

Relations between the Neural Bases of Dynamic Auditory Processing and Phonological Processing: Evidence from fMRI

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Abstract

■ Functional magnetic resonance imaging (fMRI) was used to examine how the brain responds to temporal compression of speech and to determine whether the same regions are also involved in phonological processes associated with reading. Recorded speech was temporally compressed to varying degrees and presented in a sentence verification task. Regions involved in phonological processing were identified in a separate scan using a rhyming judgment task with pseudo-words compared to a lettercase judgment task. The left inferior frontal and left superior temporal regions (Broca's and Wernicke's areas), along with the right inferior frontal cortex, demonstrated a convex response to speech compression; their activity increased as compression increased, but then de-

creased when speech became incomprehensible. Other regions exhibited linear increases in activity as compression increased, including the middle frontal gyri bilaterally. The auditory cortices exhibited compression-related decreases bilaterally, primarily reflecting a decrease in activity when speech became incomprehensible. Rhyme judgments engaged two left inferior frontal gyrus regions (pars triangularis and pars opercularis), of which only the pars triangularis region exhibited significant compression-related activity. These results directly demonstrate that a subset of the left inferior frontal regions involved in phonological processing is also sensitive to transient acoustic features within the range of comprehensible speech. ■

INTRODUCTION

Speech is composed of elementary phonetic units, which are represented by acoustic features in the auditory signal and are considered to correspond to discrete abstract linguistic entities, called phonemes. Speech perception is often characterized as the mapping of the continuous, rapidly changing acoustic signal onto phonemic representations. In order to identify phonemes, one must be able to distinguish acoustic features changing over the course of milliseconds. In particular, essential linguistic distinctions (such as differences between consonants) depend upon the ability to distinguish rapid changes in the frequencies of acoustic energy peaks known as formant transitions. Processing of such transient acoustic features (which we will refer to as dynamic auditory processing) is impaired in a number of language disorders, including developmental dyslexia (Tallal, 1980), specific language impairment (Tallal & Piercy, 1973), and pure word deafness (Phillips

& Farmer, 1990; Auerbach, Allard, Naeser, Alexander, & Albert, 1982).

Neural Substrates of Dynamic Auditory Processing

The neural substrates of the processing of transient acoustic information are not well understood, but it appears that both the left auditory and left frontal cortices may be involved. Bilateral lesions to the auditory cortex can result in a syndrome known as "pure word deafness," which is associated with deficits in speech perception and in the processing of transient acoustic information (Phillips & Farmer, 1990; Auerbach et al., 1982). Using magnetoencephalography (MEG), Nagarajan et al. (1999) demonstrated that normal subjects exhibited discrete successive left-hemisphere M100 responses to rapidly successive acoustic stimuli, whereas dyslexic subjects who were impaired on psychophysical tests of dynamic acoustic processing failed to exhibit such discrete successive responses. The M100 response is thought to arise from the auditory cortex, suggesting that auditory cortical function is closely related to psychophysical ability on tests of dynamic acoustic processing. Additional evidence from intracortical re-

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cordings in human auditory cortex demonstrates that the left auditory cortex responds differentially to acoustic stimuli depending upon the temporal arrangement of acoustic features (e.g., voiced vs. voiceless stop consonants), and that this differential response occurred both for speech and nonspeech analogue stimuli (Liegeois-Chauvel, de Graaf, Laguitton, & Chauvel, 1999).

The left prefrontal cortex has been implicated in dynamic auditory processing by studies using PET and fMRI to compare processing of sounds with either transient or steady-state acoustic features, but the localization of this function in the left prefrontal cortex has been inconsistent across studies. Fiez et al. (1995) used PET to examine the processing of both linguistic and nonlinguistic stimuli with either rapidly changing or steady-state acoustic features. A region in the left frontal operculum (BA 44) was more active during the processing of transient versus steady-state stimuli regardless of the linguistic content of the stimuli. Other studies have found activation in the left dorsolateral prefrontal cortex (BA 46/9/10) during the processing of nonspeech analogues with rapid spectral transitions using PET (Belin et al., 1998) and fMRI (Temple et al., 2000). Another study (Johnsrude, Zatorre, Milner, & Evans, 1997) examined the discrimination of pure tones with either short- or long-duration frequency glides, and found greater activation in the left orbito-frontal cortex for short-duration glides (i.e., rapid frequency transitions).

Neural Substrates of Phonological Processing

Phonological processing refers to a set of cognitive processes related to the processing of speech sounds. In speech perception, phonological processing involves the mapping of acoustic features onto linguistic representations, both at the level of single phonemes and at the level of whole words. Neuroimaging studies have examined the perception of spoken words compared to silence (Dhankhar et al., 1997; Fiez, Raichle, Gbalota, Tallal, & Petersen, 1996; Price et al., 1996; Warburton

et al., 1996; Binder et al., 1994; Mazoyer et al., 1993; Petersen, Fox, Posner, Mintun, & Raichle, 1988), words compared to reversed speech (Price et al., 1996), syllables compared to noise (Zatorre, Evans, Meyer, & Gjedde, 1992), and words in a native language compared to words in an unknown language (Schlosser, Aoyagi, Fulbright, Gore, & McCarthy, 1998). Although there is variability in the precise localization of activity across studies (cf. Demonet, Fiez, Paulesu, Petersen, & Zatorre, 1996), most of these studies have found speech-related activity in the posterior part of the superior temporal gyrus/sulcus, along with the left inferior frontal gyrus. Similar regions have been identified in studies where subjects performed phonological monitoring tasks (Demonet et al., 1992; Demonet, Price, Wise, & Frackowiak, 1994; Zatorre et al., 1992; Zatorre, Meyer, Gjedde, & Evans, 1996). These results are consistent with the finding that phonological perception is impaired in aphasic patients with either anterior or posterior lesions (see, e.g., Blumstein, 1994), and suggest that the posterior superior temporal region (“Wernicke’s area”) and inferior frontal region (“Broca’s area”) may function as an integrated network in speech perception.

Phonological processes important for reading include phonological segmentation (the explicit segmentation of a spoken word into its separate phonemes), phonological coding (the mapping of orthographic symbols onto particular phonemes), and lexical retrieval (the retrieval of phonological word forms). Phonological segmentation has not been studied extensively using neuroimaging, but one study (Burton, Blumstein, & Small, 2000) has suggested that the left inferior frontal cortex is engaged during segmentation. Phonological coding has been studied by visually presenting pseudo-words (pronounceable nonwords) in tasks involving silent reading (Herbster, Mintun, Nebes, & Becker, 1997), rhyme judgments (Pugh et al., 1996; Shaywitz et al., 1995), syllable counting judgments (Poldrack et al., 1999), and homophone decisions (Rumsey et al., 1997). Each of these studies found activity in the left

Figure 1. Spectrogram of uncompressed and compressed versions of the sentence “cats can purr.”

