Language network specializations: An analysis with parallel task designs and functional magnetic resonance imaging

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Although the classical core regions of the language system (Broca’s and Wernicke’s areas) were defined over a century ago, it took the advent of functional imaging to sharpen our understanding of how these regions and adjacent parts of the brain are associated with particular aspects of language. One limitation of such studies has been the need to compare results across different subject groups, each performing a different type of language task. Thus, this study was designed to examine overlapping versus segregated brain activations associated with three fundamental language tasks, orthography, phonology and semantics performed by the same subjects during a single experimental session. The results demonstrate a set of primarily left-sided core language regions in ventrolateral frontal, supplementary motor, posterior mid-temporal, occipito-temporal and inferior parietal areas, which were activated for all language tasks. Segregated task-specific activations were demonstrated within the ventrolateral frontal, mid-temporal and inferior parietal areas. Within the inferior frontal cortex (Broca’s regional complex), segregated activations were seen for the semantic and phonological tasks. These findings demonstrate both common and task specific activations within the language system.

Keywords: Language; Orthography; Phonology; Semantics; Functional magnetic resonance imaging

Introduction

In the latter half of the 19th century, careful case observations and remarkable insights by, Paul Broca, Carl Wernicke and others

Collectively, these results suggest that the classical language regions are not specifically devoted to single linguistic operations. Rather, it appears that they are comprised of several subregions each of which may show different specializations. Although functional imaging studies have extended our view of the language system, not all studies have shown consistent task-specific activations possibly because of the use of varying task designs and the reliance on single task subtraction methodology. In order to overcome these limitations, we have designed parallel language tasks that manipulate attention to orthographic, phonologic and semantic linguistic comparisons for single words relative to a common non-linguistic baseline task comparing letter strings. Comparisons are made within subjects using random-effects analyses with stringent statistical criteria. The results within our

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single subject group confirm and extend findings previously achieved only through the meta-analysis of multiple studies or by using disparate task designs.

Methods

Subjects

Fifteen participants were included in the analysis. There were 8 males and 7 females with a mean (standard deviation) age of 29.9 (5.9) years. Subjects had no history of significant medical, neurologic or psychiatric illness. All subjects were right-handed by self-report and their mean handedness score was 85.3 (11.9) (Oldfield, 1971). All subjects gave their written informed consent and this study was approved by the Northwestern University Institutional Review Board.

Behavioral tasks

All 15 subjects performed the orthographic, phonologic and semantic tasks, described below. Twelve of the subjects also performed a syntactic task in the same session, which is not reported in this manuscript. Fourteen subjects performed the tasks within a single session, while one subject was studied over 2 sessions.

Each task was performed as a separate functional imaging run consisting of eight alternating 30.45-s blocks of the active and control conditions. During each active task, subjects were shown two words for 3400 ms and asked to respond if the words were identical along a specified linguistic parameter. Fig. 1 illustrates the comparisons. In the orthographic task (ANA), subjects responded if the words were anagrams; in the phonologic task (HOM), subjects responded if the words were homophones; in the semantic task (SYN), subjects responded if the words were synonyms. During the control task (CON), subjects were shown pairs of consonant letter strings and asked to respond if the strings matched.

The word lists were drawn from the MRC psycholinguistic database (Coltheart, 1981). Table 1 shows the ratings of the word and letter lists along various linguistic dimensions. Approximately 90% of the words on each list were open-class and 10% were closed-class. Seventy-five to 90% were nouns or verbs, 25 to 38% were adjectives, 10 to 20% were adverbs and 0.8 to 2% were prepositions, conjunctions or pronouns. Since each word could have more than one part of speech classification (based on the MRC database), these percentages add up to more than 100%. Nouns could be concrete or abstract and were drawn from several categories. There were less than 20% irregularly spelled words as rated by two of the authors (ACN and DRG).

Because of differences in the linguistic ratings between the lists (or large standard deviations among the conditions), ratings for Kucera-Francis frequency, number of letters, familiarity, concreteness, and imageability were included as covariates of no interest in the functional imaging analysis (see below).

