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Functional Specialization for Semantic and Phonological Processing in the Left Inferior Prefrontal Cortex[1]

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Neuroimaging and neuropsychological studies have implicated left inferior prefrontal cortex (LIPC) in both semantic and phonological processing. In this study, functional magnetic resonance imaging was used to examine whether separate LIPC regions participate in each of these types of processing. Performance of a semantic decision task resulted in extensive LIPC activation compared to a perceptual control task. Phonological processing of words and pseudowords in a syllable-counting task resulted in activation of the dorsal aspect of the left inferior frontal gyrus near the inferior frontal sulcus (BA 44/45) compared to a perceptual control task, with greater activation for nonwords compared to words. In a direct comparison of semantic and phonological tasks, semantic processing preferentially activated the ventral aspect of the left inferior frontal gyrus (BA 47/45). A review of the literature demonstrated a similar distinction between left prefrontal regions involved in semantic processing and phonological/lexical processing. The results suggest that a distinct region in the left inferior frontal cortex is involved in semantic processing, whereas other regions may subserve phonological processes engaged during both semantic and phonological tasks. © 1999 Academic Press

The inferior cortex of the left frontal lobe is critically involved in language function. People with lesions to this region exhibit primary difficulties with speech production, though other aspects of language performance are impaired as well (see Damasio, 1992, for review). Neuroimaging studies have also provided evidence that the left frontal region is active during a wide range of language tasks, including those that do not involve overt production of speech (see Gabrieli *et al.*, 1998, for review).

The current understanding of the structure of language processing distinguishes a set of component linguistic functions: these include separable processes related to speech sounds (phonological processing); to the visual structure of written words (orthographic processes); to the meaning of linguistic tokens (semantic processing); to the structure of complex linguistic forms (syntactic processing); to the integration of phonological, semantic, and syntactic aspects of words (lexical processing); and to the programming of speech motor acts (articulatory processing).

Neuropsychological investigations suggest that each of these forms of processing may be individually impaired by brain damage, although large lesions often result in impairment of multiple processes (Caplan, 1992). The left frontal lobe has been primarily implicated in articulatory and phonological processing on the basis of neuropsychological studies. However, because brain lesions are often large and do not observe functional boundaries, it is difficult to determine whether separate linguistic functions are subserved by separate cortical regions in the left frontal lobe. In the present study, we used functional magnetic resonance imaging (fMRI) to investigate whether two classes of linguistic processing involved in the reading of written words, phonological and semantic processing, rely upon separate regions of the left inferior frontal cortex.

Frontal Cortex and Semantic Processing

Imaging studies using positron emission tomography (PET) and fMRI have suggested that the anterior extent of the left inferior prefrontal cortex (LIPC), corresponding to Brodmann's areas 47 and 45 in the inferior frontal gyrus, is active during word-level semantic processing, such as making semantic decisions about words (Demb *et al.*, 1995; Gabrieli *et al.*, 1996; Kapur *et al.*, 1994b; Wagner *et al.*, 1998) or generating words based on semantic relationships (Klein *et al.*, 1995; Petersen *et al.*, 1988). Demb *et al.* (1995) examined whether LIPC activation in a semantic decision task was a function of task difficulty and found that

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LIPC was activated during a semantic decision task even when the perceptual baseline task was more difficult (as measured by response time). This result rules out the possibility that brain activation in the semantic task was a function of task difficulty rather than semantic processing per se.

Evidence for the specificity of LIPC activation to semantic processing comes from a study that examined repetition priming effects in a semantic decision task (Demb *et al.*, 1995). Repetition of items in a semantic decision task (abstract/concrete judgment) resulted in reduced LIPC activation for the repeated compared to the original presentation. Performing a perceptual decision task (uppercase/lowercase) repeatedly resulted in no such changes in prefrontal activation, suggesting that the changes were specific to semantic processing. Wagner *et al.* (1997a) further examined the process specificity of such item repetition effects and found that items initially encountered in a perceptual decision task did not result in later decreases in activation on a semantic decision task, whereas items initially encountered in a semantic decision task resulted in decreases in LIPC activation when reprocessed semantically. A study by Wagner *et al.* (1997b) demonstrated the generality of LIPC involvement in semantic processing. Subjects were presented with pictures or words and made category decisions (living/nonliving) for each item. Activation of LIPC decreased with repetition both for words and for pictures, suggesting that LIPC plays a general role in semantic processing (see also Vandenberghe *et al.*, 1996).

The role of the frontal cortex in semantic processing has also been examined using other methods. A study using scalp recordings with high-density electrodes found differences in electrical activity over the frontal cortex between word reading and semantic generation tasks, with the source of the difference localized to the ventral left frontal cortex (Abdullaev and Posner, 1998). Another study using chronically implanted depth electrodes in LIPC (BA 47) found greater activity in that region related to semantic decision relative to a perceptual decision (Abdullaev and Bechtereva, 1993). In a study combining intraoperative stimulation with PET (Klein *et al.*, 1997), stimulation of an LIPC region disrupted synonym generation but not word repetition, and the same region exhibited PET activation for synonym generation compared to word repetition. Neuropsychological studies provide additional evidence that LIPC is involved in semantic processing of words. Swick and Knight (1996) examined abstract/concrete and living/nonliving judgments in patients with lesions to the LIPC, the left superior prefrontal cortex, or the right prefrontal cortex. Patients with lesions to the LIPC were impaired on the living/nonliving task relative to patients with lesions to the left superior prefrontal cortex or the right prefrontal area. These data converge with imaging studies to strongly suggest that activation in the LIPC is directly related to semantic processing of words.

Frontal Cortex and Phonological Processing

The LIPC has also been implicated in phonological processing on the basis of imaging and neuropsychological studies. Studies using PET have found activation of the LIPC during tasks that require judgments about individual phonemes, such as phonetic monitoring (Demonet *et al.*, 1992; Zatorre *et al.*, 1996), and other tasks that require processing of phonological information such as rhyming judgments (Sergent *et al.*, 1992) and the generation of rhymes (Klein *et al.*, 1995). Similar activations have been found during tasks involving visually presented nonwords (Pugh *et al.*, 1996). Tasks involving the reading of nonwords are thought to require phonological recoding in order to translate novel orthographic information into phonological information, whereas tasks involving familiar words can be performed by direct retrieving phonological representations from the lexicon (Coltheart, 1985).

Lesions to the LIPC may also impair phonological processing. Fiez and Petersen (1998) have reviewed the evidence for phonological dyslexia (an impairment in the ability to derive phonological information from orthographic information) in patients with damage to the left inferior frontal region. Across studies, six of seven patients with confirmed damage to the left frontal region (sometimes accompanied by other lesions) exhibited deficits in reading nonwords, erroneously producing real words in response to visually presented nonwords. This review provides preliminary evidence in favor for a role of the left frontal cortex in phonological processing, though further work is necessary to fully characterize the anatomical and linguistic nature of the deficit.

Phonological vs Semantic Processing in Frontal Cortex

One important question regards whether semantic and phonological processing relies upon separate functional regions in the LIPC. Resolving this question is not only important from a brain-mapping perspective, but can also shed light upon the basic structure of language processing. Common activations for phonological and semantic processing in the LIPC would suggest common underlying cognitive processes, whereas separate activations suggest distinct processes.

There are reasons to believe that semantic and phonological processing might be closely related. The first is the well-known automaticity of semantic processing (Neely, 1977). It may be the case that words that are processed to the level of phonology are automatically processed semantically as well, whereas words processed in a superficial visual manner (as in a case judgment task) might not engender the same level of automatic semantic processing. Conversely, phonological information may exert an automatic influence on semantic processing. Van Orden *et al.* (1988) found that subjects made phonologically driven false alarms in a category decision task, such as accepting "rows" as a flower, suggesting that phonological information automatically influenced performance on the semantic task. Such findings have led some (e.g., Van Orden *et al.*, 1988) to argue that reading words for meaning is mediated by phonological processing; however, neuropsychological evidence shows that patients with impairments in phonological processing may perform well on semantic tasks (Hanley and McDonnell, 1997; Shelton and Weinrich, 1997), suggesting that phonological mediation may not be necessary. Functional neuroimaging can help address this issue by determining the degree to which semantic and phonological processing results in distinct patterns of neural activation.

The Current Study

The study presented here directly examined the role of LIPC in semantic and phonological processing using fMRI. Several previous imaging studies directly comparing semantic and phonological processing have not found differences in inferior frontal activation between semantic and phonological tasks (Klein *et al.*, 1995; Price *et al.*, 1997; Pugh *et al.*, 1996). Other studies have found regions of greater activation for semantic processing relative to phonological processing (Shaywitz *et al.*, 1995). We attempted to clarify these previous studies by presenting four scans with task comparisons designed to isolate specific classes of linguistic processing. One scan compared a semantic decision (abstract/concrete decision) with a perceptual decision task (uppercase/lowercase decision) in order to isolate semantic, phonological, and lexical processing. Another scan compared a phonological task (syllable counting) with the same perceptual decision task in order to isolate phonological processing of words, which may involve direct retrieval of phonological word-form information. A third scan compared a phonological task (syllable counting) using nonwords with the perceptual baseline task; because reading nonwords likely requires translation of orthographic to phonological features, this task was thought to isolate phonological recoding operations. A fourth scan directly compared the semantic decision task with the phonological task (with words), in order to directly isolate the regions involved specifically in semantic or phonological processing. These are referred to as the *semantic*, *phonological*, *pseudoword phonological*, and *direct comparison* scans, respectively. Together these scans allow the determination of the whether separate regions in the LIPC subserve these linguistic processes.

