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The role of inferior frontal cortex in phonological processing

Martha W. Burton*

*Department of Neurology, University of Maryland School of Medicine, 12-011 Bressler Research Building,
655 W Baltimore Street, Baltimore, MD 21201-1559, USA*

Abstract

Recent neuroimaging studies of language processing are examining the neural substrate of phonology because of its critical role in mapping sound information onto higher levels of language processing (e.g., words) as well as providing codes in which verbal information can be temporarily stored in working memory. However, the precise role of the inferior frontal cortex in spoken and written phonological tasks has remained elusive. Although lesion studies have indicated the presence of selective deficits in phonological processing, the location of lesions underlying these impairments has not revealed a consistent pattern. Despite efforts to refine methods and tasks, functional neuroimaging studies have also revealed variability in activation patterns. Reanalysis of evidence from these neuroimaging studies suggests that there are functional subregions within the inferior frontal gyrus that correspond to specific components of phonological processing (e.g., orthographic to phonological conversion in reading, and segmentation in speech). © 2001 Cognitive Science Society, Inc. All rights reserved.

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1. Introduction

With the recent availability of neuroimaging techniques for studying cognitive function, a rapidly growing number of studies are attempting to define the neurobiological underpinnings of language. Two imaging techniques, functional magnetic resonance imaging (fMRI)

* Tel.: +1-410-706-8690; fax: +1-410-706-0324.

E-mail address: burton@cortex.neurology.umaryland.edu (M.W. Burton).

and positron emission tomography (PET), are currently widely used to show the location and magnitude of changes in blood flow/oxygenation associated with brain activity during cognitive processes. Although many studies have focused on identifying the location of brain activity during cognitive tasks, a recent challenge in these investigations is whether functional neuroimaging can reveal not only where a cognitive process takes place, but also how it is accomplished.

Some recent neuroimaging studies of language processing have concentrated on the role of phonology because of its critical role in mapping sound information onto higher levels of language processing (e.g., words) as well as providing codes in which verbal information can be temporarily stored in working memory. Phonological processes in spoken language are used to map the acoustic signal onto more abstract representations of sound (e.g., features and phonemes). For example, one type of phonological process that has been hypothesized is “segmentation” in which listeners must separate speech sounds from the continuous acoustic signal.

In reading, phonological (sound) information as well as orthographic (spelling) information may provide routes to word recognition (Coltheart, Curtis, Atkins, & Haller, 1993). Readers associate spelling with sounds, which may then be used to access lexical information, particularly for less familiar words. Although phonological processing plays a role in both spoken and written language, it is not yet clear the extent to which phonological processes used in speech, such as segmentation, rely on the same neural substrate as those in print, such as orthographic-to-phonological conversion.

Lesion studies have suggested that phonological processes can be selectively impaired, indicating that it may be possible to locate the underlying neural substrate of sound processes. However, analyses of the location of lesions in patients with phonological impairments have not demonstrated any straightforward relationship between phonological processes and frontal cortex. Recent neuroimaging studies have attempted to build on neuropsychological studies of the neural bases of phonological processing by revealing regions of activity during processing in normal subjects. These studies have shown promising results, suggesting for example, that the inferior frontal gyrus and the posterior superior temporal gyrus show increased activity during tasks that involve sounds and words (Binder et al., 1997; Price et al., 1992; Price et al., 1996b; Zatorre, Evans, Meyer, & Gjedde, 1992; Zatorre, Meyer, Gjedde, & Evans, 1996). However, the precise role of the inferior frontal cortex in spoken and written phonological tasks (and in language processing in general) has remained elusive. The current review examines (1) what neuroimaging studies have revealed about the neural underpinnings of sound processing in the inferior frontal cortex; and (2) how new approaches that investigate subcomponents of phonological processing with potentially different neural substrates, are shedding light on the role of inferior frontal cortex in phonological processes.