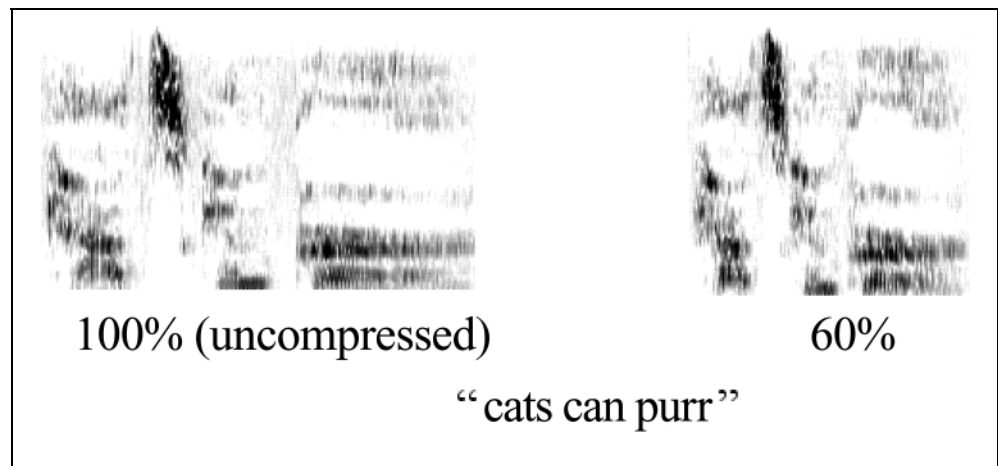


Table 1. Stereotactic Locations of Significant Activations ($p < .001$ Uncorrected and at Least 10 Contiguous Voxels) for Rhyme Judgment and Sentence Verification Scans

<i>Task/Region</i>	<i>X</i>	<i>Y</i>	<i>Z</i>	<i>No. of Voxels</i>	<i>Max Z</i>
<i>Rhyme Judgment</i>					
L IFG	-48	34	12	22*	4.31
L IFG (operculum)	-52	16	0	22*	3.98
<i>Compression-Related Decrease</i>					
R STG/planum temporale	40	-14	16	175*	4.40
R precuneus	6	-68	20	12	4.22
White matter	-26	0	24	14	3.75
L STG	-46	-32	12	14	3.73
R lingual gyrus/parahippocampal	32	-50	-8	16	3.66
L MTG angular gyrus	-46	-70	20	11	3.63
R STG	46	-12	-4	17	3.60
<i>Compression-Related Increase</i>					
L MFG	-28	54	16	86*	4.81
R IFG/insula	34	26	-4	25*	4.11
anterior cingulate	4	32	20	29*	4.11
R striatum	18	4	8	25*	3.99
R STG	66	-40	8	16	3.95
<i>Convex Compression Response</i>					
L STG/Wernicke's	-64	-24	0	82*	4.29
L IFG/MFG	-52	22	12	16	4.23
L IFG	-34	14	20	25*	4.15
R IFG	36	26	8	22*	3.76
L IFG insula	-38	34	8	14	3.65

XYZ coordinates refer to the MNI305 stereotactic space. Clusters noted with an asterisk (*) survived correction for multiple comparisons ($p < .05$).

inferior frontal cortex related to pseudoword processing, with less consistent activation in the temporal cortex. This result is consistent with evidence (reviewed by Fiez & Petersen, 1998) that left inferior frontal lesions can result in phonological dyslexia. Lexical retrieval has been examined by comparing the processing of words with either regular or irregular pronunciations; regular words (e.g., MINT) can be pronounced either using rules that map orthography onto phonology (assembled phonology) or using direct retrieval of the phonological word form (addressed phonology), whereas irregular words (e.g., PINT) require the use of

addressed phonology. Neuroimaging studies of irregular word processing have found activation in the fusiform gyrus (Herbster et al., 1997; Rumsey et al., 1997). Thus, phonological processing in reading seems to rely upon some common regions (inferior frontal cortex) and some distinct regions (inferior temporal cortex) compared to phonological processing in speech perception.

Relations Between Phonological and Rapid Auditory Processing

There is evidence that phonological processing in reading may be related to perception of transient acoustic signals. In particular, a large body of evidence demonstrates that individuals with reading disorders suffer from deficits in both phonological coding and perception of transient acoustic features (reviewed by Wright et al., 2000; Farmer & Klein, 1995). These phonological and acoustic deficits are correlated within dyslexic individuals (Witton et al., 1998). Furthermore, psychoacoustic performance on tests of dynamic acoustic processing predicts reading ability in unselected normal readers, both for children (Talcott et al., 2000) and adults (Ahissar, Protopapas, Reid, & Merzenich, 2000), suggesting that there is a fundamental relationship between these processes. Functional imaging has also shown that the neural processing of rapidly changing acoustic signals is disrupted in adults with reading disorders (Temple et al., 2000). The present study examined whether common neural processes are involved in the processing of rapidly transient acoustic signals in speech perception and in phonological coding during reading. Evidence from previous neuroimaging studies (reviewed above) suggests that similar regions may be involved, but no studies have directly examined both phonological processing and rapid acoustic processing.

To determine the neural response to increasingly transient changes in the speech signal, we used a speech-compression algorithm that manipulated the rate of acoustic changes in recorded speech while maintaining the spectral features of the speech signal (see Figure 1). Compression using this method results in more rapid acoustic transitions in the speech stream. During fMRI scanning, subjects performed a

Table 2. Behavioral Data for Compressed Sentence Verification Task Performed During fMRI Scanning

<i>Compression (% of Original Length)</i>	<i>Accuracy</i>
60	.83 (.03)
45	.85 (.07)
30	.72 (.05)
15	.53 (.03)

Means with standard deviation in parentheses.