The syllable-counting task used in the present study differs from the tasks used in a number of previous studies of phonological processing, such as phoneme monitoring or rhyme judgments. Whereas phoneme monitoring tasks require access to individual phonemes, the syllable-counting task requires access to individual syllables, which are composed of clusters of phonemes. The syllabic level of representation is important during both language comprehension and language production. For example, the syllable is thought to be the basic unit of organization for phonological encoding, which is the stage in speech production at which a phonetic plan is assembled (Levelt, 1993). This suggests that the syllable-counting task might engage frontal regions involved in speech production, and one previous study (Price *et al.*, 1997) found activation of the left prefrontal cortex during syllable counting (at a lenient threshold). Rhyme judgments may be more similar to syllable counting than phoneme discrimination, since rhyme judgments also involve processing of features greater than a single phoneme. The syllable-counting task introduces an additional requirement to maintain a count, which is not required for other phonological tasks. However, the small number of syllables involved (one to three) suggests that subjects may subitize the units (i.e., enumerate them without counting). When performed with pseudowords, the syllable-counting task also requires additional phonological processing in the form of phonological recoding, which may result in activation of additional regions.

METHODS

Subjects

Subjects were eight volunteers (five male and three female, seven right-handed and one left-handed) from the Stanford community who participated for $30. All subjects were native speakers of English. Informed consent was obtained from each subject prior to the experiment.

Materials

Three 144-word lists were constructed from a previously used set of abstract and concrete words (see Gabrieli *et al.*, 1996); these word lists are presented in Appendix A. Word frequency and word length did not differ significantly between lists (P's > 0.2). Across lists, mean word frequency (Kucera and Francis, 1982) was 63.4 for abstract words and 47.0 for concrete words. Each list was broken into 12 blocks of 12 words; each block consisted of half abstract and half concrete words, half uppercase and half lowercase words, and half two-syllable and half one- and three-syllable words. Thus, each list could be used interchangeably in each of three tasks: abstract/concrete judgment, case judgment, and syllable counting. Pseudowords used in the experiment were chosen from a set of pronounceable nonwords created by changing one consonant in a set of medium-frequency English words; these nonwords are also presented in Appendix A. Each item appeared only once during the entire experiment for each subject.

Procedure

Subjects participated in one scanning session lasting approximately 90 min. Four functional scans were administered during the session; the order of these scans in the session and the assignment of word lists to particular scans was counterbalanced across subjects. Across the four scans, the subjects performed three tasks in different combinations. In the *case judgment* task, the subject pressed a response button depending upon the case of the letters in which the word was presented. In the *category judgment* task, the subject pressed the response button depending upon whether the word was abstract or concrete. In the *syllable judgment* task, the subject pressed the response button depending upon the number of syllables in the word or pseudoword. Half of the subjects pressed the response button for abstract words, uppercase words, and two-syllable words. The other half of the subjects pressed the response button for concrete words, lowercase words, and words that did not have two syllables.

In each scan, the two tasks being compared were alternated each 34.17 s for six cycles of alternation. In the *Semantic* scan, the semantic judgment and case judgment tasks were alternated. In the *Phonological* scan, the syllable judgment (on real words) and case judgment tasks were alternated. The *Pseudoword Phonological* scan was identical in procedure to the Phonological scan, except that the stimuli were pronounceable nonwords. In the *Direct Comparison* scan, the semantic judgment task and syllable judgment task (with real words) were alternated in order to directly compare semantic and phonological processing. Each individual item was presented for 1.5 s with a 1.13-s interstimulus interval. An instruction card was presented at the beginning of each block of trials, with the same timing as the stimuli.

Stimuli were generated by a Macintosh computer and back projected onto a screen located above the subject's neck via a magnet-compatible projector; the projected image appeared on a mirror mounted above the subject's head. Subjects responded by pressing an optical switch with the right hand. The responses were collected by a computer interfaced with the optical switch using the PsyScope button box (Cohen *et al.*, 1993).

fMRI Procedures

Imaging was performed with a 1.5-T whole-body MRI scanner (GE Medical Systems Signa). A prototype receive-only whole-head coil was used for signal reception. Head movement was minimized using a "bite-bar" formed with each participant's dental impression. A T2*-sensitive gradient-echo spiral sequence (Glover and Lai, 1998) was used for functional imaging with parameters of TE = 40 ms, TR = 900 ms, flip angle = 70°, FOV = 36 cm, and inplane resolution = 2.35 mm. Four spiral interleaves were obtained for each image, for a total acquisition time of 360 ms per image slice (3600 ms per image volume). The onset of the scanning session was controlled by the experimental presentation program via a TTL output, allowing precise synchronization of the stimulus presentation and scanner onset.

In each experiment, ten 6-mm-thick slices were acquired separately in the coronal plane of the Talairach and Tournoux (1988) atlas from the anterior commissure to the frontal pole, with a 1-mm interslice interval. Figure 1 presents an example of such a set of slices overlaid on a saggital localizing image. Functional images were acquired continuously every 3.6 s over the course of each 410-s experiment, for a total of 114 images. T1-weighted flow-compensated spin-echo anatomy images were acquired for each of the slices imaged in the functional scans.

A feature of the spiral acquisition technique is that off-resonance resulting from magnetic field heterogeneity or T2* variations causes only image blurring rather than spatial distortions as in echo-planar imaging or conventional gradient-recalled methods (Noll *et al.*, 1992). This blurring was corrected during reconstruction from a field map made using phase images obtained at two different echo times for each spatial slice (Irarrazabal *et al.*, 1996) Registration of the functional images and the spin-echo anatomic images required no correction for distortion.

Data Analysis

Functional image processing was performed offline after transferring the raw data to a Sun SparcStation. Raw functional images were motion corrected in the inplane dimensions using AIR 3.0 (Woods *et al.*, 1992) and then spatially filtered in three dimensions using a Gaussian filter (5 mm full width at half-maximum). The data were then analyzed using the cross-correlation method described by Friston *et al.* (1994). The activity of each pixel was correlated to a reference function obtained by convolving the square wave describing the task alternation with an estimate of the participant's hemodynamic response function. For each scan in the present experiment, the frequency of the square wave describing the task alternation was 0.014634 Hz (6 cycles/410 s). These correlation values were then normalized to create a functional image (SPM{Z}) for each individual scan for each subject.

Averaged functional images across the eight subjects

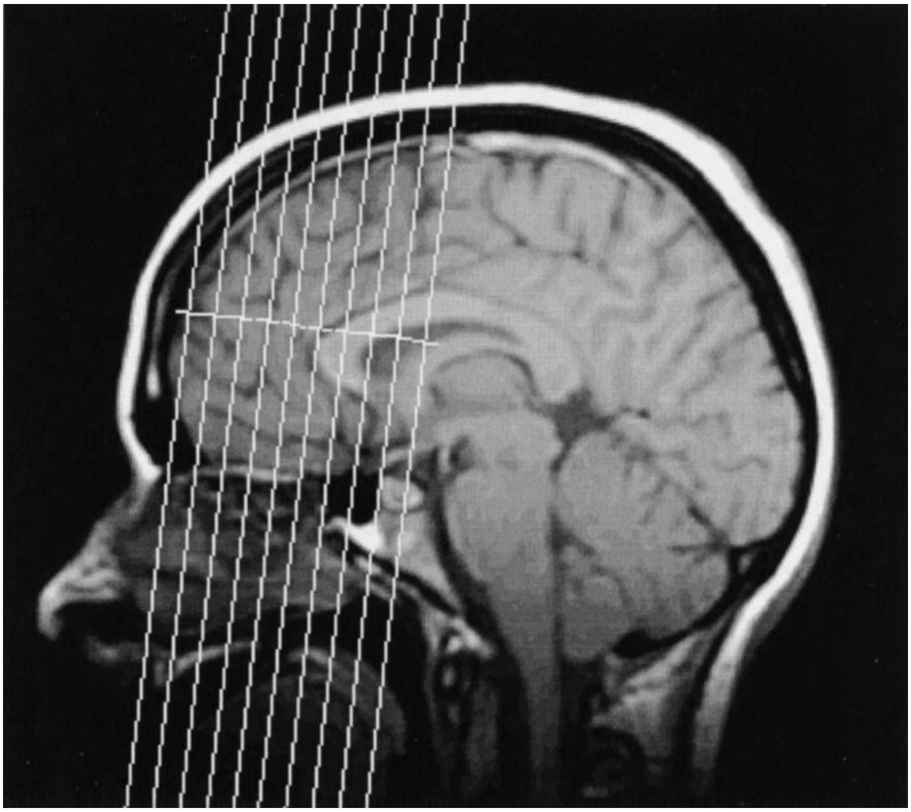

FIG. 1. Example of fMRI slice selection.

were formed for each scan by warping the functional images for each participant onto a reference template from the Talairach and Tournoux (1988) atlas using the nonlinear WARP_TRI procedure in IDL (Research Systems, Inc., Boulder, CO). Functional activation maps were constructed by selecting pixels whose averaged correlation values exceeded a criterion of $Z \geq 1.96$ ($P = 0.05$, two-tailed), along with a median filter of three pixels. Cluster maxima were included in the activation tables below if they had a Z value of at least 1.96 and a cluster size of at least six inplane voxels and were at least two slices away from the nearest maximum in the same cluster.

Data were also analyzed using a paired comparison approach, which was performed using double subtraction between pairs of scans; this approach allows comparison of activations across separate task comparisons (cf. Poldrack *et al.*, 1998). In this case, the approach allowed examination of convergence of comparisons across scans with the results from individual scans. After warping to the reference template, Z maps from each of the two scans being compared were subtracted and then averaged across subjects. The resultant map is distributed under the null hypothesis as a standard normal variate with mean of zero and standard deviation of sqrt(N) where N is the number of subjects. Two comparisons were examined using this analysis for comparison with the Direct Comparison scan (Semantic − Syllable judgment): Semantic versus Phonological scans [(Semantic − Case) − (Syllable − Case)] and Semantic versus Pseudoword Phonological [(Semantic − Case) − (Pseudoword Syllable − Case)].

RESULTS

Behavioral Results

Response times and accuracy for each of the four scans are presented in Table 1. Case judgments were faster than semantic decisions in the Semantic scan, $t(7) = 7.15$, $P < 0.001$, and were faster than phonological decisions in the Phonological scan, $t(7) = 5.49$, $P < 0.001$. In the Direct Comparison scan, there was no significant difference between response times for phonological and semantic decisions, $t(7) = 0.059$, $P > 0.95$; five subjects were slower on semantic decisions and three were slower on phonological decisions. In the Pseudoword Phonological scan, phonological decisions were slower than case judgments, $t(7) = 7.12$, $P < 0.001$.