2. Lesion studies

Although there is controversy over how to divide language and its components into subcomponents, particularly for the purposes of neurobiological study, there do seem to be

processes that are specific to phonology. Lesion studies have demonstrated that damage to different brain regions selectively impair specific types of phonological processes. For example, some patients have particular difficulty with phonological output, resulting in speech errors that follow specific patterns (Gandour, 1998). This type of expressive deficit typically occurs with damage to the left hemisphere and often in Broca's area (defined as incorporating Brodmann Areas 44 and 45 and including the pars triangularis and pars opercularis of the left inferior frontal gyrus) (Benson, 1988). In receptive aphasia, patients with damage to the left superior posterior temporal regions may also have impairments in processing of speech sounds (Basso, Casati, & Vignolo, 1977; Benson, 1988; Blumstein, Cooper, Zurif, & Caramazza, 1977; Carpenter & Rutherford, 1973; Miceli, Caltagirone, Gainotti, & Payer-Rigo, 1978; Oscar-Berman, Zurif, & Blumstein, 1975; Riedel & Studdert-Kennedy, 1985; Tallal & Newcombe, 1978). These patients may have difficulty mapping speech sounds onto linguistically relevant categories, such as sound segments and words (Blumstein, 1998; Caplan, 1992). However, the traditional characterization of expressive aphasia being associated with anterior lesions and receptive aphasia associated with posterior lesions has been challenged on a number of grounds (e.g., Mohr et al., 1978). Particularly relevant to the nature of phonological impairments is evidence of patients with anterior lesions showing speech discrimination deficits (Blumstein, 1998). Although patients with lesions in the temporal lobe might be expected to show speech discrimination deficits because primary auditory areas are located in the temporal lobe and, thus, have direct connections to the auditory association areas, less anticipated is that patients with anterior lesions also manifest such impairments.

Other lesion studies have investigated difficulties with phonological processing involving segmental (e.g., /b/) or higher level phonological units (e.g., syllable) (Berndt, Haendiges, Mitchum, & Wayland, 1996). For example, patients may have difficulty with auditory rhyme judgments (Blumstein et al., 2000; Gordon & Baum, 1994), and segmental manipulation or blending (addition or deletion of segments) (Berndt et al., 1996). Difficulty in blending tasks may occur in patients who have acquired phonological dyslexia (particular difficulty reading nonwords), suggesting an important relationship between reading and auditory phonological processing, specifically in tasks that rely on correspondences between graphemes and phonemes. The location of damage in cases of phonological dyslexia has not revealed a consistent pattern. In a review of 14 studies of patients with phonological dyslexia in which neuroanatomical descriptions of the location of lesions in 32 cases were provided, only three patients had lesions contained within the frontal lobe. For the rest, the damage extended into the parietal and/or temporal cortices or was limited to the parietal/temporal and or occipital lobes (Fiez & Petersen, 1998). Thus, although lesion studies have provided evidence that processing of sound may be selectively impaired, the neural substrate of phonological processing remains unclear.

3. Neuroimaging studies

A topic of recent debate has concerned the ability of neuroimaging studies to identify the neural substrate of phonological processes (Démonet, Fiez, Paulesu, Petersen, & Zatorre,

1996; Poeppel, 1996). With current methods of imaging, high-resolution spatial information about the underlying substrate of normal human cognition has become possible for normal adults. Both PET and fMRI serve as the basis of task-dependent or activation-based functional neuroimaging. Both of these methods involve imaging some (presumed) correlate of neural activity during performance of a cognitive task in order to observe the particular areas of the brain that play the largest role(s) in that cognitive task. These methods offer the potential for revealing areas of the brain that are active during a task, yet when damaged may not impair performance of language functions. Thus, information from imaging methods may complement information from lesion studies by revealing the set of areas that are active during cognitive processes in normal adults. The question is whether specific areas can be shown to correspond to a cognitive function or more likely, a component of a cognitive function.

Although functional imaging offers much promise in understanding language function in the brain, one complication in activation-based studies has been the design of experimental tasks. Typically, the design of an activation-based experiment in language (or other type of cognition) requires the comparison of at least two conditions, that is, changes in brain activity during some task compared to another task (or rest). In the study of language, task design is particularly complex, since the components of the language system(s) are controversial.