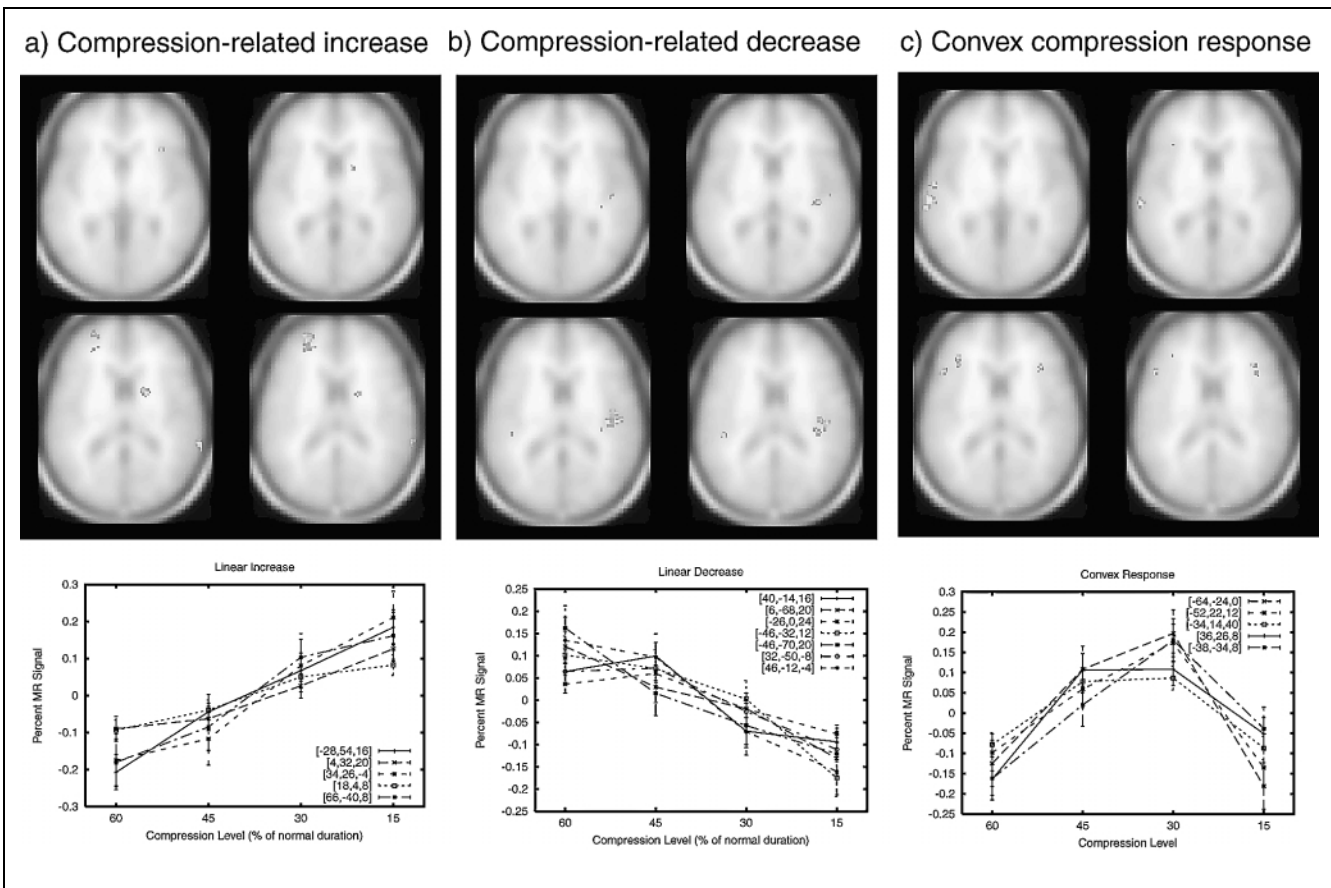


Figure 2. Regions exhibiting significant compression-related modulation during sentence verification ($p < .001$, uncorrected and at least 10 contiguous voxels). First row depicts activation map, second row presents signal from each significantly active cluster across levels of compression. (a) Compression-related decrease (contrast: 1, 1/3, -1/3, -1). (b) Compression-related increase (contrast: -1, -1/3, 1/3, 1). (c) Increase from 60% to 30%, decrease from 30% to 15% (convex response) (contrast: -3/4, 1/4, 5/4, -3/4). The right side of the figure corresponds to the right hemisphere of the brain.

comprehension task with sentences at four different levels of compression. This technique allowed us to separate language comprehension and rapid auditory processing: By compressing speech until it was incomprehensible, we were able to separately identify brain regions sensitive to the rate of acoustic changes and those that were additionally sensitive to language comprehension.

To independently identify regions involved in phonological processes associated with reading, we performed a separate scan in which subjects performed a rhyming judgment task on visually presented pseudowords compared to a lettercase judgment. Rhyme judgments require the formation of a phonological representation for each of the words and a comparison of those phonological representations in working memory, and this task has been used to examine phonological processing in neuroimaging (e.g., Pugh et al., 1996). Pseudowords were used in this study because they do not have preexisting lexical representations and, thus, encourage the use of assembled phonology in performance of the rhyme judgment task. This scan allowed us to determine whether regions engaged by phonological processing

were also sensitive to the rate of transient acoustic signals in speech perception.

RESULTS

Stereotactic locations for all significant activations are presented in Table 1.

Behavioral data for compressed sentence verification are presented in Table 2; data were not available for two subjects due to button box malfunction. Accuracy decreased significantly with increasing sentence compression, linear trend $F(1,5) = 103.4, p < .001$, and was only marginally greater than chance for 15% compression, $t(1,5) = 2.35, p > .07$. There were significant differences in accuracy between the 45% and 30% levels and the 30% and 15% levels ($ps < .01$) whereas there was no difference between accuracy at the 60% and 45% levels ($p > .8$).

Compression-Related Activity

The fMRI results for each contrast and plots of the activity in significantly active regions are presented in Figure 2.