Subjects responded by pressing a button held in their right hand. Reaction times were recorded for all responses. Task accuracy was determined from the percentage of correct behaviors, that is, (number of hits + number of correct rejections)/total no. of stimuli. Stimuli were presented and responses were collected using Superlab software (Cedrus, San Pedro, CA) running on a Power Macintosh computer (Apple, Cupertino, CA). The stimuli were projected onto a custom-designed nonmagnetic rear projection screen using an active matrix liquid crystal display projector. Subjects viewed the screen, located approximately 170 cm from their eyes, through a non-magnetic mirror.

Ultimate inclusion of subjects in the group analysis was dependent on above-chance performance (≥62.5% accuracy, 24/40 correct), on each of the three tasks during the experimental session. The accuracy cut-off was based on the binomial test. This criterion was met by 14 of the 15 subjects.

MR imaging—anatomical scans

T1 weighted anatomic images were obtained on the 1.5 T Siemens Vision scanner, using a 3D FLASH sequence with the following parameters: TR/TE, 15 ms/6 ms; flip angle, 20°; FOV, 220 mm; matrix, 256 × 256; slice thickness, 1.0 mm. All anatomic and functional scans were obtained in transaxial planes parallel to the AC-PC line.

MR imaging—functional scans

Functional MRI volumes were acquired as thirty-two 4-mm slices using a single-shot EPI method (TR/TE, 4350/40 ms; flip angle, 90°; matrix, 64 × 64; FOV, 220 mm). For all functional runs, the signal was allowed to reach a steady state over four initial volumes that were excluded from the analysis.

Subjects had their head immobilized with a vacuum pillow (Vac-Fix, Bionix, Toledo, OH) and the restraint calipers built into the head coil. They were given a non-magnetic button, which

![Fig. 1. Examples of stimuli in the three language tasks and the control condition.](image-url)
Table 1
Linguistic parameters for word and letter lists

<table>
<thead>
<tr>
<th></th>
<th>Num. letters</th>
<th>Kucera-Francis</th>
<th>Familiarity</th>
<th>Concreteness</th>
<th>Imageability</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANA words</td>
<td>4.06 (0.85)</td>
<td>184.1 (882.08)</td>
<td>543.2</td>
<td>471.7</td>
<td>491.2 (98.38)</td>
</tr>
<tr>
<td>ANA letters</td>
<td>4.67 (0.471)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>HOM words</td>
<td>4.4 (0.82)</td>
<td>132.9 (387.91)</td>
<td>522.7</td>
<td>456.3</td>
<td>471.9 (100.09)</td>
</tr>
<tr>
<td>HOM letters</td>
<td>4.66 (0.655)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>SYN words</td>
<td>4.4 (0.74)</td>
<td>95.5 (123.20)</td>
<td>553.26 (64.39)</td>
<td>393.9 (85.77)</td>
<td>451.4 (67.72)</td>
</tr>
<tr>
<td>SYN letters</td>
<td>4.89 (0.439)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

All values are reported as mean (standard deviation). Letter condition comparisons used a one-way ANOVA and post-hoc Tukey HSD; word condition comparisons used a multivariate ANOVA and post-hoc Tukey HSD.

*a* \( P < 0.001\) number of letters, ANA words vs. HOM words.

*b* \( P = 0.001\) number of letters, ANA words vs. SYN words.

*c* \( P < 0.001\) concreteness, ANA words vs. SYN words.

*d* \( P = 0.011\) imageability, ANA words vs. SYN words.

*e* \( P = 0.003\) number of letters, ANA letters vs. SYN letters.

*f* \( P < 0.001\) concreteness, HOM words vs. SYN words.

*g* \( P = 0.002\) number of letters, HOM letters vs. SYN letters.

enables recording of their responses. A vitamin E capsule was taped to the left temporal region to mark laterality for image processing.

**MR imaging—data analysis**

The preprocessing and analysis of fMRI data were performed using the SPM-2 software (Wellcome Department of Imaging Neuroscience, London, UK, http://www.fil.ion.ucl.ac.uk/spm) running under the MATLAB environment (Mathworks Inc., Sherborn, MA) (Friston et al., 1995a,b; Worsley and Friston, 1995) on a PC workstation.