Despite efforts to refine methods and tasks, it remains difficult to draw conclusions from the literature about the areas involved in phonological processes. Investigators attribute “phonological processing” to areas such as “Broca’s area,” “inferior frontal gyrus,” “Brodmann Areas 44/45/46,” yet the precise location of activation within the frontal cortex varies across studies as well as the tasks used to identify these areas. One possible contribution to the variability across studies may be intersubject differences in the anatomic structures and in the location of cytoarchitectonic borders of Broca’s area, such as Brodmann areas 44 and 45 reported in functional studies (Amunts et al., 1999). In addition, “phonology” has been isolated using “verb generation,” “phoneme monitoring,” “visual rhyming,” or “syllable counting” typically compared to passive listening or reading tasks, sensory tasks, or rest. The phonological tasks used in these studies often do not separate production and receptive components or consider similarities/differences in spoken versus written language. Collapsing together these studies without regard to these issues is unlikely to result in increased understanding of the involvement of particular areas. The challenge is to determine whether the differences in location of activation correspond to particular cognitive functions engaged by the phonological tasks and furthermore, whether there are differences in the neural substrate between phonological recoding processes engaged by reading versus speech. Below we will examine theoretical issues related to the processing of sound information in speech and print and the circumstances under which inferior frontal regions are activated by considering recent neuroimaging studies of phonological processing. We will discuss how some of our recent data contribute to specifying the role of the inferior frontal gyrus in processing of sound information, and finally consider possible phonological processes that activate subregions of the inferior frontal gyrus.

In our consideration of neuroimaging studies, we will focus primarily on those studies that rely on phonological judgments to reveal brain activation patterns. We will not emphasize studies that involve elements of word production (e.g., word generation, word reading) (see

Fiez & Petersen, 1998; Poldrack et al., 1999 for reviews). While these studies are helpful in revealing the distributed pattern of activation in reading tasks and tasks that require overt articulation, in many cases, they do not allow isolation of phonological processing from other linguistic components, especially articulation, which may also activate regions such as Broca's area.

We will further focus on studies that report inferior frontal gyrus activation during phonological processing. A number of studies have shown that other areas of the brain are specifically involved in phonological subprocesses. For example, in the auditory modality, speech tasks often show activation of primary auditory cortex and auditory association areas due to initial acoustic/phonetic processing (Price et al., 1992; Zatorre et al., 1996). In tasks that require short-term storage of phonological information, there is often inferior parietal activation (Awh, Smith, & Jonides, 1995; Jonides et al., 1998; Paulesu, Frith, & Frackowiak, 1993; Paulesu et al., 1996). These studies demonstrate the location of neural correlates for elements of phonological processing, namely early perceptual processing of speech and short-term storage of verbal information. The question considered here is whether the same approach of identifying areas participating in subcomponents of phonological processing will reveal the role of inferior frontal cortex in phonological processing.

3.1. Phonology in reading

In reading, there is much controversy over the paths from the written word to word recognition. Dual route models include a direct visual access route in which the orthographic information is mapped onto word representations without reference to phonological information. A second optional route is mediated by phonological information (see Coltheart et al., 1993 for a review). According to some models, phonological codes may be automatically activated whether or not a task requires explicit word recognition (Perfetti & Bell, 1991; Perfetti, Bell, & Delaney, 1988). By contrast, connectionist models of word recognition do not explicitly perform any orthography to phonology mapping. Instead, they capture effects of regular correspondences between spelling and sound with a single process that is sensitive to statistical relationships between spelling and sound that develop through repeated word exposure (Seidenberg, 1987; Seidenberg & McClelland, 1989). These models have led to different predictions about activation of the inferior frontal cortex depending on the extent of orthographic to phonological transformation (Fiez, Balota, Raichle, & Petersen, 1999; Fiez & Petersen, 1998).