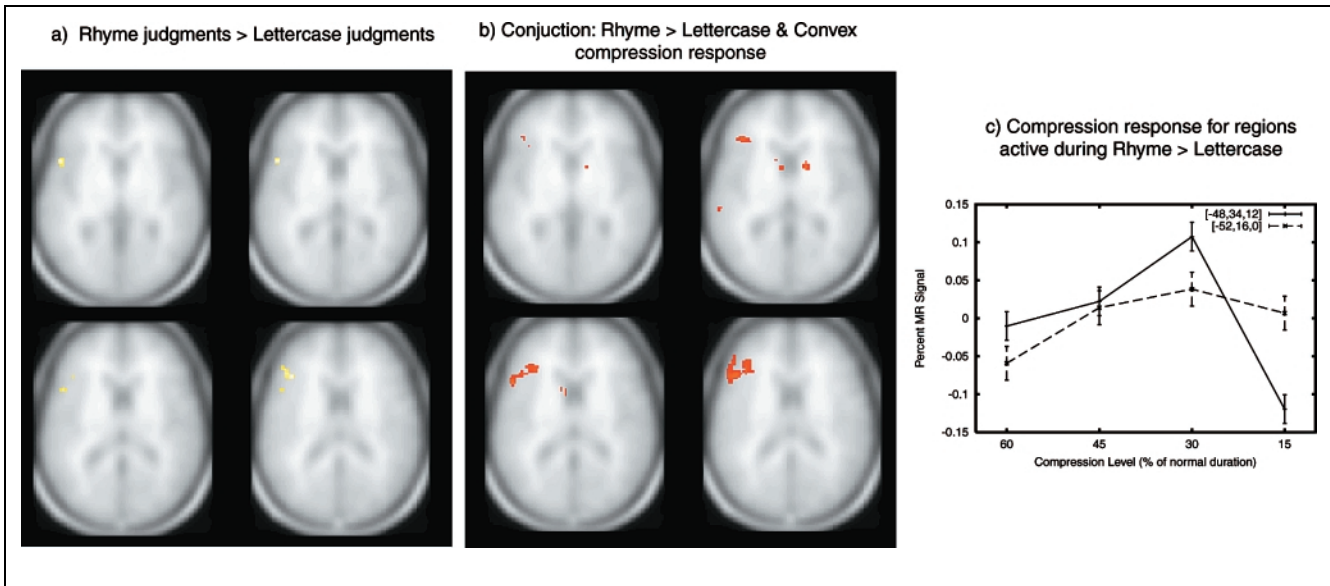


Figure 3. (a) Regions exhibiting significant activation during rhyme judgments compared to case judgments ($p < .001$, uncorrected and at least 10 contiguous voxels). (b) Regions exhibiting significant response for conjunction of rhyme > lettercase judgments and convex compression response. (c) Compression response for regions active during rhyme judgments.

Increases

A significant compression-related increase occurred in the middle frontal gyrus (BA 46/10). A more posterior region in the right inferior frontal gyrus also showed this pattern. Other regions demonstrating compression-related increases were in the right superior temporal gyrus, anterior cingulate, and right striatum.

Convex Responses

Five regions, four of which were in the left hemisphere, exhibited a significant convex function of compression, increasing from 60% to 30% and then decreasing at 15%. One was located in the left posterior superior temporal gyrus (BA 21/22) in the region traditionally known as Wernicke's area. Three regions were located in the left inferior frontal gyrus (BA44/45) in or near the region traditionally known as Broca's area. The right inferior frontal gyrus also exhibited this pattern of activity.

Decreases

The largest region of compression-related decrease was located in the right superior temporal plane, spanning the posterior insula, transverse temporal gyrus, and planum temporale. A similar but smaller decrease was observed in the left superior temporal cortex. Decreases were also observed in the left angular gyrus region (BA 39), right lingual gyrus, and right precuneus.

Phonological Activity

Accuracy was greater on the lettercase judgment task (100%) than the rhyme judgment task (88%). The only

significantly activated region during the rhyme task compared to the baseline (lettercase judgment) task encompassed the posterior section of the left inferior frontal gyrus including Broca's area (BA 44/45; see Figure 3A). This activation comprised two separate clusters of activation at the chosen threshold. One cluster was located in the LIFG pars triangularis (45/46), whereas the other cluster encompassed the LIFG pars opercularis including the frontal operculum (BA 44/45/47).

Conjunction Analysis

In order to systematically determine whether regions involved in phonological processing were also sensitive to transient acoustic features, we performed a conjunction analysis across the rhyme judgment and sentence

Table 3. Stereotactic Locations of Significantly Active Regions for Conjunction of Rhyme > Lettercase and Each Compression Response

Task/Region	X	Y	Z	No. of Voxels
<i>Convex Compression Response and Rhyme > Lettercase</i>				
L IFG	-54	18	8	172
L IFG	-38	12	20	53
R striatum	14	8	4	10
<i>Increasing Compression Response and Rhyme > Lettercase</i>				
L MFG	-40	32	4	18
R striatum	14	8	4	14

$p < .001$, uncorrected and at least 10 contiguous voxels.

compression scans (Price & Friston, 1997). The results of this analysis are presented in Table 3 and Figure 3B. There were three regions that conjointly demonstrated activation for rhyme judgments compared to case judgments and a convex compression response function, two in the left inferior prefrontal cortex and one in the right basal ganglia. There were two regions that showed conjoint rhyme activation and linearly increasing compression response, in the left dorsolateral prefrontal cortex (anterior to the regions with convex response) and in the right basal ganglia. No regions exhibited a significant conjunction between rhyme judgments and decreasing compression response.

Region-of-Interest Analysis

To further determine the relationship between the rhyme judgment and sentence compression tasks, regions exhibiting significant activation in the rhyme judgment task were used to interrogate the data from the sentence compression scan. These data are presented in Figure 3C. The region in the inferior frontal gyrus pars triangularis (centered at $-48, 34, 12$) exhibited a significant effect of compression, $F(3,21) = 3.11, p < .05$, whereas the region in the frontal operculum (centered at $-52, 16, 0$) did not exhibit a significant effect of compression, $F(3,21) = 0.44$.

DISCUSSION

The neural response to temporal compression of speech and its relationship to phonological processing was examined using fMRI. The results demonstrated that left inferior frontal and left posterior temporal cortices (Broca's and Wernicke's areas), along with a right-hemisphere inferior frontal homologue, exhibited sensitivity to transient acoustic features when contained in comprehensible speech. Both conjunction analysis and independent region-of-interest (ROI) analysis identified a region in the left inferior frontal cortex that was active for rhyme judgments and that exhibited a convex sentence compression response, demonstrating a brain region involved in phonological processing that was also sensitive to transient acoustic signals. This is the first demonstration of common neural responses for phonological processing and dynamic acoustic processing. In contrast to the convex response of the inferior frontal cortex, a region in the left middle frontal gyrus exhibited increasing activity with speech compression even when the speech signal was no longer comprehensible. These results demonstrate that distinct regions in left frontal cortex exhibit qualitatively different responses to speech compression.

Frontal Cortex and Rapid Auditory Processing

Previous studies have found activation of the left prefrontal cortex associated with transient acoustic signals,

but localization has varied across studies (as described above). The present results extend previous findings by Belin et al. (1998) and Fiez et al. (1995) by demonstrating left frontal sensitivity to rapidly transient signals in meaningful speech (as opposed to tones or individual syllables), and by demonstrating overlap between phonological processing of written stimuli and processing of rapid acoustic signals in speech. Our results further suggest that the previous findings of Belin et al. and Fiez et al. may represent separate responses to transient acoustic signals. The middle frontal gyrus activation found by Belin et al. for fast spectral transitions compared to rest overlapped with the region exhibiting increasing compression response in the present study, suggesting that this region is sensitive to rapidly changing acoustic features in both language and nonlanguage stimuli. The frontal opercular region found by Fiez et al. to be active for rapidly changing acoustic stimuli was near the region found to exhibit a convex compression function in the present study (12 mm between maxima), and may thus be sensitive to the particular range of frequency transitions that occur in natural speech. Differences between the Fiez et al. and Belin et al. studies may reflect the different types of stimuli or differences between passive listening and active processing. The role of the orbito-frontal region identified by Johnsrude et al. (1997) is unclear, as no other studies have found similar activation related to rapid acoustic processing. However, signal from the orbito-frontal cortex was limited in the present study by magnetic susceptibility artifacts, so activation in that region may have been missed.