Preprocessing steps included slice-timing correction, motion correction within functional runs, coregistration between the functional and anatomic images within each subject and normalization to the Montreal Neurological Institute standard template brain (MNI-305) (Ashburner et al., 1997; Friston et al., 1995a,b). This template approximates the space described in the atlas of Talairach and Tournoux (1988). Functional data were then smoothed with a 10-mm FWHM isotropic Gaussian kernel, to enable intersubject comparisons.

Because the word and letter lists differed between tasks along various linguistic dimensions, these ratings were included as covariates of no interest in each subject’s design matrix. This was done by calculating an average for each of the ratings in each of the condition blocks. These block-specific values for each rating were then included as parametric regressors for each condition. The letter blocks had only the number of letters as a regressor, while the word blocks included the number of letters, Kucera-Francis frequency, and ratings of familiarity, concreteness, and imageability.

SPM uses the technique of statistical parametric mapping and references the probabilistic behavior of a stationary Gaussian field for defining the probability density function of an image. It employs the general linear model for testing hypotheses at each voxel. Contrasts were set up to test for voxelwise effects of signal differences between the word and letter conditions, and statistical parametric maps were calculated in each subject (Friston et al., 1995b).

Random effects analyses were computed by generating for each subject parameter effect images for the three main contrasts (ANA-CON, HOM-CON and SYN-CON). The parameter effects images were then entered into a second-level, one-way ANOVA with the language task as the grouping factor. A non-sphericity correction was included in the analysis to account for the use of the same subjects in all tasks (Friston et al., 2002).

Common areas of activation across all tasks were identified using a random effects conjunction analysis. Specialization within the word processing network was revealed by inclusive masking the main effect of one task (active task minus control) with its differential effects compared with the other tasks. For example, specialization within the network for orthography was identified by inclusively masking ANA-CON with ((ANA-CON) – (HOM-CON)) and with ((ANA-CON) – (SYN-CON)). This had the effect of showing activations in the (ANA-CON) contrast only where ANA-CON was more active than HOM-CON and SYN-CON. Similar analyses were performed for the other tasks. These contrasts will be referred to as masked analyses.

Voxels were considered significant at \( P < 0.05 \) after correction for multiple comparisons using the False Discovery Rate (FDR) (Genovese et al., 2002). The FDR is able to appropriately control the false positive rate while being less likely to result in Type II errors than the Family-wise Error. The conjunction analysis was considered significant at a corrected threshold of 0.05 based on corrected significance levels in the component contrasts. This ensured that voxels were significant in all contrasts comprising the conjunction (Nichols et al., 2005).

**Results**

**Behavioral data**

Fourteen of fifteen subjects met the inclusion criterion. One subject performed at chance on the ANA task (55% correct) so all their runs were excluded from analysis in order to maintain a balanced design. The mean response times and accuracies are shown in Table 2. Overall subjects were highly accurate on both the active and control tasks. There was a significant effect of condition on reaction time in the active condition, \( F_{2,41} = 5.18, P < 0.01 \). A post-hoc Tukey test showed that the difference was between the ANA and SYN conditions, \( P < 0.01 \). There was also an effect of condition on accuracy in the control task, \( F_{2,41} = 6.65, P < 0.01 \). Subjects were slightly more accurate during the control
periods for the ANA and HOM tasks than for the SYN task. This may be related to the slightly longer letter string length in the SYN task, Table 1.

**fMRI results**

The conjunction of all three conditions versus their respective controls showed that voxels that were significantly activated in all three tasks, Fig. 2 and Table 3. This analysis showed activations primarily within the left inferior and middle frontal gyri and lateral orbital gyrus overlying portions of Brodmann areas 6, 9, 10, 45, 46 and 47. Activations were also seen in the left anterior insula, supplementary motor area and right cerebellum, Fig. 2.

For the individual task activations, the masked ANA contrast, Fig. 3-top and Table 4, demonstrated frontal activations in the left anterior inferior frontal gyrus and bilateral frontal eye field regions. Bilateral activations were seen in the posterior parietal cortex, which were more extensive on the left. The right cerebellum was also activated (not shown).

The masked HOM contrast showed activations at the junction of the left posterior inferior frontal gyrus and precentral sulcus corresponding to the pars opercularis region of Broca’s complex, and the left superior precentral gyrus, Fig. 3-middle and Table 5. On the right, activations were seen in the orbital gyrus, ventral insula and parahippocampal gyrus (not shown).

