32]. Direct comparisons between speech and melody processing, however, have failed to show significant differences in either the left or the right temporal lobe [16–19], despite a general consensus that speech engages the left hemisphere more than the right, and music engages the right hemisphere more than the left [33,34].

Implications for functional and physiological models

At a functional level, recognition of speech relative to other acoustic signals: (i) is more dependent on the precise temporal arrangement of spectro-temporal features, such as noise bursts, silent gaps and formant transitions; (ii) is most intrinsically linked to speech production processes [35,36]; and (iii) has the richest, most subject-independent, conceptual associations. Our point is that none of these characteristics necessitate brain regions dedicated to speech processing. The neural substrate analyzing frequency and amplitude changes could, for example, be the same for speech, environmental sounds and music

processing with greater demands on this system during speech. Linguistic experience modulates neuronal responses [37,38] but this could reflect changes in synaptic efficacy (the strength of synaptic connections), synaptic density (the number of axonal terminals), and/or the timing of neuronal responses [39,40] within processing regions that are shared by several functional systems. Likewise, the strong motor and conceptual activation evoked by speech input [36] might reflect experience-dependent connections to speech production and semantic areas.

Our claims might appear to conflict with neuropsychological reports that speech deficits can dissociate from deficits in music or environmental sound processing [41,42] (although see [43]). The classic interpretation of selective speech deficits is that a lesion has damaged cortical areas or connections that are necessary for the processing of speech but not sounds. How can the apparent discrepancy between neuropsychological and functional imaging results be resolved? One possibility is that, although speech processing areas are activated by non-speech stimuli, these areas are necessary only for speech recognition but not for music/sound recognition [44]. Alternatively, it might be that functional specialization for speech or music processing does not rely on specific, discrete cortical regions in the vicinity of the superior temporal sulcus but rather on the functional connections between auditory association cortices and high-level integrative networks involved in decision-making, response planning, motor processing, and so forth. Hence, lesions that disrupt speech comprehension more than music could conceivably be a consequence of damage to the connections between speech perception areas and speech production areas in the left hemisphere, whereas lesions that disrupt music more than speech could be a consequence of damage to limbic connections in the right hemisphere. Similarly, lesions that selectively disrupt environmental sound processing might be a consequence