The present results, along with other recent findings (Temple et al., 2000; Belin et al., 1998), expand the domain of processes associated with the dorsolateral prefrontal cortex (DLPFC) to include auditory processing. Cognitive neuroimaging studies have focused primarily on the role of the DLPFC in verbal and visuospatial working memory and executive control processes (e.g., Smith & Jonides, 1999) and long-term memory processes (e.g., Wagner, Desmond, Glover, & Gabrieli, 1998). However, there are several lines of evidence that are suggestive of the involvement of dorsolateral prefrontal cortex in auditory processing. First, there is extensive anatomical connectivity in macaques between the auditory cortex and DLPFC regions (Romanski, Bates, & Goldman-Rakic, 1999; Romanski, Tian, et al., 1999; Hackett, Stepniewska, & Kaas, 1999; Deacon, 1992), providing an anatomical substrate for prefrontal participation in auditory processing. Second, neurophysiology in macaques has identified neurons in the DLPFC that exhibit responses to auditory stimuli (Suzuki, 1985; Azuma & Suzuki, 1984). Third, lesions to the DLPFC in humans result in alterations of early auditory evoked potentials (Knight, Scabini, & Woods, 1989; Chao & Knight, 1998) and reductions in mismatch negativity to auditory stimuli (Alain, Woods, & Knight, 1998), suggesting that the DLPFC modulates early audi-

tory processing in a top-down manner. Further studies will be necessary to determine the exact role of the DLPFC in auditory processing in humans.

It is not possible to determine whether the convex compression response in left frontal and temporal regions reflect the cause or the consequence of changes in comprehension related to sentence compression. These regions may become more active due to increased effort to comprehend more compressed sentences (until comprehension breaks down at the most compressed levels). It is also not possible to determine the degree to which the effects of comprehension are specific to particular classes of speech sounds such as consonants versus vowels; e.g., the shortening of vowels could adversely affect comprehension in addition to the shortening of formant transitions in some consonants.

Relations Between Dynamic Acoustic and Phonological Processing

The present study found that one of the left frontal regions engaged during rhyming judgments also exhibited sensitivity to sentence compression within the range of comprehensible speech. This is consistent with previous neuroimaging studies that have separately demonstrated activation in this region for phonological processing (Poldrack et al., 1999) and rapid auditory processing (Fiez et al., 1995). The results provide a neural basis for the previously observed correlation between dynamic auditory processing and reading ability in dyslexic adults (Witton et al., 1998) and unselected normal children (Talcott et al., 2000) and adults (Ahissar et al., 2000). The ontogeny of this relationship is unclear; there is evidence that deficits in dynamic acoustic processing are present in infants at risk for language disorder (Benasich & Tallal, 1999), but this has not been established for reading ability.

The rhyme judgment task may engage processes (such as decision and executive control processes) that are additional to those engaged during normal reading, so that brain regions engaged during rhyme judgments may reflect these other processes rather than the phonological assembly processes engaged during normal reading. However, studies of rhyming and other reading tasks (cited above) suggest that the left inferior frontal cortex is generally engaged during tasks involving phonological processes involved in reading.

There is extensive evidence for left lateralization both for processing of rapidly changing acoustic signals and for phonological processing. Studies using dichotic listening (Schwartz & Tallal, 1980), intracortical recording (Liegeois-Chauvel et al., 1999), and brain imaging (Belin et al., 1998; Fiez et al., 1995) have all suggested that the left hemisphere is preferentially responsive to rapidly changing acoustic signals, and it has been suggested in turn that this hemispheric specialization may underlie

the left lateralization of phonological processing (Schwartz & Tallal, 1980; Teuber, 1974). Our results qualify these previous results by suggesting that the left-hemisphere specialization for rapid auditory processing in Broca's and Wernicke's areas may be limited to the range of temporal modulation frequencies that occur in natural speech; activation increased in these regions with increasing temporal modulation, but then decreased when modulation became too fast for comprehension. Right hemisphere frontal regions also exhibited compression-related increases in activity, although this activity was weaker and less extensive than the analogous left frontal increase. This is consistent with the relatively small lateralization effects found in dichotic listening studies, suggesting that lateralization of rapid processing is not absolute.

Auditory Cortex and Rapid Processing

The auditory cortex exhibited a significant compression-related decrease bilaterally, with a stronger decrease in the right hemisphere. It is possible that this decrease simply reflects a decrease in the amount of auditory stimulation with increasing compression. However, the decrease in auditory cortical activity was driven primarily by a large drop in activity between 45% to 30% compression, suggesting that the drop-off did not simply reflect decreasing stimulation time. This decrease may have arisen because the temporal frequency of changes in the acoustic signal in highly compressed speech may be outside the frequency range of auditory cortical entrainment responses (i.e., the range over which neural response can faithfully follow the acoustic signal). In A1, entrainment responses are low pass with a cutoff of 8–10 Hz (Kilgard & Merzenich, 1998; Schreiner & Langner, 1988), which may be lower than the frequency of relevant changes in highly compressed speech; e.g., a formant transition lasting 30 msec in normal speech would last less than 5 msec in speech compressed to 15% of original length, placing it outside the bandpass of the A1 entrainment response. Another possibility is that the response of the auditory cortex consists mostly of invariant onset responses (Eggermont, 1995; Eggermont, 1998; Schreiner & Urbas, 1988). Although there were nominally more sentences in the highly compressed condition, it is possible that the less compressed sentences were responded to as trains of separate stimuli (resulting in trains of separate onset responses) whereas the highly compressed sentences were more often responded to as a single stimulus (resulting in fewer onset responses per sentence). These issues can be best addressed using neuroimaging methods with higher temporal resolution, such as MEG (e.g., Nagarajan et al., 1999) or intracortical recording (Liegeois-Chauvel et al., 1999), because the neural responses in question fall far below the temporal resolution of the fMRI signal.