Finally, the masked SYN contrast showed activations in the left lateral orbital and inferior frontal gyrus (pars orbitalis and pars triangularis regions of Broca’s complex), a region in the left posterior superior temporal gyrus consistent with Wernicke’s area, and several additional regions in the middle and anterior temporal cortex, Fig. 3-bottom and Table 6. Other areas of activation included the left supplementary motor cortex, right

<table>
<thead>
<tr>
<th>Location</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>Z</th>
<th>P (voxel corrected)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left PreCS (BA 6)</td>
<td>–36</td>
<td>3</td>
<td>39</td>
<td>3.89</td>
<td>0.0011</td>
</tr>
<tr>
<td>Left MFG (BA 9)</td>
<td>–51</td>
<td>24</td>
<td>30</td>
<td>6.54</td>
<td>2.43E–09</td>
</tr>
<tr>
<td>Left IFG (BA 45)</td>
<td>–48</td>
<td>33</td>
<td>18</td>
<td>5.19</td>
<td>4.31E–06</td>
</tr>
<tr>
<td>Left IFG (BA 47)</td>
<td>–51</td>
<td>27</td>
<td>–3</td>
<td>4.77</td>
<td>3.25E–05</td>
</tr>
<tr>
<td>Left LOG (BA 10/46)</td>
<td>–45</td>
<td>48</td>
<td>0</td>
<td>5.11</td>
<td>6.48E–06</td>
</tr>
<tr>
<td>Left anterior insula</td>
<td>–30</td>
<td>21</td>
<td>3</td>
<td>3.36</td>
<td>0.0066</td>
</tr>
<tr>
<td>SMA (BA 8/32)</td>
<td>–3</td>
<td>15</td>
<td>51</td>
<td>4.36</td>
<td>1.83E–04</td>
</tr>
<tr>
<td>Right cerebellum</td>
<td>15</td>
<td>–78</td>
<td>–33</td>
<td>3.42</td>
<td>0.0054</td>
</tr>
<tr>
<td>(crus I/lobule VI)</td>
<td>27</td>
<td>–69</td>
<td>–42</td>
<td>3.71</td>
<td>0.0021</td>
</tr>
<tr>
<td></td>
<td>36</td>
<td>–69</td>
<td>–45</td>
<td>3.96</td>
<td>8.71E–04</td>
</tr>
</tbody>
</table>

*P < 0.05 ANA vs. SYN post-hoc Tukey-HSD.

**Table 2**

| Response time (milliseconds) and accuracy (%) for the task and control conditions |
|---------------------------------|----------|----------|----------|
| ANA (mean ± SD)                | HOM (mean ± SD) | SYN (mean ± SD) |
| Active task                    | 1728 ± 221* | 1558 ± 181 | 1473 ± 235* |
| Control task                   | 1750 ± 259  | 1948 ± 299 | 1827 ± 241  |
| Accuracy: ANA                  | 92.7%      | 90.9%     | 93.0%      |
| Accuracy: HOM                  | 97.0%      | 97.7%     | 92.9%      |
| Accuracy: SYN                  | 97.0%      | 97.7%     | 92.9%      |

**Table 3**

*Fig. 2. Random effects conjunction of ANA, HOM and SYN tasks. All regions shown are significant at *P* < 0.05 corrected for each of the components in the conjunction. The activations are clearly left sided. The upper row shows a lateral rendered view of the activations on the mean brain of all subjects. The lower row shows the activations overlaid on axial slices. Key: CB (I/VI) = cerebellum (crus I/lobule VI); IFG = inferior frontal gyrus; INS = insula; LOG = lateral orbital gyrus; MFG = middle frontal gyrus; PCS = precentral sulcus; SMA = supplementary motor area.*
Discussion

The current study has provided evidence of both general and task specific activations while subjects performed tasks of orthographic,
Reported activations are significant at this case 12.4 mm.