FMRI Results: LIPC

Table 2 presents the Talairach locations for significant clusters of activation and deactivation in each of

TABLE 1

Response Time and Accuracy for Each Scan (Standard Error in Parentheses)

Scan and task	RT	Accuracy
Semantic vs Case		
Case	527 (31)	0.99 (0.005)
Category	843 (51)	0.89 (0.038)
Phonological vs Case		
Case	537 (24)	0.99 (0.007)
Syllable	805 (43)	0.96 (0.023)
Semantic vs Phonological		
Syllable	830 (70)	0.91 (0.036)
Category	835 (41)	0.81 (0.048)
Pseudoword Phonological vs Case		
Case	497 (29)	0.91 (0.082)
Nonword Syllable	907 (54)	0.75 (0.089)

the four scans for the entire scan volume averaged over all subjects; regions outside the inferior frontal cortex are included for completeness but will not be discussed here. Figure 2 presents the averaged functional activation maps over all subjects for the region encompassing the left inferior frontal cortex, whereas Fig. 3 presents data from an individual subject for each scan. There was significant LIPC activation in the Semantic scan, which compared the abstract/concrete decision to the uppercase/lowercase decision. This activation extended through Brodmann's areas 44, 45, and 47. Significant activation was also present in the right inferior prefrontal cortex (RIPC); this bilateral pattern of activation in the Semantic scan was observed in six of the eight participants. Other studies of semantic processing have also found RIPC activation during semantic processing (e.g., Wagner *et al.*, 1998). The LIPC activation in the Semantic scan extended anteriorly to the frontal pole, as did RIPC activation.

In the Phonological scan, there was a limited region of activation in the dorsal portion of the left inferior frontal gyrus, near the inferior frontal sulcus (BA 45). Activation was also found in the right inferior frontal gyrus (BA 44).

In the Direct Comparison scan, there were significant regions of activation in the anterior LIPC (BA 47/45) and posterior LIPC (BA 44) for semantic processing compared directly to phonological processing. There was no evidence for greater phonological-related activation than semantic-related activation in the left inferior frontal gyrus. However, the right inferior frontal cortex exhibited greater activation for the phonological task compared to the semantic task.

In the Pseudoword Phonological condition, there was significant activation of the inferior frontal gyrus during phonological decisions when compared to case judgments; this activation fell near the inferior frontal sulcus in the dorsal aspect of the gyrus. Activation was also observed in the superior and posterior section of the inferior frontal gyrus (BA 44/45). Significant right inferior frontal activation was also observed during this task.

Between-Scan Comparisons

Task comparisons across separate scans were performed using double subtraction as described above; activations and deactivations for these comparisons are listed in Table 2. Activation in the Semantic scan was first compared to activation in the Phonological scan. There was an area of significantly greater activation for semantic processing extending along the left inferior frontal gyrus for several centimeters, through BA 44, 45, 47, and 10. There were also two regions of significantly greater semantic activation in the right inferior frontal gyrus, posteriorly in BA 44 and anteriorly in BA 47. The double subtraction results thus confirmed the results from the individual scan comparisons between semantic and phonological processing.

Activation in the Semantic scan was also compared to that in the Pseudoword Phonological scan to determine whether the heightened phonological demands of the pseudoword task would offset the activation in left inferior prefrontal regions in the semantic task. There was significantly greater activation in the left inferior prefrontal region for semantic processing, extending through BA 45 and 47. There was also a region of greater activation for semantic processing in the right inferior frontal cortex.

DISCUSSION

Our examination of semantic and phonological processing in the left inferior prefrontal cortex demonstrated the existence of a region in the left inferior frontal gyrus whose activity was specifically related to semantic processing. The anterior/ventral extent of the gyrus was more active during semantic than phonological processing, whereas a more posterior/dorsal region (near the inferior frontal sulcus) was active in relation to both semantic and phonological processing. There was no evidence of greater activation in the left inferior frontal gyrus for phonological relative to semantic processing. Comparisons between scans provided converging evidence with the results from individual scans, demonstrating that semantic processing resulted in greater activity in the anterior/inferior LIFG than phonological processing for either words or pseudowords. These results suggest that phonological processing is automatically engaged during the performance of a semantic task, but that some regions in the LIPC are specifically related to semantic processing. The dissociation between anterior/ventral and posterior/dorsal regions is also consistent with the framework proposed by Fiez (1997) for semantic and phonological processing in the frontal cortex.

TABLE 2

Stereotactic Locations of Cluster Maxima

Comparison	Talairach coordinates x	y	z	Maximum Z
Semantic > Case				
L inf frontal gyr (BA 47)	−46	20	−3	7.3
Ant cingulate (BA 32)	−1	20	42	6.96
L inf frontal gyr (BA 44)	−49	8	26	6.14
R mid frontal gyr (BA 10)	38	50	15	5.91
Sup frontal gyr (BA 8)	−1	35	47	5.15
Ant cingulate (BA 24/32)	−2	8	45	5.09
R inf frontal gyr (BA 45/47)	34	20	0	5.06
R orbitofrontal cortex (BA 11)	7	60	−18	4.72
R inf frontal gyr (BA 44)	52	8	26	4.53
L inf frontal gyr (BA 10)	−46	50	1	4.41
L inf frontal gyr (BA 47)	−35	35	−1	4.38
R inf frontal gyr (BA 45)	43	35	13	4.24
R caudate	12	8	12	4.13
L caudate	−12	0	18	3.87
L sup frontal gyr (BA 10)	−23	60	−7	3.82
L orbitofrontal cortex (BA 11)	−25	50	−16	3.53
L sup frontal gyr (BA 9)	−5	50	33	3.22
L caudate	−10	16	11	3.05
L mid frontal gyr (BA 6)	−39	0	47	2.8
Case > Semantic				
L mid frontal gyr (BA 8/9)	−36	35	37	3.73
Med frontal gyr (BA 10)	0	55	0	3.54
Ant cingulate (BA 32/24)	−2	40	0	3.28
Phonological > Case				
White matter	32	35	22	3.62
Ant cingulate (BA 24/32)	−3	8	36	3.22
R mid frontal gyr (BA 8/9)	38	20	33	3.14
L inf frontal gyr (BA 45)	−47	28	16	2.86
Ant cingulate (BA 24/32)	5	20	30	2.85
R inf frontal gyr (BA 44)	60	8	27	2.69
L premotor (BA 6)	−46	0	24	2.35
Case > Phonological				
L sup/mid frontal gyr (BA 8/9)	−23	40	34	3.31
Med frontal gyr (BA 9)	−1	40	20	3
L sup frontal gyr (BA 8)	−17	28	43	2.77
R mid frontal gyr (BA 10)	30	55	20	2.77
R sup frontal gyr (BA 10)	22	60	−10	2.69
Med frontal gyr (BA 9/10)	−1	55	5	2.57
Semantic > Phonological				
Sup frontal gyr (BA 9)	−7	50	31	4.69
Medial frontal gyrus (BA 8)	−4	35	48	4.61
L inf frontal gyr (BA 44)	−53	16	25	3.68
L sup frontal gyr (BA 6)	4	20	56	3.39
L inf frontal gyr (BA 47)	−37	28	−9	3.31
L inf frontal gyr (BA 47)	−42	40	−8	2.74
Phonological > Semantic				
L mid frontal gyr (BA 9/46)	−42	35	26	4.02
R premotor (BA 6)	49	0	16	3.68
Corpus callosum	15	35	3	3.37
R inf/mid frontal gyr (BA 45/9)	33	20	41	3.17
L premotor (BA 6)	−47	0	13	3.11
R inf frontal gyr (BA 45)	48	35	7	3.03
R inf frontal gyr (BA 44)	47	8	37	3
Gyrus rectus	0	50	−26	2.97
Med frontal gyr (BA 10)	10	50	4	2.94
R inf frontal gyr (BA 10)	41	50	2	2.72
R sup frontal gyr (BA 10)	27	60	5	2.5
Ant cingulate/med frontal gyr (BA 32/6)	−1	0	47	2.46
Pseudoword Phonological > Case				
L inf frontal gyrus (BA 44)	−56	8	23	6.65
R inf frontal gyr (BA 45)	39	28	16	6.19
Ant cingulate/med frontal gyr (BA 24/32)	0	8	43	6.05
Ant cingulate (BA 32)	0	20	42	5.91
R premotor (BA 6)	42	0	25	5.91
L inf frontal gyrus (BA 45)	−48	20	26	5.12
R inf/mid frontal gyr (BA 46/10)	43	40	12	5.09