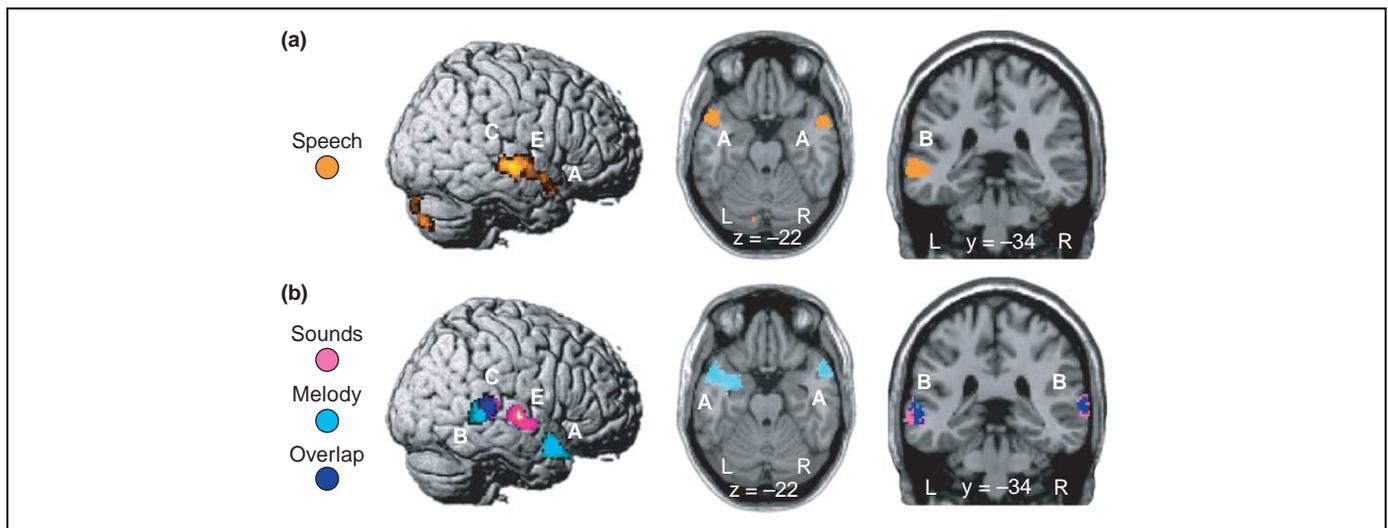


Figure 2. Right hemisphere response to auditory stimuli. (a) Activation for speech compared with environmental sounds [12]. Areas A, C and E correspond to their homologues in Figure 1. (b) Activation for environmental sounds compared with noise (pink) [12]; melody emergence (light blue) [23]; and the overlap (dark blue). Left panels in both (a) and (b): activation rendered onto the surface of a canonical model of the right hemisphere. Middle panels: axial slices (z plane) 22 mm below the ac–pc line [54]. Right panels: coronal slices (y plane) 34 mm posterior to the ac–pc line. L = left hemisphere; R = right hemisphere. (As in Figure 1, the threshold for activation ranged from $t = 3.1$ to 4.7).

of damage to right hemisphere connections to and from a widespread conceptual system. Indeed, it is well-established that top-down regulation from higher level integrative regions plays a fundamental role in perception [45,46].

Top-down regulation from high-level integrative regions can also explain the categorical nature of speech perception as illustrated by phenomena such as the bistable perception of 'sine-wave' speech [47]. Recent work [48] implicates the inferior frontal cortex in such categorical sorting. In our model, speech recognition is considered to emerge from the connectivity between (generic) auditory areas and such frontal lobe regions. To summarize, we believe that to build functional and physiological models of auditory speech processing, we require a better understanding of functional connectivity, synaptic efficacy, and neuronal transients in addition to the characterization of the processes that drive activation in discrete cortical regions.

Conclusions

In this article, we have argued that there are no macro-anatomical structures dedicated to speech in the human brain. This does not exclude the possibility that other neurophysiological techniques such as depth electrode recordings could, in the future, reveal local functional specialization at a smaller, micro-anatomical scale (see Box 1). Nevertheless, we can accommodate the absence of speech-specific brain regions by hypothesizing that speech processing emerges from differential demands on resources shared by both verbal and non-verbal auditory processing. In other words, we are claiming that speech and linguistic processing stem from changes in the functional integration among acoustic and conceptual regions that are also engaged by non-verbal stimuli. More generally, our arguments challenge the notion that language functions can simply be localized in dedicated cortical structures.

Further experiments are required for a better specification of anatomical connections between the brain areas activated by higher cognitive operations. Such investigations could be based on neuroanatomy, *in vivo* neurophysiology, diffusion tensor imaging, or a combination of these techniques. Equally crucial is the specification of the functional connectivity between brain areas during speech processing as compared with other tasks [32]. This in turn should lead to models of speech comprehension that integrate data from both functional and physiological approaches.

Acknowledgements

C.P. and T.G. are supported by the Wellcome Trust. G.T. is supported by the BBSRC and the ESRC.