In the visual modality, phonological processing has been explored primarily using rhyme judgments (Paulesu et al., 1993; Petersen, Fox, Posner, Mintun, & Raichle, 1989; Pugh et al., 1996; Sergent, Zuck, Lévesque, & MacDonald, 1992; Shaywitz et al., 1995). Studies using nonword rhyming pairs and letters (e.g., does "g" rhyme with "b"?) have found inferior frontal cortex activation. However, not all of this frontal activation falls within Broca's area (Sergent et al., 1992). The predominant interpretation of these visual rhyme judgment studies is that the inferior frontal gyrus activation can be attributed to phonological rehearsal processes that are used to maintain verbal information for short periods of time. Baddeley has proposed such a rehearsal system in which there is a limited duration phonological storage component (buffer) and an articulatory rehearsal process that maintains the stored informa-

tion (Baddeley, 1986). Thus, in the rhyme judgment task, participants must maintain phonological information about the first stimulus for later comparison to the second in order to make a rhyme judgment. However, as Pugh et al. point out, in some of these studies, the visual stimuli were presented simultaneously (Pugh et al., 1996). It is difficult to see what role rehearsal would play in such a task. Second, the stimuli in these studies vary widely. In some cases, the stimuli were words, while in others, the rimes (vowel-consonant portion of the syllable) of the nonwords were spelled differently (e.g., *gooz-rews*), and in yet other cases, subjects were expected to judge whether letter names rhyme.

Such differences in types of stimuli have not been systematically explored in rhyme judgment. However, differences between reading of words and pseudowords and between sets of words with carefully controlled properties such as frequency and consistency of sound to spelling mapping are now being explored in word reading tasks (Fiez et al., 1999; Hagoort et al., 1999; Paulesu et al., 2000). Inferior frontal activation has emerged in conditions such as reading nonwords that require an increased amount of grapheme to phoneme conversion compared to reading words. In a cross-linguistic comparison between Italian and English readers, Paulesu et al. (2000) found greater inferior frontal activation for readers of English compared to readers of Italian, particularly for nonword reading. The two languages differ in the consistency of orthography, suggesting possible increased activation from the more complicated mapping of orthographic information in English. Thus, some recent studies have attributed to the left inferior frontal gyrus a role in spelling-to-sound conversion.

3.2. *Phonology in speech*

Other neurobiological studies have focused on a fundamental issue in speech perception, that is, how listeners map the incoming speech stream onto linguistically relevant units (Burton, Small, & Blumstein, 2000; Zatorre et al., 1992; Zatorre et al., 1996). The motor theory of speech claims that these units correspond to articulatory gestures (Liberman & Mattingly, 1985). Zatorre et al. have argued that this articulatory mapping process (or segmentation) activates Broca's area. Other models of speech perception map acoustic input directly onto syllables (Klatt, 1979) without reference to articulatory gestures. Such models would predict that activation in areas associated with articulation (i.e., inferior frontal cortex) is not necessary during the course of everyday speech perception. Instead, phonological areas associated with mapping sound onto meaning (i.e., posterior temporal areas) are activated according to such theories. Thus, models of speech perception make different predictions about areas that will be activated during speech perception tasks.

Zatorre et al. presented subjects with pairs of spoken consonant-vowel-consonant sequences (e.g., *fat-tid*) and asked whether the final consonant was the same or different (Zatorre et al., 1992; Zatorre et al., 1996). This task was then compared with subjects' responses to a pitch discrimination task and a passive listening task. Importantly, in the final consonant discrimination task of Zatorre et al., the vowel preceding the critical consonant in the stimulus pairs was never the same. This ensured that subjects needed to separate the final consonant from the vowel, which requires analyzing speech sounds that are differently encoded (i.e., consonant transitions vary as function of vowel context). The results showed activation of the left frontal cortex in the phonetic discrimination task, but there was no such

activation in Broca's area under passive listening conditions to the same stimuli. They propose that Broca's area activation occurs when more fine-grained phonetic analysis is required and subjects must make phonetic judgments. In their view, to accomplish such analysis, listeners must access articulatory representations. It is this recoding process from acoustics to articulatory gestures that is said to require Broca's area involvement. Such an articulatory recoding process is thought to take place in Broca's area because of its traditional association with articulatory deficits in neuropsychological studies of aphasic patients, although it should be noted that recent evidence has indicated that lesions to Broca's area do not necessarily result in articulatory impairment (Dronkers, 1996).