TABLE 2—*Continued*

Comparison	Talairach coordinates x	y	z	Maximum Z
R inf frontal gyr (BA 44/9)	48	16	24	4.98
L inf frontal gyrus (BA 45)	−50	35	12	4.55
R caudate	12	0	14	3.93
L putamen	−17	8	7	3.65
Sup frontal gyr (BA 8)	0	35	46	3.08
R mid frontal gyr (BA 10)	41	55	5	3.08
White matter	−17	28	2	2.83
Case > Pseudoword Phonological				
Med frontal gyr (BA 10)	−2	55	−10	4.95
R mid/sup frontal gyr (BA 8/9)	18	40	43	3.85
L mid frontal gyr (BA 8/9)	−27	20	43	3.71
Ant cingulate (BA 32)	−3	40	−3	3.68
Med frontal gyr (BA 9)	1	50	21	3.65
Ant cingulate (BA 24/32)	−7	28	−6	3.39
Ant insula	33	8	−8	3.14
L mid/sup frontal gyr (BA 8/9)	−22	35	49	3.03
Semantic > Phonological (double subtraction)				
L inf frontal gyr (BA 45/47)	−44	20	−1	6.25
R inf/mid frontal gyr (BA 9/44)	49	16	30	5.74
R inf frontal gyr (BA 47)	47	28	−9	5.2
R inf frontal gyr (BA 47)	39	40	−10	5.15
R sup frontal gyr (BA 11)	15	55	−14	4.92
L inf frontal gyr (BA 44)	−47	8	21	4.86
R caudate	10	8	11	4.84
L sub frontal gyr (BA 11)	−24	50	−16	4.58
R mid frontal gyr (BA 10)	34	55	7	4.53
Med frontal gyr (BA 9/10)	−5	55	20	4.5
L inf frontal gyr (BA 45/47)	−35	35	−2	4.5
L sub frontal gyr (BA 11)	−22	60	−8	3.96
White matter	−12	0	23	3.62
L caudate	−12	16	12	3.59
Ant cingulate (BA 32)	−9	40	10	3.42
Corpus callosum	−8	28	12	2.52
Phonological > Semantic (double subtraction)				
L mid frontal gyr (BA 8/9)	−36	35	38	4.04
R mid frontal gyr (BA 8/9)	32	28	32	3.93
R premotor (BA 6)	55	0	11	3.17
Semantic > Pseudoword Phonological (double subtraction)				
L sup frontal gyr (BA 6/8)	−10	28	54	6.05
Med frontal gyr/ant cingulate (BA 32/8)	−7	35	34	5.49
L inf frontal gyr (BA 45)	−55	20	17	5.09
L sup frontal gyr (BA 6)	−6	16	54	4.78
L sup frontal gyr (BA 9)	−13	55	24	4.7
R sup frontal gyr (BA 8)	17	40	42	4.5
L inf frontal gyr (BA 10)	−43	50	0	4.41
L inf frontal gyr (BA 47)	−33	35	−9	4.21
L mid frontal gyr (BA 6)	−39	0	55	3.87
R inf frontal gyr (BA 47)	49	20	−7	3.73
L inf frontal gyr (BA 44)	−44	8	26	3.34
R inf frontal gyr (BA 47)	41	35	−8	3.17
L caudate	−12	16	13	3
R inf/mid frontal gyr (BA 6/44)	52	8	39	2.97
R caudate/putamen	3	16	4	2.91
R sup frontal gyr (BA 10)	15	60	24	2.72
R mid frontal gyr (BA 10)	32	55	5	2.66
Ant insula	−34	8	−6	2.4
Pseudoword Phonological > Semantic (double subtraction)				
R premotor (BA 6)	40	0	25	5.63
R mid frontal gyr (BA 8/9)	33	28	38	5.15
R mid frontal gyr (BA 8/9)	−37	35	36	4.5
R mid frontal gyr (BA 9/46)	39	40	22	4.16
R mid frontal gyr (BA 6)	29	0	61	4.02
R ant cingulate (BA 24)	8	8	31	3.93
R ant insula (BA 13)	37	16	9	3.65
Med/sup frontal gyr (BA 6)	3	0	70	3.22
L ant insula (BA 13)	−32	16	10	2.89
White matter	30	0	5	2.6

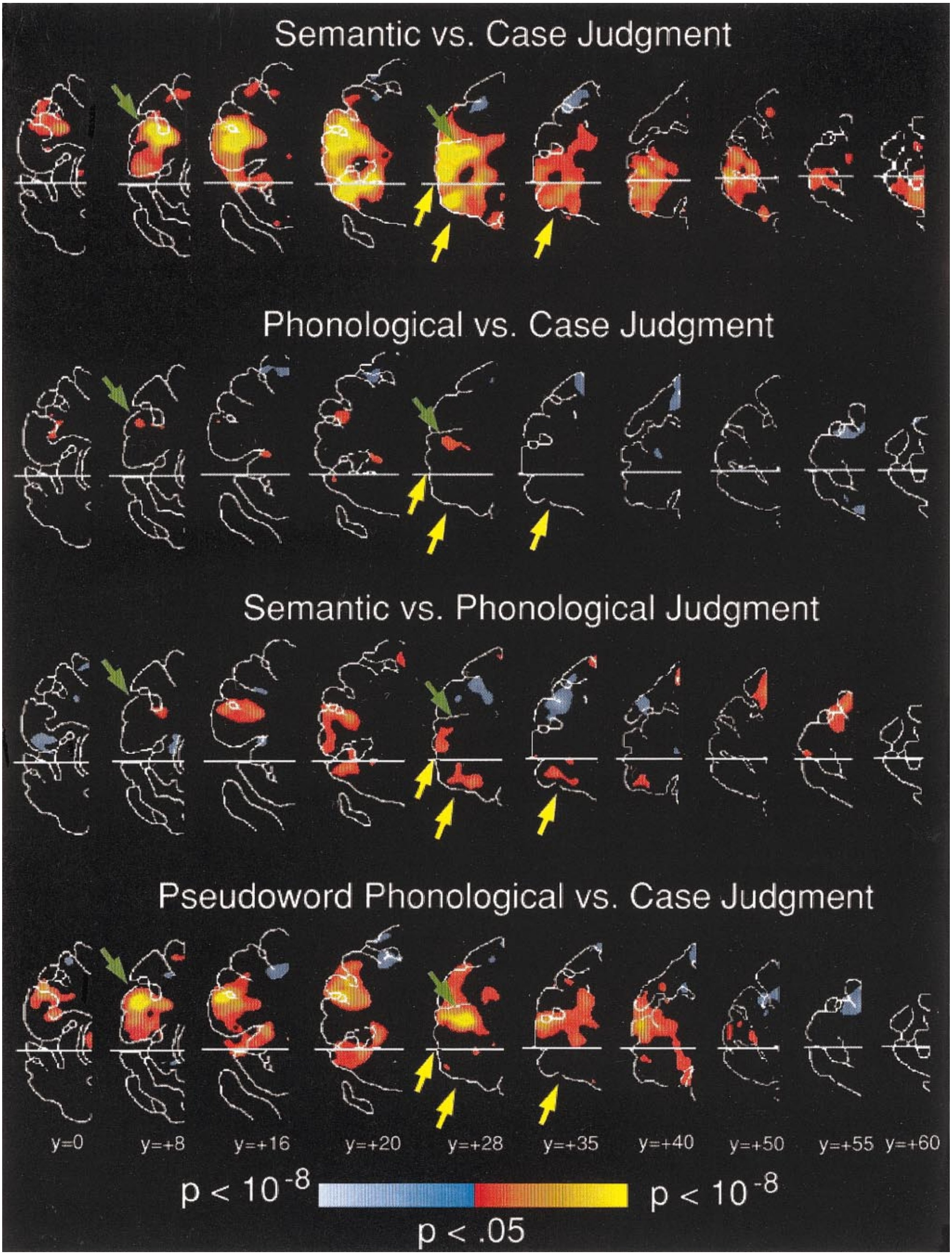

FIG. 2. Regions of significant activation in the left prefrontal cortex for each scan, averaged across subjects. Regions displayed in red-yellow were more active for semantic than perceptual decision (row 1), phonological than perceptual decision (row 2), semantic than phonological decision (row 3), and nonword phonological than perceptual decision (row 4). Semantic processing led to greater

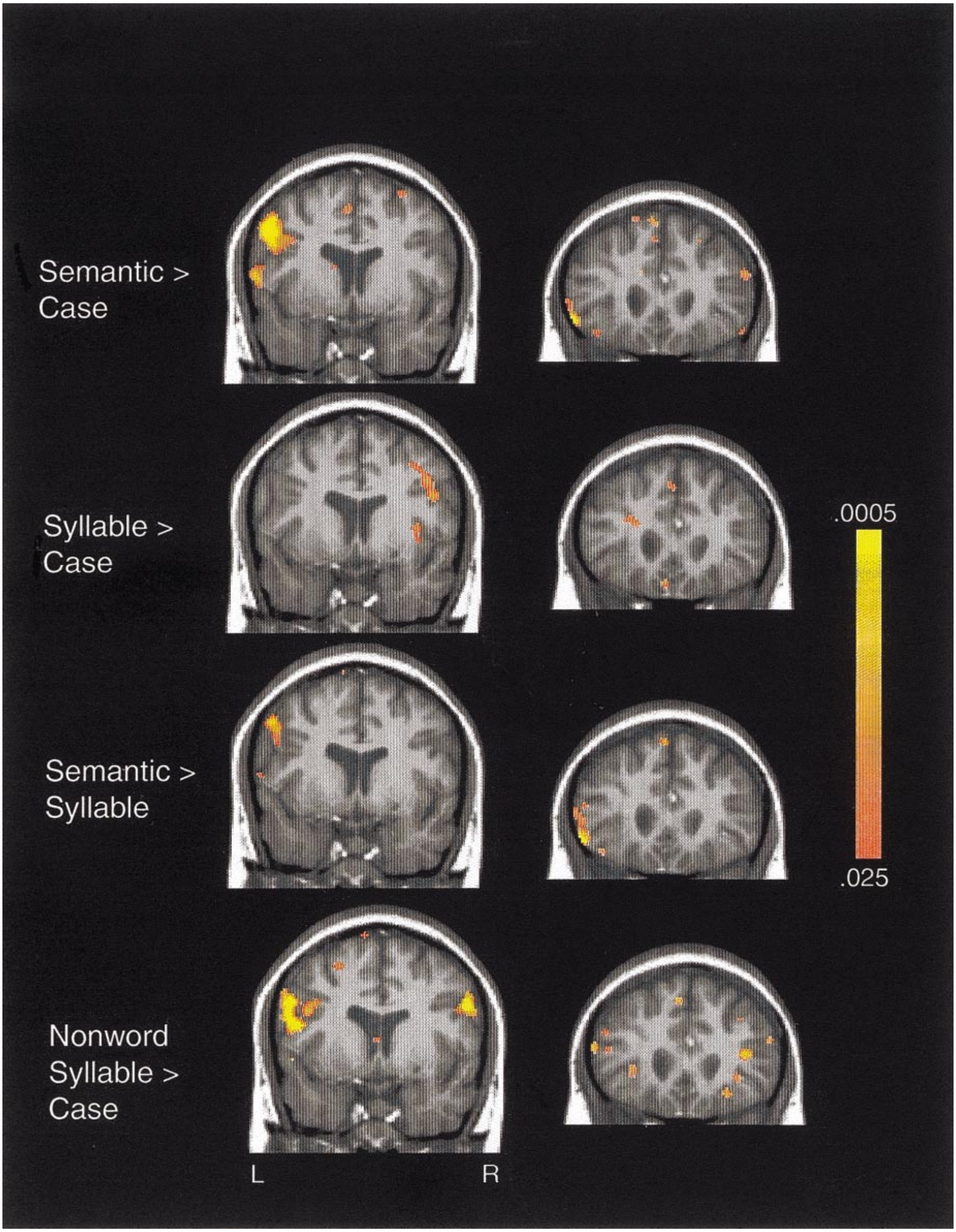

FIG. 3. Regions of significant activation in two selected slices for one individual subject in each scan. Images are presented in neurological convention (left side of image represents left hemisphere).