Right Cerebellum
Right ITG (BA 37) 51
Right IPS (BA 7) 39
Left IPS (BA 7) 30
Left SMG (BA 7/40) 30 30 4.77 0.0058 37
Left SPL (BA 7) 36 30 5.09 7.13E-05 50
Right IFS (BA 46) 42 33 5.09 7.13E-05 50

Zatorre et al., 1992) and semantics (Binder et al., 1997; Chee et al., 1999; De´monet et al., 1992, 1994; Martin et al., 1995; Petersen et al., 1989, 1990). Devlin et al., 2003; Fiez, 1997; Gold and Buckner, 2002; Kapur et al., 1994a,b; Martin et al., 1995; Petersen et al., 1989, 1990). Devlin and colleagues have further demonstrated the critical and specific involvement of BA 47 in semantics by showing that transcranial magnetic stimulation (TMS) over BA 47 selectively slows semantic but not phonological processing. In fact, the specific involvement of BA 47 in semantics by showing the engagement of different subregions based on the linguistic goals of the task. More anterior aspects of Broca’s region, within the anatomical regions of the pars triangularis and pars orbitalis (see Devlin et al., 2003, for definitions), were activated in the semantic task more than in either the phonological or the orthographic tasks. These results are consistent with several previous reports demonstrating activations particularly within the BA 47 region, and also BA 45, as being linked to semantics (Buckner et al., 1995a,b; Dapretto and Bookheimer, 1999; Demb et al., 1995; Demontet et al., 1992; Devlin et al., 2003; Fiez, 1997; Gold and Buckner, 2002; Kapur et al., 1994a,b; Martin et al., 1995; Petersen et al., 1989, 1990). Devlin and colleagues have further demonstrated the critical and specific involvement of BA 47 in semantics by showing that transcranial magnetic stimulation (TMS) over BA 47 selectively slows semantic but not phonological processing. In fact, the location of their mean stimulation site (x = −52, y = +24, z = −2) was less than 4 mm from the most significant site of activation for the semantic task in the current study, Table 6 (x = −51, y = +27, z = −3), providing a nice convergence of results (Devlin et al., 2003).

The BA 47 region activation was also within 1 cm of the activation reported by Hagoort et al., as an area integrating word meaning with world knowledge (Hagoort et al., 2004). The similar activation in this study may relate to subjects having to compare the meanings of different words.

Inferior frontal cortex

This study was also able to demonstrate regional specializations within the language system. Specialization was found specifically within Broca’s complex by showing the engagement of different subregions based on the linguistic goals of the task. More anterior aspects of Broca’s region, within the anatomical regions of the pars triangularis and pars orbitalis (see Devlin et al., 2003, for definitions), were activated in the semantic task more than in either the phonological or the orthographic tasks. These results are consistent with several previous reports demonstrating activations particularly within the BA 47 region, and also BA 45, as being linked to semantics (Buckner et al., 1995a,b; Dapretto and Bookheimer, 1999; Demb et al., 1995; Demontet et al., 1992; Devlin et al., 2003; Fiez, 1997; Gold and Buckner, 2002; Kapur et al., 1994a,b; Martin et al., 1995; Petersen et al., 1989, 1990). Devlin and colleagues have further demonstrated the critical and specific involvement of BA 47 in semantics by showing that transcranial magnetic stimulation (TMS) over BA 47 selectively slows semantic but not phonological processing. In fact, the location of their mean stimulation site (x = −52, y = +24, z = −2) was less than 4 mm from the most significant site of activation for the semantic task in the current study, Table 6 (x = −51, y = +27, z = −3), providing a nice convergence of results (Devlin et al., 2003).

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Thompson-Schill and colleagues have suggested that the inferior frontal cortex may be linked to semantic choice rather than semantic retrieval, per se (Thompson-Schill et al., 1997). Although, our task design itself would not exclude this interpretation, the area of activation in the Thompson-Schill et al. study (mean $x = 44$, $y = 9$, $z = 30$, inferior frontal sulcus), while partly overlapping the frontal activation in the conjunction analysis, did not overlap the activations for either the masked semantic or phonological analyses. This also suggests that the region activated by the conjunction is engaged by all three language tasks, rather than specifically supporting just phonology or semantics, again consistent with a potential general role in post-lexical processing.