We recently completed a study investigating the conditions under which frontal areas are activated in speech discrimination tasks using fMRI (Burton et al., 2000). The purpose of this research was to investigate whether Broca's area will always show activation in an overt speech discrimination task in which subjects are required to make a same/different judgment about phonetic segments. We expected that Broca's area would only be involved when the subject must perform a task that requires articulatory recoding, namely, segmentation of speech stimuli wherein subjects separate the individual sounds from the whole stimulus. If there are a number of differences in the segments in the stimuli, but the task involves the initial sound for discrimination, then it appears likely that the subject must overtly identify the initial segment of the first stimulus and compare it to the initial segment of the second stimulus in order to make a same/different judgment. In contrast, if there is only one phonetic difference in the discrimination pair, such as in phonetic voicing, as is often the case in traditional speech perception experiments, there is in theory no need for segmentation since the subject only has to perceive a single phonetic difference between the stimulus pairs to make a decision.

In a series of two fMRI experiments, we examined the discrimination of voicing in stop consonants (e.g., *t-d*, *k-g*) in tasks that either do or do not require overt segmentation. Specifically, we compared "same/different" judgments of the first sound of pairs of words in two speech experiments, which differed in segmental task demands. Pairs of speech stimuli either required segmentation of the initial phoneme from the rest of the word (e.g., *dip-doom*, *dip-tomb*) or did not require overt segmentation (e.g., *dip-dip*, *dip-tip*). These speech conditions were compared in two experiments to a tone control task where subjects discriminated between pairs of tones with either same or different pitch. For each experiment, eight native speakers of English were presented with one of the speech conditions and the tone condition. Behavioral data showed that subjects were highly accurate in both experiments (greater than 96% correct), but revealed that response times for the "different" pairs were significantly slower than the "same" pairs *only* when segmentation of the speech sounds was required. No other significant differences in response times in any of the other conditions emerged. Functional image acquisition and analysis were performed according to methods described in Burton et al. (2000). The imaging data from group and individual subject analysis showed that whereas both speech conditions showed bilateral superior temporal activation when compared to tone discrimination, only the condition requiring overt segmentation showed evidence of frontal activity. Importantly, the activation difference between the two groups of subjects was statistically significant when directly compared. Taken together, the behavioral and imaging data indicate that phonological processing, and in this

case, phonetic judgments, may invoke different neural mechanisms depending on task demands. More specifically, tasks that invoke segmentation (e.g., discrimination of the initial consonant in *dip-doom* pairs) activated inferior frontal cortex, whereas those that do not require such processes (e.g., discrimination of *dip-tip*) did not.

Other studies of auditory phonological processing have compared phoneme monitoring for sequences of sounds (Demonet et al., 1992; Demonet, Price, Wise, & Frackowiak, 1994) or auditory detection of speech stimuli (e.g., vowels, consonant-vowel (CV) syllables, and CVC words) (Fiez et al., 1995) to passive or sensory (tone) tasks. Both the phonetic discrimination tasks in Zatorre et al. (1992; Zatorre et al. 1996) and in Burton et al. (2000) and the phoneme monitoring tasks of Demonet et al. (1992, 1994) involve segmentation of speech sounds and comparison of stimuli for a decision (either between two consonants in a pair of syllables or between a consonant and a target phoneme). These tasks have shown significant increases in activity in the inferior frontal gyrus relative to passive or sensory conditions.

4. Functional subregions within the inferior frontal gyrus

Thus, auditory and visual phonological judgments as well as reading tasks have all shown participation of the inferior frontal gyrus in processing of sound information. However, some recent studies have suggested that there may be differences in location of left frontal activation depending on the type of processing. For example, Fiez and Petersen (1998) and Poldrack et al. (1999) have argued that there may be subdivisions within left frontal/prefrontal areas. Specifically, semantic processes have been located more anteriorly within the ventral prefrontal cortex (Brodmann Area 47), whereas phonological processing have been attributed to more posterior locations within the triangular and opercular portions of the inferior frontal gyrus (BA 44/45) (Fiez, 1997). Zatorre et al. have further hypothesized that there may be functional subregions within Broca's area specifically related to phonetic operations (Zatorre et al., 1996).