References

- Cohen, L. *et al.* (2000) The visual word form area: spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain* 123, 291–307
- Amedi, A. *et al.* (2002) Convergence of visual and tactile shape processing in the human lateral occipital complex. *Cereb. Cortex* 12, 1202–1212
- Scott, S.K. *et al.* (2000) Identification of a pathway for intelligible speech in the left temporal lobe. *Brain* 123, 2400–2406
- Davis, M.H. and Johnsrude, I.S. (2003) Hierarchical processing in spoken language comprehension. *J. Neurosci.* 23, 3423–3431
- Joanisse, M.F. and Gati, J.S. (2003) Overlapping neural regions for processing rapid temporal cues in speech and nonspeech signals. *Neuroimage* 19, 64–79
- Binder, J.R. *et al.* (2000) Human temporal lobe activation by speech and nonspeech sounds. *Cereb. Cortex* 10, 512–528
- Crinion, J.T. *et al.* (2003) Temporal lobe regions engaged during normal speech comprehension. *Brain* 126, 1193–1201
- Giraud, A.L. and Price, C.J. (2001) The constraints functional neuroimaging places on classical models of word processing. *J. Cogn. Neurosci.* 13, 1–12
- Giraud, A.L. *et al.* (2004) Contributions of sensory input, auditory search and verbal comprehension to cortical activity during speech processing. *Cereb. Cortex* 14, 247–255
- Jancke, L. *et al.* (2002) Phonetic perception and the temporal cortex. *Neuroimage* 15, 733–746
- Mummery, C.J. *et al.* (1999) Functional neuroimaging of speech perception in six normal and two aphasic subjects. *J. Acoust. Soc. Am.* 106, 449–457
- Thierry, G. *et al.* (2003) Hemispheric dissociation in access to the human semantic system. *Neuron* 38, 499–506
- Vouloumanos, A. *et al.* (2001) Detection of sounds in the auditory stream: event-related fMRI evidence for differential activation to speech and nonspeech. *J. Cogn. Neurosci.* 13, 994–1005
- Narain, C. *et al.* (2003) Defining a left-lateralized response specific to intelligible speech using fMRI. *Cereb. Cortex* 13, 1362–1368
- Specht, K. and Reul, J. (2003) Functional segregation of the temporal lobes into highly differentiated subsystems for auditory perception: an auditory rapid event-related fMRI-task. *Neuroimage* 20, 1944–1954
- Hickok, G. *et al.* (2003) Auditory-motor interaction revealed by fMRI: speech, music, and working memory in area Spt. *J. Cogn. Neurosci.* 15, 673–682
- Hugdahl, K. *et al.* (1999) Brain activation during dichotic presentations of consonant-vowel and musical instrument stimuli: a ¹⁵O-PET study. *Neuropsychologia* 37, 431–440
- Tervaniemi, M. *et al.* (2000) Lateralized automatic auditory processing of phonetic versus musical information: a PET study. *Hum. Brain Mapp.* 10, 74–79
- Zatorre, R.J. *et al.* (1992) Lateralization of phonetic and pitch discrimination in speech processing. *Science* 256, 846–849
- Koelsch, S. *et al.* (2002) Bach speaks: a cortical 'language-network' serves the processing of music. *Neuroimage* 17, 956–966
- Koelsch, S. *et al.* (2004) Music, language and meaning: brain signatures of semantic processing. *Nat. Neurosci.* 7, 302–307
- Maess, B. *et al.* (2001) Musical syntax is processed in Broca's area: an MEG study. *Nat. Neurosci.* 4, 540–545
- Griffiths, T.D. *et al.* (1998) Analysis of temporal structure in sound by the human brain. *Nat. Neurosci.* 1, 422–427
- Price, C.J. *et al.* (1996) Hearing and saying: the functional neuroanatomy of auditory word processing. *Brain* 119, 919–931
- Patel, A.D. and Daniele, J.R. (2003) An empirical comparison of rhythm in language and music. *Cognition* 87, B35–B45
- Thompson, W.F. *et al.* (2003) Perceiving prosody in speech. Effects of music lessons. *Ann. N. Y. Acad. Sci.* 999, 530–532
- Warren, J.D. *et al.* (2003) Separating pitch chroma and pitch height in the human brain. *Proc. Natl. Acad. Sci. U. S. A.* 100, 10038–10042
- Vandenberghe, R. *et al.* (1996) Functional anatomy of a common semantic system for words and pictures. *Nature* 383, 254–256
- Vandenberghe, R. *et al.* (2002) The response of left temporal cortex to sentences. *J. Cogn. Neurosci.* 14, 550–560
- Gorno-Tempini, M.L. *et al.* (1998) The neural systems sustaining face and proper-name processing. *Brain* 121, 2103–2118
- Wernicke, C. (1874) *Der Aphasische Symptomenkomplex*, Cohen & Weigert
- Kriegstein, K.V. and Giraud, A.L. (2004) Distinct functional substrates along the right superior temporal sulcus for the processing of voices. *Neuroimage* 22, 948–955
- Zatorre, R.J. *et al.* (2002) Structure and function of auditory cortex: music and speech. *Trends Cogn. Sci.* 6, 37–46
- Hickok, G. and Poeppel, D. (2000) Towards a functional neuroanatomy of speech perception. *Trends Cogn. Sci.* 4, 131–138