The present study did not find left lateralization of auditory cortical response to rapidly changing acoustic signals, in contrast to a previous study of rapid auditory processing using PET (Belin et al., 1998). Rather, both left and right auditory cortices exhibited compression-related decreases in activity, primarily reflecting decreases at 15% compression compared to all other levels. There are several possible reasons for this discrepancy. First, the total amount of auditory stimulation decreased with compression, which may have offset any increases related to processing of transient acoustic inputs. This question is difficult to address directly, because compression by necessity reduces the time of auditory stimulation, but studies using event-related fMRI could be used to independently vary word length and auditory compression to determine the roles of these factors. Second, the background acoustic noise from the MR scanner may have altered the response of auditory cortex (whereas the Belin et al., 1998 study used PET, which creates no background noise). Further studies using auditory stimulation interleaved with gradient noise will be necessary to fully address this question.

METHODS

Participants

Eight normal, native English-speaking adults (four male, four female, age range 20–29) participated in the experiment. Right-handedness was confirmed in all participants with the Annett (1967) handedness inventory, and informed consent was obtained prior to the fMRI scan.

Imaging Methods

Imaging was performed on a GE Signa MR scanner at 1.5 T with a standard GE head coil. Eight slices (24 cm FOV, 6 mm slice thickness, 1 mm skip) were imaged parallel to the AC–PC line, covering a region from the level of the inferior temporal cortex to the level of the superior parietal cortex. T1-weighted spin-echo structural images were collected for the in-plane slices. One volume (eight slices) was acquired every 1.44 sec using a T2*-weighted gradient-echo spiral pulse sequence (Glover & Lai, 1998) with parameters of TR = 720 msec, TE = 40 msec, flip angle = 70°, and two spiral interleaves. Three dummy images (4.32 sec) were collected and discarded at the beginning of each scan, and stimulus presentation did not begin until after that period, allowing for the dissipation of auditory cortical activity induced initially by gradient noise (Bandettini, Jesmanowicz, Van Kylen, Birn, & Hyde, 1998).

Tasks

Participants engaged in two separate fMRI scans examining speech perception and phonological processing. The order of scans was constant across participants, whereas the order of task conditions within each scan

was counterbalanced across participants. Auditory stimuli were delivered binaurally using the Resonance Technology (Van Nuys, CA) auditory system; the sound level was adjusted for each participant such that they were able to comfortably hear the stimuli during scanning. Auditory stimuli were presented over the constant sound of the scanner gradients. Visual stimuli were delivered via back projection onto a built-in mirror on the head coil. Responses were collected during scanning using a hand-held fiber-optic response button.

Compressed Sentence Verification

Processing of auditorily presented sentences at varying levels of temporal compression was examined using a sentence verification task. Sentences were compressed to four levels (60%, 45%, 30%, and 15% of original length) using a phase-vocoder algorithm employing a short-term Fourier transform (Portnoff, 1981). Compression levels were alternated every 28.8 sec for a total scan length of 460.8 sec; order of compression levels across the scan was counterbalanced across subjects. Participants responded to sentences that were semantically true (e.g., “Cats have four legs”) by pressing a button, and withheld responses for sentences that were semantically false (e.g., “People have four legs”). They were instructed to guess for sentences that were unintelligible. Sentences were presented with a constant 1700-msec interstimulus interval to equalize the amount of poststimulus processing time per sentence across levels of compression; the number of sentences in each 28.8-sec block thus increased with greater compression (with the exact number of sentences depending upon the length of individual sentences in the block), and the total time of acoustic stimulation per block decreased with greater compression.

Rhyme Judgment

Phonological processes associated with reading were examined by alternating every 25.92 sec between a rhyming task in which participants judged whether each pair of visually presented pseudowords did or did not rhyme (e.g., stroat and snote), and a baseline task in which participants judged whether each pair of visually presented consonant strings were or were not printed in identical lettercase (e.g., bbTT and bbTt) (see Pugh et al., 1996). Stimuli were presented once every 3.24 sec, with a total of eight stimuli in each block; the entire scan lasted 311.04 sec.

Data Analysis

Data were preprocessed using SPM96 (Wellcome Department of Cognitive Neurology, London, UK) implemented in MATLAB (Mathworks, Sherborn, MA). Following image reconstruction and motion correction (Woods, Cherry, & Mazziotta, 1992), all images were normalized into the

MNI305 stereotactic space (which approximates the space of Talairach & Tournoux, 1988) by aligning each image to a normalized template using an eight-parameter linear transformation (with pitch constrained to zero). Normalized images were then smoothed using a 6-mm full width at half maximum (FWHM) Gaussian kernel. Data were analyzed according to a mixed-effects model treating subjects as a random effect using SPM99. For each subject, adjusted mean images were created for each condition after removing global signal and low-frequency covariates. Condition and covariate effects were then estimated according to the general linear model at each voxel. To test hypotheses about regionally specific condition effects, the estimates were compared using linear contrasts. The resulting set of voxel values for each contrast constitute a statistical parametric map (SPM $\{t\}$) that was thresholded at $p = .001$ (uncorrected for multiple comparisons) with a cluster extent threshold of 10 voxels. The statistical significance of the resulting statistical maps was then characterized using distributional approximations from the theory of Gaussian fields (Friston et al., 1995) in terms of the probability that an observed cluster size could have occurred by chance across the entire imaged volume at $p < .05$ (i.e., a corrected p value). Conjunction analyses were further performed using SPM99, and ROI analyses were performed using the volume of interest (VOI) extraction tool in SPM99.

The inclusion of four different levels of compression allowed examination of both linear and convex fMRI responses to sentence compression. Contrasts were performed on the sentence compression data to test for linear increase (contrast: $-1, -1/3, 1/3, 1$), linear decrease (contrast: $1, 1/3, -1/3, -1$), and a particular convex relationship in which activity increased from 60% to 30% compression and then decreased at 15% (contrast: $-3/4, 1/4, 5/4, -3/4$). Given that the threshold for comprehensibility in normal subjects fell between 15% and 30% compression, this convex pattern represented brain activity that increased with temporal compression while stimuli were comprehensible and then decreased once stimuli became incomprehensible.

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The data reported in this experiment have been deposited in the National fMRI Data Center (<http://www.fmridc.org>). The accession number is 2-2001-111KR.

REFERENCES

Ahissar, M., Protopapas, A., Reid, M., & Merzenich, M. M. (2000). Auditory processing parallels reading abilities in

adults. *Proceedings of the National Academy of Sciences, U.S.A.*, *97*, 6832–6837.

Alain, C., Woods, D. L., & Knight, R. T. (1998). A distributed cortical network for auditory sensory memory in humans. *Brain Research*, *812*, 23–37.

Annett, M. (1967). The binomial distribution of right, mixed, and left handedness. *Quarterly Journal of Experimental Psychology*, *19*, 327–333.