Closer inspection of the foci of activation in phonological studies suggests an organization of foci of activation corresponding to different subprocesses. Fig. 1 shows a schematic drawing of a portion the inferior frontal and middle gyri with a plot of the location of activation in phonological judgment studies that report standardized coordinates (Talairach & Tournoux, 1988). Table 1 lists the studies, tasks, and location of activation included in the analysis. In addition, based on a review by Fiez and Petersen (1998) of six studies (Bookheimer, Zeffiro, Blaxton, Gaillard, & Theodore, 1995; Fiez, unpublished data; Herbster, Mintun, Nebes, & Becker, 1997; Price, Moore, & Frackowiak, 1996a; Price et al., 1996b; Rumsey et al., 1997), the average activation and standard deviation for reading aloud tasks compared with passive or sensorimotor is included for comparison purposes. The studies are organized by modality (i.e., auditory vs. visual). However, essentially all of the visual studies involve a rhyme judgment, whereas the auditory studies mostly involve segmentation. Thus, based on current studies, effects of modality are difficult to separate from the type of phonological process. Although it is possible that the differences between the auditory and visual phono-

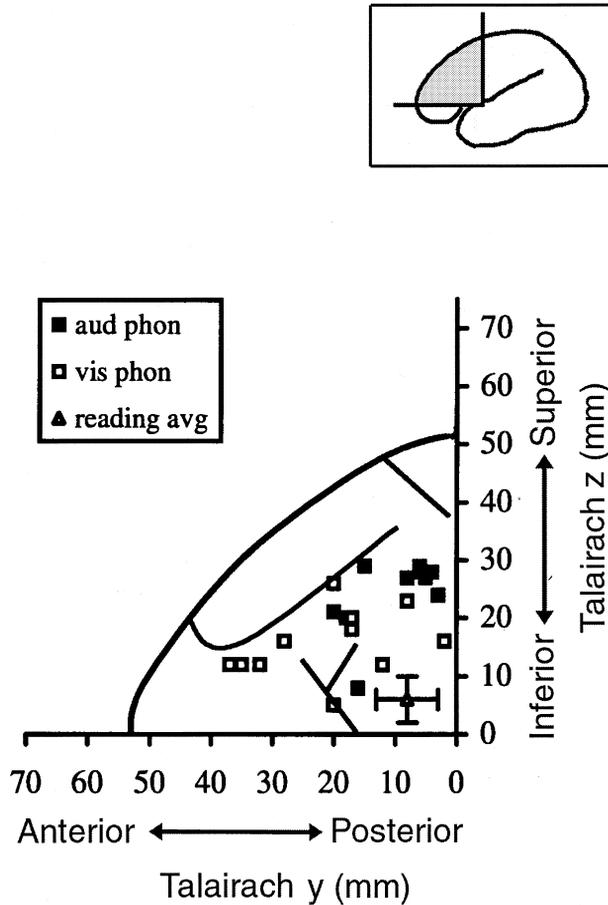


Fig. 1. The chart depicts a magnification of the shaded area of the lateral view of the brain shown inside the box at top right. The chart includes the left inferior and middle frontal gyri and depicts the location of foci of activation in auditory and visual phonological studies shown in Table 1. The scale is based on the standard stereotactic coordinates in the Talairach and Tournoux (1988) atlas with the abscissa showing the y coordinate (anterior-posterior) and the ordinate showing the z coordinate (inferior-superior). The location of the sulci separating the inferior and middle frontal gyri (curved line) and between the pars triangularis and opercularis (backwards Y) was approximated assuming a lateral (x) coordinate of 47, the average of all studies in Table 1. Filled squares indicate auditory phonological studies. Unfilled squares represent visual phonological studies. The unfilled triangle shows the location of average activation in reading studies reviewed by Fiez and Petersen (1998). The bars attached to the triangle indicate the standard deviation.

logical studies are related to modality of presentation, it appears to be more likely that they are due to differences in the type of phonological processing invoked by the different tasks used in each modality.