The frontal activation associated with phonology in the current study was located at the junction of the precentral sulcus and posterior IFG within the pars opercularis region (see Devlin et al., 2003). Similar activations have been reported in other studies using tasks of phonological perception (Démonet et al., 1992, 1994; Devlin et al., 2003; Fiez, 1997; Fiez et al., 1995; Gold and Buckner, 2002; Paulesu et al., 1997; Rumsey et al., 1997; Zatorre et al., 1996). Part of this activation extended towards but did not overlap with the anterior insula, which has been suggested in both lesion...
(Dronkers, 1996) and functional neuroimaging studies (Riecker et al., 2000a,b; Wise et al., 1999) to be closely linked with articulation. However, a recent study by Hillis et al., did not find an association between the anterior insula and articulation (Hillis et al., 2004). In the HOM task, subjects had to make phonological judgments without overt articulation, which may account for the absence of left insular activation. Another possibility, given the activation of the anterior insula in the conjunction analysis, is that the anterior insula may also be associated with general aspects of post-lexical processing or attention in all three tasks rather than articulation (Riecker et al., 2000a,b).

Other frontal activations

Supplementary motor cortex activation was seen in the conjunction and masked SYN analyses. Other studies have noted SMA activations for a variety of language tasks involving semantic, phonologic, and orthographic operations (Binder et al., 1997; Booth et al., 2002a,b; Buckner et al., 1995a; Chee et al., 1999; Kuo et al., 2004; Poldrack et al., 1999; Siok et al., 2003). Anterior SMA activations \((y = +10 \text{ to } +40)\) have been associated with semantic (Binder et al., 1997; Booth et al., 2002a; Buckner et al., 1995a; Poldrack et al., 1999) and syllabic processing tasks (Kuo et al., 2004; Siok et al., 2003). Posterior activations \((y = -22 \text{ to } 0)\) have been seen less consistently across studies, but have occurred in tasks involving word recall and repetition (Buckner et al., 1995a) or processing of letters/syllables compared with semantics (Booth et al., 2002a; Poldrack et al., 1999). Data from primates shows that anterior SMA has robust connections with anterior prefrontal and inferior frontal areas, while posterior SMA is connected to motor and posterior premotor regions (Rizzolatti et al., 1996). There are also connections with cerebellum. With respect to language, the SMA has been hypothesized to play a role in covert articulation and internally versus externally guided word generation (Fiez and Raichle, 1997). However, it has also been activated in motor planning and “complex” motor behaviors (Vorobiev et al., 1998).

Temporal cortex

In the masked semantic task, several regions of activation were seen in the lateral temporal lobe. The temporal cortex has been associated with semantics based on data from lesion (Damasio et al., 1996; Hart and Gordon, 1990), degenerative (Mummery et al., 1999) and multiple functional imaging studies (Démonet et al., 1992; Shaywitz et al., 1995a,b; Vandenberghe et al., 1996). A recent study by Hagoort et al. has further suggested that temporal cortex activity may be more specifically associated with the retrieval of word meaning (Hagoort et al., 2004). The current study is entirely consistent with these findings and provides a robust demonstration of the significant temporal activation found in semantic tasks.

Several functional imaging studies have also implicated middle and anterior portions of the temporal lobe in phonological processing (Démonet et al., 1992, 1994; Paulesu et al., 1993; Shaywitz et al., 1995a,b; Sergent et al., 1992). Anterior temporal activation was not seen in the masked phonology analysis. However, the phonology task used visual rather than auditory stimuli and did not involve word generation. Furthermore, the analysis technique stringently controlled for semantic processing. These factors suggest that the non-auditory regions of temporal lobe may not be involved in phonologic processing, although it is possible that our criteria were so strict as to result in a Type 2 error.

Parietal cortex

Several studies have suggested that the supramarginal gyrus likely plays a role in the short-term storage of verbal information (Binder et al., 1997; Paulesu et al., 1993; Warrington et al., 1971). This role is consistent with the design of our tasks in which subjects would have maintained the phonological or semantic information of one word while looking at the other, or would have held online several letters while looking at the spelling of the second word. Activation in semantic tasks has not generally been seen unless the task includes a working memory component (Cabeza and Nyberg, 2000). In the current study, the activation of the inferior and medial parietal cortex in the semantic task therefore may have been related to greater working memory requirements during this condition.