Auerbach, S. H., Allard, T., Naeser, M., Alexander, M. P., & Albert, M. L. (1982). Pure word deafness. Analysis of a case with bilateral lesions and a defect at the prephonemic level. *Brain*, *105*, 271–300.

Azuma, M., & Suzuki, H. (1984). Properties and distribution of auditory neurons in the dorsolateral prefrontal cortex of the alert monkey. *Brain Research*, *298*, 343–346.

Bandettini, P. A., Jesmanowicz, A., Van Kylen, J., Birn, R. M., & Hyde, J. S. (1998). Functional MRI of brain activation induced by scanner acoustic noise. *Magnetic Resonance in Medicine*, *39*, 410–416.

Belin, P., Zilbovicius, M., Crozier, S., Thivard, L., Fontaine, A., Masure, M. C., & Samson, Y. (1998). Lateralization of speech and auditory temporal processing. *Journal of Cognitive Neuroscience*, *10*, 536–540.

Benasich, A. A., & Tallal, P. (1996). Auditory temporal processing thresholds, habituation, and recognition memory over the 1st year. *Infant Behavior and Development*, *19*, 339–357.

Binder, J. R., Rao, S. M., Hammeke, T. A., Yetkin, F. Z., Jesmanowicz, A., Bandettini, P. A., Wong, E. C., Estkowski, L. D., Goldstein, M. D., Houghton, V. M., & Hyde, J. S. (1994). Functional magnetic resonance imaging of human auditory cortex. *Annals Of Neurology*, *35*, 662–672.

Blumstein, S. E. (1994). Impairments of speech production and speech perception in aphasia. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *346*, 29–36.

Burton, M. W., Small, S. L., & Blumstein, S. E. (2000). The role of segmentation in phonological processing: An fMRI investigation. *Journal of Cognitive Neuroscience*, *12*, 679–690.

Chao, L. L., & Knight, R. T. (1998). Contribution of human prefrontal cortex to delay performance. *Journal of Cognitive Neuroscience*, *10*, 167–177.

Deacon, T. W. (1992). Cortical connections of the inferior arcuate sulcus cortex in the macaque brain. *Brain Research*, *573*, 8–26.

Demonet, J.-F., Chollet, F., Ramsay, S., Cardebat, D., Nespoulous, J.-L., Wise, R., Rascol, A., & Frackowiak, R. (1992). The anatomy of phonological and semantic processing in normal subjects. *Brain*, *115*, 1753–1768.

Demonet, J. F., Fiez, J. A., Paulesu, E., Petersen, S. E., & Zatorre, R. J. (1996). PET studies of phonological processing: A critical reply to Poeppel. *Brain and Language*, *55*, 352–379.

Demonet, J. F., Price, C., Wise, R., & Frackowiak, R. S. (1994). A PET study of cognitive strategies in normal subjects during language tasks. Influence of phonetic ambiguity and sequence processing on phoneme monitoring. *Brain*, *117*, 671–682.

Dhankhar, A., Wexler, B. E., Fulbright, R. K., Halwes, T., Blamire, A. M., & Shulman, R. G. (1997). Functional magnetic resonance imaging assessment of the human brain auditory cortex response to increasing word presentation rates. *Journal of Neurophysiology*, *77*, 476–483.

Eggermont, J. J. (1995). Representation of a voice onset time continuum in primary auditory cortex of the cat. *Journal of the Acoustical Society of America*, *98*, 911–920.

Eggermont, J. J. (1998). Representation of spectral and temporal sound features in three cortical fields of the cat. Si-