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activity in ventral regions of the left inferior frontal gyus (BA 45/47, yellow arrows, slices 5 and 6), whereas both semantic and phonological processing engaged a dorsal region of the inferior frontal gyrus near the inferior frontal sulcus (BA 44/45, green arrows, slices 2 and 5).

A report by Roskies *et al.* (1996) confirms the results of the present study. During PET scanning, four tasks were administered: easy and difficult semantic decision tasks, a synonym judgment task, and a rhyme judgment task. The LIPC was active during both the semantic decision and synonym tasks, and two regions in the LIPC were modulated by semantic task difficulty. Activation in the anterior/ventral region of LIPC (BA 47) was significant for the synonym task compared to fixation but not for the rhyme task compared to fixation, confirming the present results and previous findings by Shaywitz *et al.* (1995). Another study (Price *et al.*, 1997) that compared phonological processing (syllable counting) and semantic processing (living–nonliving decision) found greater activation in BA 47 for semantic processing and greater activation in BA 44 for phonological processing when a lenient threshold was used.

Process Specificity in Frontal Cortex: A Review

In order to determine whether the observed difference in LIPC activation between semantic and phonological processing was evident across previous studies, we conducted a literature search in an attempt to find all brain imaging studies employing task comparisons designed to isolate semantic, phonological, or lexical processing. We characterized each task comparison in terms of several different categories: semantic decision (e.g., living–nonliving decision), semantic production (e.g., verb generation), lexical retrieval (i.e., word/nonword decision, word-stem completion), phonological processing (e.g., phoneme monitoring or nonword processing), overt speech (e.g., word repetition or naming), and silent viewing of words. Activations were identified that fell roughly in the left frontal cortex (Talairach coordinates $X < -15$, $Y > 0$, all Z), and these activations plotted in saggital projection on a standard brain are presented in Fig. 4; a complete list of the studies included in this figure is provided in Appendix B.

This review demonstrates a great deal of overlap between the posterior regions active during semantic, phonological, and lexical processing (denoted by red circle in Fig. 4). However, a ventral and anterior region of the inferior frontal cortex (denoted by green circle in Fig. 4) was preferentially active during the performance of tasks requiring overt semantic processing. This region corresponds approximately to Brodmann's area 47/45 and is located in the ventral extent of the inferior frontal gyrus, in the region where our study found activation for semantic relative to phonological processing. Semantic decision and generation tasks both resulted in activation of this region across studies, whereas there was little activity in this region during the performance of phonological and lexical tasks. There was, however, a significant amount of overlap in more posterior sections of the frontal cortex for semantic processing with those areas active for phonological and lexical processing, suggesting that semantic processing automatically engages those processes as well. Conversely, some activation on lexical and phonological tasks may reflect automatic semantic processing engaged during performance of those tasks, although this does not seem to be a common finding.

The LIPC in Semantic Processing

Given the current evidence that the LIPC is directly involved in semantic processing, it is important to ask what specific role it might play in this processing. Neuropsychological data demonstrate that patients with lesions to the LIPC, while being impaired on some tests of semantic processing (Swick and Knight, 1996), do not exhibit severe disturbances of semantic knowledge such as those seen following temporal lobe lesions. This suggests that the LIPC likely does not subserve the primary storage of semantic knowledge representations; rather, these representations are likely supported by temporal cortex (Damasio *et al.*, 1996; Price *et al.*, 1997). The LIPC may serve instead as a semantic working memory system or semantic executive system (e.g., Gabrieli *et al.*, 1996; Kapur *et al.*, 1994b; Wagner *et al.*, 1997a). The role of such a system would be to access, maintain, and manipulate semantic representations which are represented elsewhere in the cortex. This function is a semantic analogue to the spatial and object working memory functions that have been suggested for the prefrontal cortex on the basis of neurophysiology (Goldman-Rakic, 1987) and neuroimaging (Smith and Jonides, 1997).

The semantic executive system may be engaged by three related forms of processing: retrieval, selection, and evaluation. Retrieval involves the arrangement of search cues and the querying of semantic storage for representations matching those cues. Selection involves the resolution of competition between retrieved representations and selection of the task-relevant attributes of these representations. Evaluation involves the synthesis of the information chosen through the retrieval and selection processes and use of this information to determine the proper response. Semantic tasks requiring a greater amount of semantic information require a greater amount of retrieval, whereas semantic tasks with many equally dominant competing responses, or those tasks involving decisions based upon specific attributes of the stimulus, require a greater amount of selection. The difficulty of evaluation processes should vary both with the amount of retrieved information and with the difficulty of the task (which may be related to selection).

It may be difficult to differentiate these processes, because increased retrieval necessarily results in increased selection and may also increase the load on the evaluation process. However, an fMRI study by Thompson-Schill *et al.* (1997) has suggested that activation of the LIPC is related to selection processes, specifically those processes related to the selection of task-relevant stimulus attributes. This study examined performance on semantic decision tasks in which certain features were selected and others had to be ignored (the High-Selection condition) and compared this to tasks in which all of the semantic features of the stimulus were relevant to task performance (the Low-Selection condition).

Comparison of these tasks demonstrated a region of the LIPC that was specifically related to selection demands when the difficulty of the high-selection and low-selection tasks (in terms of response time) was equated. This study is noteworthy in its attempt to further specify the processes that result in LIPC activation. However, the region found to be related to selection in the study by Thompson-Schill *et al.* (1997) fell predominantly in the posterior and dorsal portion of the inferior frontal gyrus (BA 44/45), which the review above suggested may be related to phonological or lexical processing. In one comparison there was a selection-related activation nearer to the anterior/ventral inferior frontal region; this finding suggests that the selection hypothesis remains viable as an explanation of anterior/ventral LIPC activation, and further work must be done to ascertain whether the functional characteristics of this frontal region are consistent with this hypothesis. However, it is unclear whether tasks that require increased selection would also require increased semantic retrieval and/or evaluation processes. In addition, Vandenberghe *et al.* (1996) found activation of the LIPC in a task comparison that varied semantic retrieval demands but kept selection demands constant, suggesting that activation of this region may be directly related to retrieval rather than selection.

Right Hemisphere Activations

Although our study focused on the particular role of the left inferior prefrontal cortex in semantic and phonological processing, consistent activation of the right inferior prefrontal region was also observed for both semantic and phonological processing compared to case judgments. A majority of participants exhibited bilateral activation for the semantic task compared to case judgment. Previous studies have found bilateral frontal activation for both semantic (e.g., Wagner *et al.*, 1998) and phonological (e.g., Pugh *et al.*, 1996) processing.

The right and left hemispheres may play different roles in the processing of phonological information. A study by Pugh *et al.* (1997) examined the relationship between lateralization of phonological processing using fMRI and regularity effects on lexical decision in the same subjects. Regularity effects refer to greater difficulty on a lexical decision task for irregular words, which do not follow orthographic-to-phonologic conversion rules (e.g. pint), compared to regular words, which follow these rules (e.g., lint). These effects are thought to reflect the operation of phonological recoding, in that the results of orthographic-to-phonologic conversion rules and the results of direct lexical access are in conflict for irregular items, resulting in extended response times. Pugh *et al.* (1997) found that the amount of right hemisphere activation during phonological processing was related to the size of regularity effects on a lexical decision task performed independently outside the scanner: Significant regularity effects were only found in subjects who exhibited bilateral inferior frontal activation. Effects of word length, which are also thought to reflect the operation of (serial) conversion rules, were also greater in subjects with greater right hemisphere activation.

These data suggest that the two hemispheres may process information differently during reading. Pugh *et al.* (1997) suggest that the two hemispheres may differ in the "grain size" of their processing, with the right hemisphere processing relatively small phonological units (such as individual phonemes) and the left hemisphere processing relatively large units (such as syllable onsets and rimes). The results of the present study suggest that the grain size of phonological processing in the right hemisphere may be larger than a single phoneme, since significant right hemisphere activation was found during performance of a task that required attention to larger phonological features. However, further experiments that directly manipulate critical word features (such as word length and regularity) are necessary to fully address this question.

Frontal Regions and Phonological Processing

The present findings extend previous results which had suggested a specific role for LIPC in phonological processing (e.g., Demonet *et al.*, 1992; Zatorre *et al.*, 1992) by suggesting that separate areas in the LIPC may be functionally specialized for semantic and phonological processing (cf. Fiez, 1997). The posterior and dorsal region of the left IFG, corresponding to BA 44/45, may be specialized for phonological processing whereas the anterior region of the IFG (corresponding to BA 47/45) may be specialized for semantic processing. The present results also suggest that the syllable-counting task engages regions of the left frontal cortex that are roughly similar to those engaged by other phonological tasks, with greater activation during processing of pseudowords than real words.