The location of activation in both the auditory and visual phonological judgment tasks appears to be predominantly superior to the reading tasks reviewed by Fiez and Petersen (1998), which involve conversion of orthographic information to phonological codes and overt articulation. Interestingly, the location of activation in the auditory judgment tasks

Table 1
Summary of inferior frontal cortex activation in auditory and visual phonological judgment studies

Author	Year	Experimental task ^a	Control task ^b	x	y	z ^c
Auditory studies^d						
Burton et al.	2000	Phon. Discrim. (segmentation)	Tone Discrim.	-47	15	29
Demonet et al.	1992	Phon. Monitor.	Tone Monitor	-50	18	20
Demonet et al.	1994	Phon. Monitor. (seq)	Tone Monitor	-40	4	28
Demonet et al.	1994	Phon. Monitor. (seq)	Phon. Monitor. (no seq)	-42	6	28
Fiez et al.	1995	Target Detection	Fixation	-40	16	8
Fiez et al.	1995	Target Discrim.	Passive Speech	-37	16	8
Zatorre et al.	1992	Phon. Discrim.	Passive Speech	-48	3	24
Zatorre et al.	1996	Phon. Monitor	Passive Speech	-44	8	27
Zatorre et al.	1996	Phon. Discrim.	Passive Speech	-35	20	21
Zatorre et al.	1996	Phon. Discrim.	Noise Discrim.	-43	5	27
Zatorre et al.	1996	Phon. Discrim.	Pitch Discrim.	-56	6	29
Visual studies						
Paulesu et al.	1993	Letter rhyme	Shape judgment	-46	2	16
Paulesu et al.	1996	Letter rhyme	Shape judgment	-46	12	12
Poldrack et al.	1999	Syllable counting	Case Judgment	-47	28	16
Poldrack et al.	1999	Syllable counting	Case Judgment	-48	20	26
Poldrack et al.	1999	Syllable counting	Case Judgment	-50	35	12
Poldrack et al.	1999	Syllable counting	Case Judgment	-56	8	23
Sergent et al.	1993	Letter-sound rhyme	Letter orient.	-44	37	12
Sergent et al.	1993	Letter-sound rhyme	Letter orient.	-52	17	18
Sergent et al.	1993	Letter-sound rhyme	Letter orient.	-54	20	5
Shaywitz et al.	1995	Rhyme	Case Judgment	-50	18	20

^aPhon. Discrim = Phonetic Discrimination, Phon. Monitor = Phoneme Monitoring, Discrim = discrimination, seq = in a sequence (e.g., is there a “b” that follows a “d”).

^bOrient = Orientation, no seq = not in a sequence (e.g., is there a “b”).

^cThe location of activation is given in standard stereotactic coordinates (x, y, and z) (Talairach & Tournoux, 1988).

^dStudies are organized by modality in alphabetical order.

tends to cluster in posterior and superior aspect of the inferior frontal gyrus, whereas the activation in the visual phonological judgment studies (rhyme and syllable judgment), while more widespread, appears to be more anterior and inferior to the speech tasks. An average of the anterior-posterior coordinates (y) and inferior-superior coordinates (z) by study indicates such a difference with the auditory activation more posterior (auditory = 12; visual = 18) and more superior (auditory = 23; visual = 16). These averages appear to be strongly affected by two exceptions, Paulesu et al. (1993) in the visual modality, and Fiez et al. (1995) in the auditory modality. Without including these two studies, the differences in the anterior to superior and inferior to superior planes become more clear-cut (y: mean auditory location = 22, SD = 2.8; mean visual location = 11, SD = 5.4; z: mean auditory location = 26 mm, SD = 3.5; mean visual location = 16, SD = 4.5). The task comparison reported in the Paulesu et al. (1993) between letter rhyme judgment and Korean letter shape judgment, in

fact, showed more anterior activation when repeated in a later study, suggesting the most posterior center of activation ($-46, 2, 16$) may be somewhat misleading.

The activity associated with the auditory detection task reported by Fiez et al. (1995), which is located in the left frontal opercular zone, is somewhat more puzzling. Fiez et al. have proposed that the left frontal opercular region is important for certain types of auditory/temporal analysis, and, in particular, for processing stimuli containing rapid temporal changes often in conjunction with tasks that require articulatory rehearsal strategies. The stimuli in Burton et al. (2000) also relied on rapid temporal changes, but showed frontal activation at the border of the inferior and middle frontal gyri and not in the frontal operculum. It is possible that the differences that have emerged across experiments reflect different task demands, and in particular, the extent to which the tasks require verbal rehearsal processes to perform monitoring or detection tasks such as those used by Fiez et al. (1995).