- milarities outweigh differences. *Journal of Neurophysiology*, *80*, 2743–2764.
- Farmer, M. E., & Klein, R. M. (1995). The evidence for a temporal processing deficit linked to dyslexia: A review. *Psychonomic Bulletin and Review*, *2*, 460–493.
- Fiez, J. A., & Petersen, S. E. (1998). Neuroimaging studies of word reading. *Proceedings of the National Academy of Sciences, U.S.A.*, *95*, 914–921.
- Fiez, J. A., Raichle, M. E., Miezin, F. M., Petersen, S. E., Tallal, P., & Katz, W. F. (1995). PET studies of auditory and phonological processing: Effects of stimulus characteristics and task design. *Journal of Cognitive Neuroscience*, *7*, 357–375.
- Fiez, J. A., Raichle, M. R., Gbalota, D. A., Tallal, P., & Petersen, S. E. (1996). Pet activation of posterior temporal regions during auditory word presentation and verb generation. *Cerebral Cortex*, *6*, 1–10.
- Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J. P., Frith, C. D., & Frackowiak, R. S. J. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping*, *2*, 189–210.
- Glover, G. H., & Lai, S. (1998). Self-navigated spiral fMRI: Interleaved versus single-shot. *Magnetic Resonance in Medicine*, *39*, 361–368.
- Hackett, T. A., Stepniewska, I., & Kaas, J. H. (1999). Prefrontal connections of the parabelt auditory cortex in macaque monkeys. *Brain Research*, *817*, 45–58.
- Herbster, A. N., Mintun, M. A., Nebes, R. D., & Becker, J. T. (1997). Regional cerebral blood flow during word and non-word reading. *Human Brain Mapping*, *5*, 84–92.
- Johnsrude, I. S., Zatorre, R. J., Milner, B. A., & Evans, A. C. (1997). Left-hemisphere specialization for the processing of acoustic transients. *NeuroReport*, *8*, 1761–1765.
- Kilgard, M. P., & Merzenich, M. M. (1998). Plasticity of temporal information processing in the primary auditory cortex. *Nature Neuroscience*, *1*, 727–731.
- Knight, R. T., Scabini, D., & Woods, D. L. (1989). Prefrontal cortex gating of auditory transmission in humans. *Brain Research*, *504*, 338–342.
- Liegeois-Chauvel, C., de Graaf, J. B., Laguitton, V., & Chauvel, P. (1999). Specialization of left auditory cortex for speech perception in man depends on temporal coding. *Cerebral Cortex*, *9*, 484–496.
- Mazoyer, B. M., Dehaene, S., Tzourio, N., Frak, V., Murayama, N., Cohen, L., Levrier, O., Salamon, G., Syrota, A., & Mehler, J. (1993). The cortical representation of speech. *Journal of Cognitive Neuroscience*, *5*, 467–479.
- Nagarajan, S., Mahncke, H., Salz, T., Tallal, P., Roberts, T., & Merzenich, M. M. (1999). Cortical auditory signal processing in poor readers. *Proceedings of the National Academy of Sciences, U.S.A.*, *96*, 6483–6488.
- Petersen, S. E., Fox, P. T., Posner, M. I., Mintun, M., & Raichle, M. E. (1988). Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature*, *331*, 585–589.
- Phillips, D. P., & Farmer, M. E. (1990). Acquired word deafness, and temporal grain of sound representation in the primary auditory cortex. *Behavioural Brain Research*, *40*, 85–94.
- Poldrack, R. A., Wagner, A. D., Prull, M. W., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1999). Functional specialization for semantic and phonological processing in the left inferior frontal cortex. *NeuroImage*, *10*, 15–35.
- Portnoff, M. R. (1981). Time-scale modification of speech based on short-time Fourier analysis. *IEEE Transactions on Acoustics, Speech, and Signal Processing*, *234*, 243–248.
- Price, C. J., & Friston, K. J. (1997). Cognitive conjunction: A new approach to brain activation experiments. *Neuroimage*, *5*, 261–270.
- Price, C. J., Wise, R. J. S., Warburton, E. A., Moore, C. J., Howard, D., Patterson, K., Frackowiak, R. S. J., & Friston, K. J. (1996). Hearing and saying: The functional neuro-anatomy of auditory word processing. *Brain*, *119*, 919–931.
- Pugh, K. R., Shaywitz, B. A., Shaywitz, S. E., Constable, R. T., Skudlarski, P., Fulbright, R. K., Bronen, R. A., Shankweiler, D. P., Katz, L., Fletcher, J. M., & Gore, J. C. (1996). Cerebral organization of component processes in reading. *Brain*, *119*, 1221–1238.
- Romanski, L. M., Bates, J. F., & Goldman-Rakic, P. S. (1999a). Auditory belt and parabelt projections to the prefrontal cortex in the rhesus monkey. *Journal of Comparative Neurology*, *403*, 141–157.
- Romanski, L. M., Tian, B., Fritz, J., Mishkin, M., Goldman-Rakic, P. S., & Rauschecker, J. P. (1999). Dual streams of auditory afferents target multiple domains in the primate prefrontal cortex. *Nature Neuroscience*, *2*, 1131–1136.
- Rumsey, J. M., Horwitz, B., Donohue, B. C., Nace, K., Maisog, J. M., & Andreason, P. (1997). Phonological and orthographic components of word recognition. A PET-rCBF study. *Brain*, *120*, 739–759.
- Schlosser, M. J., Aoyagi, N., Fulbright, R. K., Gore, J. C., & McCarthy, G. (1998). Functional MRI studies of auditory comprehension. *Human Brain Mapping*, *6*, 1–13.
- Schreiner, C. E., & Langner, G. (1988). Coding of temporal patterns in the central auditory nervous system. In G. Edelman, E. Gall, & M. Cowan (Eds.), *Auditory function. Neurobiological bases of hearing*. New York: Wiley.
- Schreiner, C. E., & Urbas, J. V. (1988). Representation of amplitude modulation in the auditory cortex of the cat: II. Comparison between cortical fields. *Hearing Research*, *32*, 49–63.
- Schwartz, J., & Tallal, P. (1980). Rate of acoustic change may underlie hemispheric specialization for speech perception. *Science*, *207*, 1380–1381.
- Shaywitz, B. A., Shaywitz, S. E., Pugh, K. R., Constable, R. T., Skudlarski, P., Fulbright, R. K., Bronen, R. A., Fletcher, J. M., Shankweiler, D. P., Katz, L., & et al. (1995). Sex differences in the functional organization of the brain for language. *Nature*, *373*, 607–609.
- Smith, E. E., & Jonides, J. (1999). Storage and executive processes in the frontal lobes. *Science*, *283*, 1657–1661.
- Suzuki, H. (1985). Distribution and organization of visual and auditory neurons in the monkey prefrontal cortex. *Vision Research*, *25*, 465–469.
- Talairach, J., & Tournoux, P. (1988). *A Co-Planar Stereotactic Atlas of the Human Brain*. Stuttgart: Thieme.
- Talcott, J. B., Witton, C., McLean, M. F., Hansen, P. C., Rees, A., Green, G. G., & Stein, J. F. (2000). Dynamic sensory sensitivity and children's word decoding skills. *Proceedings of the National Academy of Sciences, U.S.A.*, *97*, 2952–2957.
- Tallal, P. (1980). Auditory temporal perception, phonics, and reading disabilities in children. *Brain and Language*, *9*, 182–198.
- Tallal, P., & Piercy, M. (1973). Defects of non-verbal auditory perception in children with developmental aphasia. *Nature*, *241*, 468–469.
- Temple, E., Poldrack, R. A., Protopapas, A., Nagarajan, S., Salz, T., Tallal, P., Merzenich, M. M., & Gabrieli, J. D. E. (2000). Disruption of the neural response to rapidly transient acoustic stimuli in dyslexia: Evidence from fMRI. *Proceedings of the National Academy of Sciences, U.S.A.*, *97*, 13907–13912.
- Teuber, H.-L. (1974). Why two brains? In F. O. Schmitt & F. G. Worden (Eds.), *The neurosciences: Third study program* (pp. 71–74). Cambridge: MIT Press.

- Wagner, A. D., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. (1998). Prefrontal cortex and recognition memory. Functional-MRI evidence for context-dependent retrieval processes. *Brain*, *121*, 1985–2002.
- Warburton, E., Wise, R. J., Price, C. J., Weiller, C., Hadar, U., Ramsay, S., & Frackowiak, R. S. (1996). Noun and verb retrieval by normal subjects. Studies with PET. *Brain*, *119*, 159–179.
- Witton, C., Talcott, J. B., Hansen, P. C., Richardson, A. J., Griffiths, T. D., Rees, A., Stein, J. F., & Green, G. G. (1998). Sensitivity to dynamic auditory and visual stimuli predicts nonword reading ability in both dyslexic and normal readers. *Current Biology*, *8*, 791–797.
- Wright, B. A., Bowen, R. W., & Zecker, S. G. (2000). Nonlinguistic perceptual deficits associated with reading and language disorders. *Current Opinion in Neurobiology*, *10*, 482–486.
- Woods, R. P., Cherry, S. R., & Mazziotta, J. C. (1992). Rapid automated algorithm for aligning and reslicing PET images. *Journal of Computer Assisted Tomography*, *16*, 620–633.
- Zatorre, R. J., Evans, A. C., Meyer, E., & Gjedde, A. (1992). Lateralization of phonetic and pitch discrimination in speech processing. *Science*, *256*, 846–849.
- Zatorre, R. J., Meyer, E., Gjedde, A., & Evans, A. C. (1996). PET studies of phonetic processing of speech: Review, replication, and reanalysis. *Cerebral Cortex*, *6*, 21–30.