It is unclear why the region of LIPC activation was so restricted during syllable counting with real words when compared to case judgments in the present study; much less activation was seen for this task comparison than for the comparison of semantic and case judgments. Response times for the phonological task did not differ from the semantic decision task, suggesting that the differences in activation did not arise from differences in gross task difficulty. It is likely that posterior regions outside the current scanning range were active during syllable counting with real words (Price *et al.*,

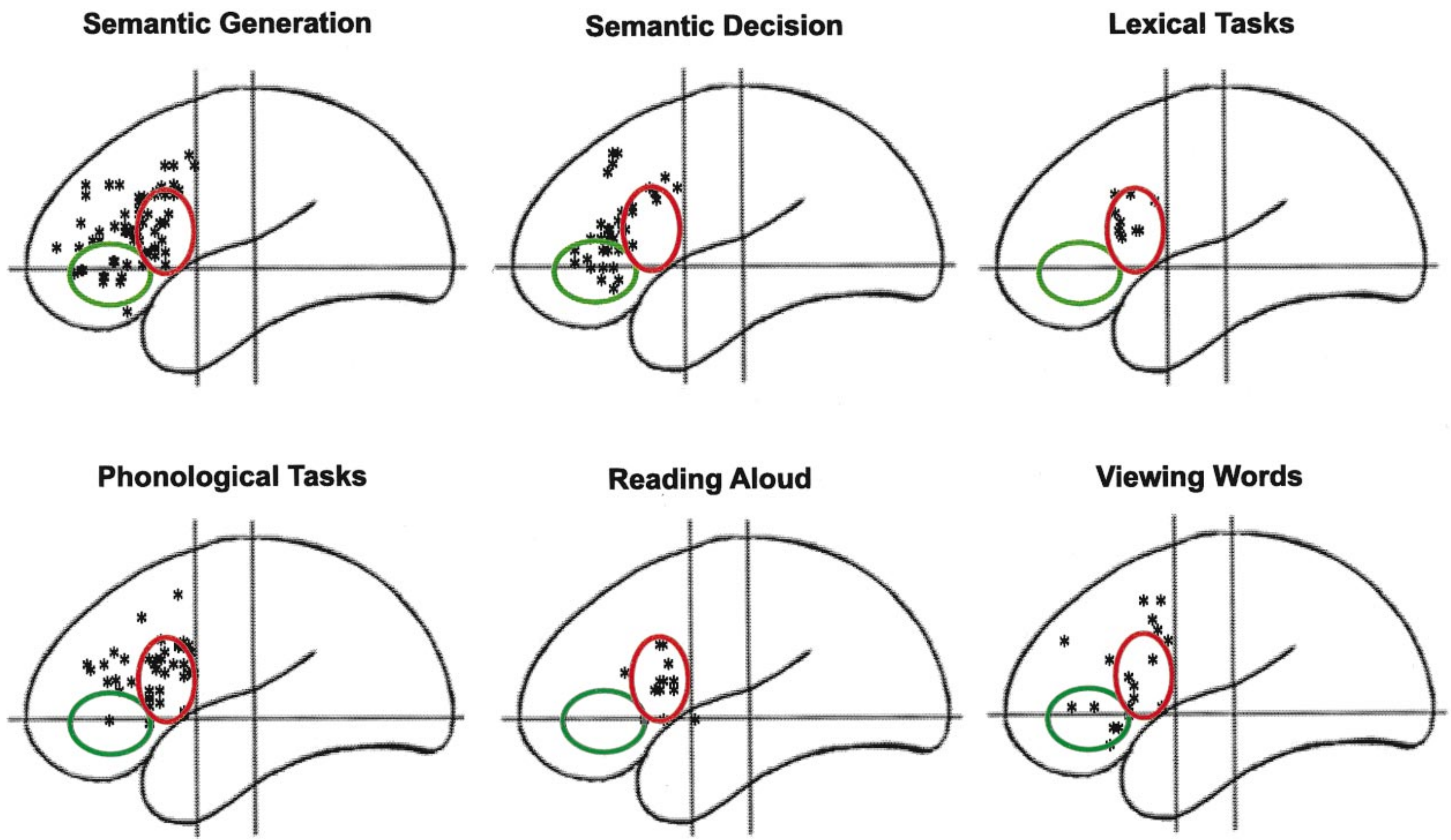

FIG. 4. Projection of left frontal activations from a number of studies of semantic, lexical, and phonological processing onto a standard saggital section (Talairach and Tournoux, 1988). Red circle denotes region common for semantic, phonological, and lexical processing, whereas green circle denotes region responsive specifically to semantic processing.

1997), and these regions may have primarily subserved task performance, with the frontal cortex playing a lesser role. The syllable-counting task using pseudowords also resulted in much greater frontal activation than the same task with real words. Syllable counting with real words may not have strongly engaged phonological recoding processes, which are necessary for the processing of pseudowords but not for real words. Syllable-counting judgments on real words may have instead been based upon orthographic knowledge; however, this is difficult to confirm on the basis of the current data.

Differences in activation were also observed between the syllable-counting tasks using words and pseudowords when each was separately compared to semantic processing using double subtraction. The largest difference between semantic and real-word syllable counting tasks was in the LIPC, whereas the strongest difference between semantic and pseudoword syllable-counting tasks was in the left superior frontal gyrus, with a weaker difference in the LIPC. It is unlikely that this difference in activations reflects qualitatively different underlying neural networks engaged in performance for real words and pseudowords during syllable counting. Rather, it is likely that the pseudoword phonological task engaged phonological processes more strongly than the real-word task. Because these phonological processes were also engaged by the semantic task, this attenuated differences in the LIPC when compared to the semantic task. The greater difference in the superior frontal cortex for the pseudoword task than for the real-word task occurred due to deactivation of the superior frontal region during pseudoword processing compared to case judgments, which may have been related to the attentional demands of the task. This suggests that common frontal regions were engaged during phonological processing on words and pseudowords, with greater engagement during the pseudoword task. Additional examination of the differences between word and pseudoword processing should shed further light upon the functional anatomy of phonological processing.

APPENDIX A: Stimulus Lists

List 1

Abstract—2 Syllable	Abstract—Not 2 Syllable	Concrete—2 Syllable	Concrete—Not 2 Syllable
access	interim	apple	ACROBAT
advice	INTERVAL	ARMY	ARM
amour	intimate	BALLOON	BAR
BURDEN	IRONY	bandit	CAR
CHAOS	joy	BARLEY	cheek
CONCEPT	LAW	baron	claw
CRISIS	legacy	BUCKET	COAST
DEMAND	LENIENCY	cabin	DROP
DEMISE	LIBERTY	circle	emperor
HEAVEN	LIFE	coffee	flood
honor	love	collar	gallery
IDEAL	LOYALTY	DIAMOND	GEESE
issue	MASTERY	finger	GIRL
LOGIC	melody	footwear	JAIL
MADNESS	MEMORY	garment	knife
MERCY	mind	glacier	ladybug
METHOD	miracle	GOBLET	lake
mischief	misery	GODDESS	LIBRARY
MOVEMENT	MISTRIAL	lemur	lip
namesake	MONTH	leopard	LUMP
PHANTOM	mood	market	MONK
REGRET	OBSTACLE	MONKEY	MUSICIAN
remorse	occasion	MOTEL	nursery
repose	opinion	NECTAR	opium
REQUEST	origin	nephew	PLATE
resolve	PAIN	noodle	rake
RESPITE	PAST	oyster	scar
RETURN	pep	pencil	SOIL
safety	perjury	PORTAL	SPATULA
snorkle	phobia	portrait	spoon
sorrow	PHONETICS	sandals	STREET
STANDARD	pledge	sergeant	TANK
SUBSTANCE	poetry	SHOTGUN	TEA
syntax	POLICY	SPIDER	thorn
torment	position	steamer	TOMB
VISION	POVERTY	trolley	TRACT

APPENDIX A—*Continued*

List 2

Abstract—2 Syllable	Abstract—Not 2 Syllable	Concrete—2 Syllable	Concrete—Not 2 Syllable
action	direction	BLIZZARD	admiral
amount	disaster	bottle	AVENUE
array	DISCRETION	BOULDER	banana
belief	DIVISION	COLLEGE	boy
BOREDOM	dream	CORNER	braid
censure	DRUGGERY	DEVIL	brick
CLIMAX	elegance	EXAM	cash
conquest	embargo	FABRIC	CHILD
CONTEXT	emotion	faucet	clock
debate	END	flower	DISH
deceit	EPISODE	fowl	drums
DIVORCE	equation	gazelle	FLASK
EFFORT	equity	HARDWOOD	foam
FOLLY	EXERTION	hotel	FORM
FREEDOM	FALLACY	infant	frog
FULLNESS	FANTASY	kidney	GRASS
harness	fate	LINDEN	ground
kindness	fear	LION	HOSPITAL
LIMIT	FRAUD	liver	KNIGHT
menace	fright	lobster	KOALA
MINUTE	fun	MEDAL	lawn
MOMENT	gist	monarch	MAGAZINE
OUTCOME	GORE	MONEY	meat
percept	grade	mother	NAIL
pleasure	gravity	mushroom	PLANT
practice	GREED	NOVEL	pool
PRESSURE	GRIEF	NUTMEG	POTATO
PRESTIGE	health	PALACE	SLUSH
prospect	heroism	PASTA	SNAKE
RESULT	HISTORY	pepper	squash
SCIENCE	holiness	poet	stick
SILENCE	hope	poster	stone
support	ILLUSION	RHINO	TEST
trouble	INCIDENT	SKILLET	TOMATO
VIGOR	INFERENCE	teacher	TREE
welfare	INTELLECT	TICKET	work

List 3

Abstract—2 Syllable	Abstract—Not 2 Syllable	Concrete—2 Syllable	Concrete—Not 2 Syllable
BEAUTY	abasement	BAGPIPE	ABDOMEN
blessing	ADVANTAGE	BARREL	APPLIANCE
cleanness	AFFECTION	baseline	BARNACLE
CONFLICT	AFTERLIFE	bullet	BOARD
COURAGE	age	camel	BOLT
custom	AGONY	clothing	brain
defeat	AMBITION	CRADLE	CAMP
defense	AMNESIA	DECADE	cell
DISEASE	ANARCHY	demon	CHIN
DUTY	APTITUDE	dragon	COIN
ESSENCE	AROUSAL	earring	cow
ETHICS	attention	event	CROWN
EXPENSE	attitude	FIORD	cucumber
extent	betrayal	FOIBLE	face
FEELING	BLAME	garden	fish
figment	blasphemy	gibbon	FLAMINGO
GAIETY	BRAVERY	grammar	FLEA
gender	brevity	insect	FORK
HATRED	CASUALTY	journal	GEM
MARRIAGE	CENTURY	KETTLE	ghost
meaning	chance	lemon	head
merit	choice	MAMMAL	HORSE
MORAL	CLARITY	meadow	HOUSE