- 35 Watkins, K. and Paus, T. (2004) Modulation of motor excitability during speech perception: the role of Broca's area. *J. Cogn. Neurosci.* 16, 978–987
- 36 Wilson, S.M. *et al.* (2004) Listening to speech activates motor areas involved in speech production. *Nat. Neurosci.* 7, 701–702
- 37 Naatanen, R. *et al.* (1997) Language-specific phoneme representations revealed by electric and magnetic brain responses. *Nature* 385, 432–434
- 38 Liebenthal, E. *et al.* (2003) Short-term reorganization of auditory analysis induced by phonetic experience. *J. Cogn. Neurosci.* 15, 549–558
- 39 Phillips, C. *et al.* (2000) Auditory cortex accesses phonological categories: an MEG mismatch study. *J. Cogn. Neurosci.* 12, 1038–1055
- 40 Parviainen, T. *et al.* Cortical differentiation of speech and nonspeech sounds at 100 ms: implications for dyslexia. *Cereb. Cortex* (in press)
- 41 Yaqub, B.A. *et al.* (1988) Pure word deafness (acquired verbal auditory agnosia) in an Arabic speaking patient. *Brain* 111, 457–466
- 42 Tanaka, Y. *et al.* (1987) Pure word deafness following bilateral lesions. A psychophysical analysis. *Brain* 110, 381–403
- 43 Saygin, A.P. *et al.* (2003) Neural resources for processing language and environmental sounds: evidence from aphasia. *Brain* 126, 928–945
- 44 Price, C.J. *et al.* (1999) Delineating necessary and sufficient neural systems with functional imaging studies of neuropsychological patients. *J. Cogn. Neurosci.* 11, 371–382
- 45 Silbersweig, D.A. and Stern, E. (1998) Towards a functional neuroanatomy of conscious perception and its modulation by volition: implications of human auditory neuroimaging studies. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 353, 1883–1888
- 46 Engelien, A. *et al.* (2000) The neural correlates of 'deaf-hearing' in man: conscious sensory awareness enabled by attentional modulation. *Brain* 123, 532–545
- 47 Remez, R.E. *et al.* (2001) On the bistability of sine wave analogues of speech. *Psychol. Sci.* 12, 24–29
- 48 Binder, J.R. *et al.* (2004) Neural correlates of sensory and decision processes in auditory object identification. *Nat. Neurosci.* 7, 295–301
- 49 Kim, K.H. *et al.* (1997) Distinct cortical areas associated with native and second languages. *Nature* 388, 171–174
- 50 Haxby, J.V. *et al.* (2001) Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science* 293, 2425–2430
- 51 Ishai, A. *et al.* (2000) The representation of objects in the human occipital and temporal cortex. *J. Cogn. Neurosci.* 12(Suppl 2), 35–51
- 52 Grill-Spector, K. and Malach, R. (2001) fMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychol. (Amst.)* 107, 293–321
- 53 Henson, R.N. and Rugg, M.D. (2003) Neural response suppression, haemodynamic repetition effects, and behavioural priming. *Neuropsychologia* 41, 263–270
- 54 Talairach, J. and Tournoux, P. (1988) *Co-Planar Stereotaxic Atlas of the Human Brain*, Thieme

Have you contributed to an Elsevier publication?

Did you know that you are entitled to a 30% discount on books?

A 30% discount is available to ALL Elsevier book and journal contributors when ordering books or stand-alone CD-ROMs directly from us.

To take advantage of your discount:

1. Choose your book(s) from www.elsevier.com or www.books.elsevier.com

2. Place your order

Americas:

TEL: +1 800 782 4927 for US customers

TEL: +1 800 460 3110 for Canada, South & Central America customers

FAX: +1 314 453 4898

E-MAIL: author.contributor@elsevier.com

All other countries:

TEL: +44 1865 474 010

FAX: +44 1865 474 011

E-MAIL: directorders@elsevier.com

You'll need to provide the name of the Elsevier book or journal to which you have contributed. Shipping is FREE on pre-paid orders within the US, Canada, and the UK.

If you are faxing your order, please enclose a copy of this page.

3. Make your payment

This discount is only available on prepaid orders. Please note that this offer does not apply to multi-volume reference works or Elsevier Health Sciences products.

For more information, visit www.books.elsevier.com