In the case of the masked orthographic contrast, this condition activated the supramarginal gyrus on the left and the intraparietal sulcus bilaterally. Although the parietal and frontal eye field activations could just reflect recruitment of the spatial attention network, we hypothesize this may represent a form of material specific spatial attention processing. In both the orthographic and control tasks, subjects had to decide if the stimulus pairs contained the same letters. Subjects found the tasks equally difficult as reflected by the similar reaction time and accuracy measures; however, greater activations were seen in the ANA task (vs. the control), suggesting that the processing of word stimuli may have enhanced any activity related to spatial attention, consistent with a material specific stimulus effect.

Cerebellum

When functional imaging was first used to study language in the 1980s, one surprising finding was the activation of the cerebellum in apparently non-motor linguistic tasks. Many subsequent studies have demonstrated cerebellar activations in both motor and non-motor aspects of language including articulation, semantics, verbal fluency, response selection, sequence learning, and verbal working memory (see Fiez and Raichle, 1997, for a review). In the current study, cerebellar activations were seen on the right in crus I/lobule VI for the conjunction analysis, crus I/lobule VI for the masked orthographic analysis, and the right dentate nucleus and crus I/II for the masked semantic analysis. These locations are based on the nomenclature of Schmahmann et al. (1999).

Some of the activations in the current study overlap cerebellar regions that may be associated with articulatory processes while others occur in regions that seem related to non-motoric aspects of language. Although subjects did not overtly articulate words in the current study, cerebellar activation has also been seen in studies employing covert articulation, and the cerebellum is hypothesized to participate in a (possibly covert) articulatory loop that includes the inferior frontal cortex and the supplementary motor area (Fiez and Raichle, 1997).

In previous studies that have used tasks which emphasized orthographic processing, cerebellar activations have been seen in right crus I (Chen et al., 2002; Fullbright et al., 1999; Rumsey et al., 1997). Semantic tasks have also shown similar cerebellar activations as in the current study. Previous studies have further shown that cerebellar activations are sensitive to semantic task
demands (Fullbright et al., 1999; Roskies et al., 2001; Xiang et al., 2003), raising the possibility that the cerebellum may directly contribute to semantic computations or selection (Xiang et al., 2003).

We consider it unlikely that the cerebellum was activated in the current study merely as a consequence of subject responses because the motor requirements of the task were well matched between the active and control conditions, and across tasks. One concern regarding cerebellar involvement in language is that cerebellar lesions do not appear to result in linguistic deficits. Further studies will be necessary to elucidate the specific role of the cerebellum in language, beyond its motor associations.

Right hemisphere

In the right hemisphere, each of the tasks had specific areas of activation, parietal and superior frontal for masked ANA, inferior frontal for masked HOM and temporal for masked SYN. Multiple studies have noted right hemisphere activations for language tasks (Chee et al., 1999; Devlin et al., 2003; Fiez et al., 1995; Heim et al., 2003; Petersen et al., 1989; Mazoyer et al., 1993; McDermott et al., 2003; Rossell et al., 2003; Rumsey et al., 1997; Tagamets et al., 2000; Turkeltaub et al., 2002). The right hemisphere has been hypothesized to be particularly activated in response to interpreting sentence content, placing information in context, detecting semantic anomalies, interpreting prosody, and understanding metaphor, none of which should activate in response to interpreting sentence content, placing information in context, detecting semantic anomalies, interpreting prosody, and understanding metaphor, none of which should be activated simply as a by-product of the current study merely as a consequence of subject responses because the motor requirements of the task were well matched between the active and control conditions, and across tasks. One concern regarding cerebellar involvement in language is that cerebellar lesions do not appear to result in linguistic deficits. Further studies will be necessary to elucidate the specific role of the cerebellum in language, beyond its motor associations.

Conclusions

Through the use of subjects performing identical tasks probing different aspects of lexical processing, this study has examined brain activations related to three fundamental language processes (orthography, phonology and semantics). The results show that a common network of brain regions supports word processing, while each task is also associated with more specific activations. The results both confirm and extend findings from multiple studies in the literature by showing the extent of functional integration and segregation in the language network.

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References