APPENDIX A—*Continued*

List 3

Abstract—2 Syllable	Abstract—Not 2 Syllable	Concrete—2 Syllable	Concrete—Not 2 Syllable
OUTCRY	clemency	PAPER	MASK
present	comedy	PICTURE	MILK
rating	CONFIDENCE	PLAZA	morgue
response	CREATION	prison	MOSS
retreat	cruelty	pupil	MULE
sadness	day	refuge	OATS
session	death	reptile	peach
STRUGGLE	DEDUCTION	sandwich	pole
theory	DEITY	STUDENT	SAUCE
UPKEEP	denial	TABLE	SCREEN
valence	density	TIGER	skull
VIRTUE	destiny	tower	steak
worry	DIFFUSION	tractor	steam

Pseudowords

2 Syllable		Not 2 Syllable	
accets	MERFER	abalyst	LABOFER
ALARV	MIBOR	ALVOHOL	LAUTH
ANCZOR	midut	AREWA	marifa
ballov	mirgor	ARPERY	milsion
baxten	motibe	barvier	NUPLEUS
boptle	OWBER	bexefit	PHOPE
CAGIN	panace	blabe	pigch
CAGTLE	parase	branf	PODCH
canver	PEPPEM	brunh	POEMRY
canyor	PILKET	CALIGER	pounf
censut	PLOTO	CHEWK	poyse
CHAVEL	REHTAL	chorp	PRESIUM
CHAVM	renime	CLITHE	quent
CIRPLE	RULIRG	CLORE	REGIVAL
coogie	SAREW	coaging	ROUNG
corfee	SARING	creat	saviot
CUSTOR	SERMOT	CRENT	SCHAP
DEVIK	shuad	crogs	SHERF
deway	sinnel	darce	SHILE
ENFINE	sinxer	dengity	SHRITE
FABOR	sixpy	DREPS	SMOLE
facen	suine	edigion	SNOVE
fanric	SUMSIT	episone	SPART
figer	TACKIC	ESPEROR	speam
FORELT	tepple	fastasy	speev
giaft	TICKEP	FILHT	stilk
heaben	TONTUE	finayce	streal
HOWOR	TREAPY	frane	STROTE
HUMOY	troply	galtery	TRAILEP
HUPTER	truca	GRAIB	twiss
imlact	tupnel	higoway	vession
LAYTAN	VECSOR	IMPORA	VETESAN
leston	VIRTIM	inquivy	wasce
LORBY	virtin	insigat	WHEEG
MASTEP	VONER	irogy	WHOKE
mealow	voyame	juive	YOUSH

APPENDIX B: Studies Included in Fig. 4

	Task comparison	*X*	*Y*	*Z*
	Semantic Generation			
Buckner *et al.*, 1995b	Verb generation > reading (females)	−49	29	−2
Buckner *et al.*, 1995b	Verb generation > reading (females)	−43	21	20
Buckner *et al.*, 1995b	Verb generation > reading (males)	−43	23	16
Buckner *et al.*, 1995b	Verb generation > reading (males)	−43	35	0
Buckner *et al.*, 1995b	Verb generation > reading (females)	−39	25	12
Buckner *et al.*, 1995b	Verb generation > reading (males)	−39	43	8
Buckner *et al.*, 1995b	Verb generation > reading (females)	−33	49	6
Buckner *et al.*, 1995b	Verb generation > reading (males)	−31	23	−2
Buckner *et al.*, 1995b	Verb generation > reading (males)	−23	47	−4
Klein *et al.*, 1995	Synonym generation > word repetition (L1)	−52	24	27
Klein *et al.*, 1995	Translation > word repetition (L1)	−48	17	29
Klein *et al.*, 1995	Synonym generation > word repetition (L2)	−48	22	26
Klein *et al.*, 1995	Synonym generation > word repetition (L1)	−46	27	12
Klein *et al.*, 1995	Synonym generation > word repetition (L2)	−44	34	15
Klein *et al.*, 1995	Translation > word repetition (L1)	−43	29	12
Klein *et al.*, 1995	Translation > word repetition (L2)	−42	24	22
Klein *et al.*, 1995	Synonym generation > word repetition (L1)	−42	39	−6
Klein *et al.*, 1995	Translation > word repetition (L1)	−42	39	−8
Klein *et al.*, 1995	Translation > word repetition (L2)	−34	15	31
Klein *et al.*, 1995	Synonym generation > word repetition (L2)	−32	58	6
Klein *et al.*, 1995	Synonym generation > word repetition (L2)	−29	48	−3
Klein *et al.*, 1995	Translation > word repetition (L2)	−28	51	−5
Klein *et al.*, 1995	Translation > word repetition (L1)	−21	29	−21
Martin *et al.*, 1995	Action word generation > object naming	−43	18	6
Martin *et al.*, 1995	Color word generation > object naming	−42	18	28
Martin *et al.*, 1995	Action word generation > object naming	−42	12	20
Martin *et al.*, 1995	Color word generation > object naming	−38	30	20
Martin *et al.*, 1995	Action word generation > object naming	−36	4	44
Martin *et al.*, 1995	Action word generation > object naming	−34	48	16
Martin *et al.*, 1995	Action word generation > object naming	−32	34	0
Martin *et al.*, 1995	Color word generation > object naming	−24	32	−8
Petersen *et al.*, 1989	Verb generation > repeat word, visual word presentation	−42	24	20
Petersen *et al.*, 1989	Verb generation > repeat word, visual word presentation	−38	24	8
Petersen *et al.*, 1989	Verb generation > repeat word, auditory word presentation	−33	31	−6
Petersen *et al.*, 1989	Verb generation > repeat word, visual word presentation	−28	38	−6
Raichle *et al.*, 1994	Verb generation > repeat noun	−43	28	13
Shaywitz *et al.*, 1995	Generate category exemplar > generate rhyme (silent)	−35	15	8
Shaywitz *et al.*, 1995	Generate category exemplar > generate rhyme (silent)	−22	40	8
Thompson-Schill *et al.*, 1997	Verb generation, high vs low selection	−49	8	30
Warburton *et al.*, 1996	Verb generation > noun generation	−52	16	16
Warburton *et al.*, 1996	Verb generation > rest (expt 3)	−52	18	12
Warburton *et al.*, 1996	Verb generation > rest	−48	14	16
Warburton *et al.*, 1996	Verb generation > rest (expt 2)	−46	24	24
Warburton *et al.*, 1996	Verb generation > listening	−46	24	24
Warburton *et al.*, 1996	Verb generation > rest (expt 3)	−44	14	28
Warburton *et al.*, 1996	Verb generation > silently repeat pseudoword	−44	18	5
Warburton *et al.*, 1996	Verb generation > rest (expt 3)	−44	22	4
Warburton *et al.*, 1996	Verb generation > rest	−42	30	14
Warburton *et al.*, 1996	Verb generation > rest	−42	22	4
Warburton *et al.*, 1996	Noun generation > rest	−42	24	24
Warburton *et al.*, 1996	Verb generation > rest	−40	10	28
Warburton *et al.*, 1996	Verb generation > verb/noun comparison	−40	20	4
Warburton *et al.*, 1996	Verb generation > rest	−40	18	2
Warburton *et al.*, 1996	Verb generation > listening	−38	10	32
Warburton *et al.*, 1996	Verb generation > silently repeat pseudoword	−38	14	−2
Warburton *et al.*, 1996	Noun generation > rest	−38	14	4
Warburton *et al.*, 1996	Verb generation > rest	−36	2	40
Warburton *et al.*, 1996	Verb generation > rest (expt 2)	−36	36	32
Warburton *et al.*, 1996	Verb generation > verb/noun comparison	−36	40	12
Warburton *et al.*, 1996	Verb generation > rest (expt 2)	−34	24	8
Warburton *et al.*, 1996	Verb generation > silently repeat pseudoword	−34	30	12
Warburton *et al.*, 1996	Verb generation > listening	−32	26	8
Warburton *et al.*, 1996	Verb generation > verb/noun comparison	−32	10	40
Warburton *et al.*, 1996	Verb generation > rest (expt 2)	−30	46	28