It is not clear from either the auditory or visual phonological studies the degree to which the inferior frontal activation is specific to phonological processes or reflects activity involved in verbal rehearsal. Verbal rehearsal has often been tested in neuroimaging using the *n*-back task, in which subjects view a sequence of single letters and decide whether each letter matches the letter a prespecified number of letters back in the sequence. The control task, in many cases, is to decide whether each letter matches a single target letter. To perform the *n*-back task, it is hypothesized that subjects continuously rehearse the letters. Thus, the areas involved in rehearsal should be revealed by the task. Smith & Jonides (1999) plotted the foci of activation of six studies using 2- and 3-back tasks (Awh et al., 1996; Braver et al., 1997; Cohen et al., 1994; Cohen et al., 1997; D'Esposito et al., 1998; Fiez et al., 1996). This analysis indicated that the activation clustered posteriorly in the frontal lobe, ranging from the premotor and supplementary motor areas ventrally to Broca's area, showing the extent of a "rehearsal circuit." Within Broca's area, the *n*-back studies have activated not only the operculum (Fiez et al., 1996), but also more superior regions (Braver et al., 1997; Cohen et al., 1994). The activity tends to be somewhat more anterior to phonological judgment studies (Braver et al., 1997; Cohen et al., 1994; Schumacher et al., 1996), but there is a great deal of overlap with the activity reviewed here. Further research is needed to determine whether phonological processes are separable from verbal rehearsal.

5. Conclusions

Re-examination of neuroimaging studies of auditory and visual phonological processes indicates that three subcomponents of phonological processing result in different patterns of activation. More specifically, speech segmentation needed to perform phoneme monitoring and phonetic discrimination tasks results in activation of the superior and posterior aspect of the inferior frontal gyrus. In studies of visual phonological judgments, such as letter or rhyme judgment, subjects convert orthographic information to phonological codes to make decisions about the sound patterns. These processes activate a region of the inferior frontal gyrus that is anterior and inferior to those seen in segmentation tasks. Studies in which subjects read aloud words and nonwords have revealed opercular activation, which does not typically

overlap with activation found in phonological judgment studies. What remains to be determined is the extent to which verbal rehearsal needed for short-term maintenance of these stimuli contributes to this inferior frontal activation. The differences in location of these three subprocesses suggests that simply attributing all of this frontal activity to the same verbal rehearsal processes is not adequate and that there are distinct phonological processes that are mediated by the inferior frontal cortex.

That these subprocesses have not been identified from lesion studies is not surprising. Structural lesions are rarely limited to such a small area of cortex (Dronkers, 1996). Thus, it would be unlikely to find a patient with a lesion that only affected the superior and posterior portion of inferior frontal cortex. Furthermore, it is unclear how lesions affect metabolic activity within the cortex. For example, a patient with a subcortical lesion may show a selective impairment of particular types of visual rhyming tasks (e.g., those in which there is a mismatch of sound and spelling information as in *chain-plane, few-sew*) (Berndt et al., 1996; Berndt & Haendiges, 2000). Thus, even though the lesion is not located near areas identified as participating in language processing, the patient, nevertheless, shows impairments in phonological processing related to converting the orthographic information in written words into sound information to perform visual rhyme judgments.

Neuroimaging studies of normal processing are contributing to progress in understanding the neural substrate of phonological processing by providing new information about the organization of subprocesses within the frontal cortex. Other studies are providing information about the time-course of phonological processes suggesting that the phonological processing proceeds from early decoding processes in the superior temporal regions to later rehearsal (and/or presumably, segmentation) processes in Broca's area (Thierry, Boulanouar, Kherif, Ranjeva, & Demonet, 1999). The combination of methods with high spatial resolution such as fMRI with those with high temporal resolution such as magnetoencephalography (MEG) and event-related potentials (ERP) promise to provide further specification of how phonological processes are accomplished.

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