APPENDIX B—*Continued*

	Task comparison	*X*	*Y*	*Z*
Warburton *et al.*, 1996	Noun generation > rest	−28	32	32
Warburton *et al.*, 1996	Verb generation > listening	−26	46	32
Wise *et al.*, 1991	Verb generation > rest	−40	14	16
Wise *et al.*, 1991	Verb generation > rest	−36	14	40
	Lexical Tasks			
Buckner *et al.*, 1995b	Stem completion > fixation (females)	−37	19	10
Buckner *et al.*, 1995b	Stem completion > fixation (males)	−37	21	12
Buckner *et al.*, 1995a	Stem completion > fixation	−37	20	11
Price *et al.*, 1994	Lexical decision > reading aloud	−52	20	16
Price *et al.*, 1994	Lexical decision > false font feature detection	−50	22	20
Price *et al.*, 1994	Lexical decision > reading aloud	−36	12	12
Price *et al.*, 1994	Lexical decision > false font feature detection	−34	14	12
Price *et al.*, 1994	Lexical decision > false font feature detection	−32	16	28
Price *et al.*, 1994	Lexical decision > reading aloud	−30	22	28
Rumsey *et al.*, 1997b	Orthographic lexical decision > fixation	−44	6	24
Rumsey *et al.*, 1997a	Orthographic lexical decision > fixation	−44	6	24
	Phonological Tasks			
Awh *et al.*, 1996	2-back > control	−42	17	22
Braver *et al.*, 1997	Monotonic increase with n-back load	−47	6	15
Braver *et al.*, 1997	Monotonic increase with n-back load	−42	23	39
Braver *et al.*, 1997	Monotonic increase with n-back load	−40	6	26
Braver *et al.*, 1997	Monotonic increase with n-back load	−38	30	22
Braver *et al.*, 1997	Monotonic increase with n-back load	−32	20	8
Cohen *et al.*, 1994	1-back > letter detection	−36	33	13
Cohen *et al.*, 1994	1-back > letter detection	−29	38	20
Demonet *et al.*, 1992	Phoneme monitor > pitch monitor	−50	18	20
Demonet *et al.*, 1994	Sequential ambig. phoneme match > tone detection	−40	4	28
Fiez *et al.*, 1995	Target detection > fixation	−40	16	8
Fiez *et al.*, 1995	Temporally changing > temporally stable	−37	16	8
Frith *et al.*, 1995	Color monitoring, novel > same pseudoword	−44	8	28
Herbster *et al.*, 1997	Speak psueodword > speak hiya repeatedly	−48	6	0
Herbster *et al.*, 1997	Speak psueodword > speak regular word	−44	4	16
Jonides *et al.*, 1997	3-back > control	−57	14	25
Jonides *et al.*, 1997	3-back > control	−44	8	27
Jonides *et al.*, 1997	3-back > control	−39	44	18
Klein *et al.*, 1995	Rhyme gen > word repetition (L1)	−44	15	30
Klein *et al.*, 1995	Rhyme gen > word repetition (L1)	−44	27	12
Klein *et al.*, 1995	Rhyme gen > word repetition (L1)	−40	36	−3
Paulesu *et al.*, 1993	(Rhyme + consonant STM) > shape judgment	−46	2	16
Price *et al.*, 1996b	Pseudowords > words, silent viewing	−42	34	24
Rumsey *et al.*, 1997b	Phonological ldt > fixation	−42	6	20
Rumsey *et al.*, 1997a	Phonological LDT > fixation	−42	6	20
Rumsey *et al.*, 1997a	Phonological LDT > fixation	−40	10	20
Rumsey *et al.*, 1997a	Phon. LDT > orthographic	−36	32	8
Rumsey *et al.*, 1997a	Phon. LDT > orthographic	−32	16	4
Sergent *et al.*, 1992	Letter-sound > object processing	−58	20	6
Sergent *et al.*, 1992	Letter-sound > spatial processing	−54	20	5
Sergent *et al.*, 1992	Letter-sound > spatial processing	−52	17	18
Sergent *et al.*, 1992	Letter-sound > object processing	−48	15	21
Sergent *et al.*, 1992	Letter-sound > spatial processing	−44	37	12
Sergent *et al.*, 1992	Letter-sound > object processing	−36	44	18
Sergent *et al.*, 1992	Letter-sound > object processing	−25	8	48
Shaywitz *et al.*, 1995	rhyme vs case	−50	18	20
Warburton *et al.*, 1996	Silently repeat pseudoword > rest	−48	14	16
Warburton *et al.*, 1996	Silently repeat pseudoword > rest	−42	6	−2
Warburton *et al.*, 1996	Silently repeat pseudoword > rest	−38	20	2
Zatorre *et al.*, 1992	Phonetic discrimination > passive speech listenening	−48	3	24
Zatorre *et al.*, 1992	Phonetic discrimination > passive speech listening	−34	45	20
Zatorre *et al.*, 1996	Phonetic discrimination > pitch disc.	−56	6	29
Zatorre *et al.*, 1996	Phonetic discrimination (half words) > listening to noise	−56	20	−5
Zatorre *et al.*, 1996	Phonetic discrimination (half words) > passive word listening	−44	8	27
Zatorre *et al.*, 1996	Phonetic discrimination (half words) > listening to noise	−43	5	27
Zatorre *et al.*, 1996	Phonetic discrimination (half words) > passive word listening	−35	20	21

APPENDIX B—*Continued*

	Task comparison	*X*	*Y*	*Z*
	Semantic Decision			
Binder *et al.*, 1996	Semantic decision > pitch decision	−46	15	30
Binder *et al.*, 1996	Semantic decision > pitch decision	−45	32	3
Demb *et al.*, 1995	Abstract/concrete decision > case judgment	−48	35	15
Demonet *et al.*, 1992	Semantic decision > pseudoword phonological decision	−20	30	44
Demonet *et al.*, 1992	Semantic decision > pseudoword phonological decision	−20	30	40
Demonet *et al.*, 1992	Semantic decision > pseudoword phonological decision	−18	32	36
Demonet *et al.*, 1992	Semantic decision > tone judgment	−16	28	44
Demonet *et al.*, 1992	Semantic decision > tone judgment	−16	30	40
Desmond *et al.*, 1995	Abstract/concrete decision > case, left-lateralized Wada patients	−45	35	9
Gabrieli *et al.*, 1996	Abstract/concrete decision > case judgment	−49	35	9
Jennings *et al.*, 1997	PLS analysis, loads on semantic processing variable	−34	28	4
Jennings *et al.*, 1997	PLS analysis, loads on semantic processing variable	−34	40	0
Jennings *et al.*, 1997	PLS analysis, loads on semantic processing variable	−24	28	−8
Kapur *et al.*, 1994b	Living/nonliving > letter detection	−38	22	20
Kapur *et al.*, 1994b	Living/nonliving > letter detection	−38	26	12
Kapur *et al.*, 1994b	Living/nonliving > letter detection	−32	34	4
Kapur *et al.*, 1994b	Living/nonliving > letter detection	−30	30	−4
Kapur *et al.*, 1994b	Living/nonliving > letter detection	−38	28	16
Kapur *et al.*, 1994b	Living/nonliving > letter detection	−28	34	−4
Pugh *et al.*, 1996	Category match > line judgment	−50	35	−8
Thompson-Schill *et al.*, 1997	Word similarity, high vs low selection	−45	4	30
Thompson-Schill *et al.*, 1997	Word similarity, high vs low selection	−41	30	8
Vandenberghe *et al.*, 1996	Word & Picture semantic match > size match	−42	22	20
Vandenberghe *et al.*, 1996	Word > picture, semantic match	−34	26	20
Vandenberghe *et al.*, 1996	Word & Picture semantic match > size match	−16	30	−12
Wagner *et al.*, 1997	First > repeated, word, living/nonliving task	−49	45	−2
Wagner *et al.*, 1997	First > repeated, picture, living/nonliving task	−49	45	4
Wagner *et al.*, 1997	First > repeated, word, living/nonliving task	−47	39	−4
Wagner *et al.*, 1997	First > repeated, picture, living/nonliving task	−47	39	8
Wagner *et al.*, 1997	First > repeated, word, living/nonliving task	−39	32	12
Wagner *et al.*, 1997	First > repeated, picture, living/nonliving task	−39	32	9
Wagner *et al.*, 1998	Abstract/Concrete decision > Fixation, single trial	−50	9	34
Wagner *et al.*, 1998	Abstract/Concrete decision > Fixation, single trial	−50	25	12
Wagner *et al.*, 1998	Abstract/Concrete decision > Uppercase/Lowercase	−43	9	34
Wagner *et al.*, 1998	Abstract/Concrete decision > Uppercase/Lowercase	−43	13	28
Wagner *et al.*, 1998	Abstract/Concrete decision > Uppercase/Lowercase	−40	22	21
Wagner *et al.*, 1998	Abstract/Concrete decision > Uppercase/Lowercase	−40	31	12
Wagner *et al.*, 1998	Abstract/Concrete decision > Fixation, single trial	−31	22	6
Wagner *et al.*, 1998	Abstract/Concrete decision > Uppercase/Lowercase	−28	22	6
Warburton *et al.*, 1996	Verb/noun comparison > rest	−40	12	24
	Reading Aloud			
Herbster *et al.*, 1997	Speak word > speak hiya repeatedly	−46	0	−4
Herbster *et al.*, 1997	Speak irregular word > speak hiya repeatedly	−40	12	−4
Martin *et al.*, 1996	Tool naming > animal naming	−52	10	20
Martin *et al.*, 1996	Tool naming > view nonsense objects	−30	8	8
Martin *et al.*, 1996	Animal naming > view nonsense objects	−28	14	8
Martin *et al.*, 1996	Object naming > view nonsense objects	−28	16	8
Martin *et al.*, 1996	Animal naming > tool naming	−26	28	16
Price *et al.*, 1994	read aloud > false font feature detection	−32	14	28
Price *et al.*, 1996a	Repeating > listening to words	−58	8	12
Price *et al.*, 1996a	Repeating words > saying crime to reversed words	−48	14	12
Price *et al.*, 1996a	Repeating words > saying crime to reversed words	−42	12	12
Price *et al.*, 1996a	Repeating words > saying crime to reversed words	−40	12	28
Rumsey *et al.*, 1997a	word > pseudoword, pronunciation	−18	20	−4
	Viewing Words			
Bookheimer *et al.*, 1995	View words > view nonsense objects	−40	26	−8
Bookheimer *et al.*, 1995	View words > view nonsense objects	−36	18	4
Bookheimer *et al.*, 1995	View words > view nonsense objects	−32	14	44
Bookheimer *et al.*, 1995	name words > view nonsense objects	−32	18	8
Menard *et al.*, 1996	View words > view X's	−49	10	36
Menard *et al.*, 1996	View words > view X's	−43	20	0

APPENDIX B—*Continued*

	Task comparison	X	Y	Z
Menard *et al.*, 1996	View words > view X's	−43	7	0
Menard *et al.*, 1996	View words > view fixation	−41	7	44
Menard *et al.*, 1996	View pictures > view fixation	−39	10	20
Menard *et al.*, 1996	View words > view fixation	−39	20	−4
Menard *et al.*, 1996	View pictures > view X's	−34	34	0
Petersen *et al.*, 1990	Real words > pseudowords	−29	43	0
Price *et al.*, 1994	Word > false font, silent viewing	−38	28	−16
Price *et al.*, 1996b	Word > false font, silent viewing	−48	8	32
Price *et al.*, 1996b	Word > letter string, silent viewing	−42	28	20
Price *et al.*, 1996b	Word > letter string, silent viewing	−40	4	28
Price *et al.*, 1996b	Word > false font, silent viewing	−38	20	12
Price *et al.*, 1996b	Word > pseudowords	−26	46	28
Price *et al.*, 1996b	Word > pseudowords	−22	24	−8

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