Segregating Semantic and Syntactic Aspects of Processing in the Human Brain: an fMRI Investigation of Different Word Types

The processing of single words that varied in their semantic (concrete/abstract word) and syntactic (content/function word) status was investigated under different task demands (semantic/ syntactic task) in an event-related functional magnetic resonance imaging experiment. Task demands to a large degree determined which subparts of the neuronal network supporting word processing were activated. Semantic task demands selectively activated the left pars triangularis of the inferior frontal gyrus (BA 45) and the posterior part of the left middle/superior temporal gyrus (BA 21/22/37). In contrast, syntactic processing requirements led to an increased activation in the inferior tip of the left frontal operculum (BA 44) and the cortex lining the junction of the inferior frontal and inferior precentral sulcus (BA 44/6). Moreover, for these latter areas a word class by concreteness interaction was observed when a syntactic judgement was required. This interaction can be interpreted as a prototypicality effect: non-prototypical members of a word class, i.e. concrete function words and abstract content words, showed a larger activation than prototypical members, i.e. abstract function words and concrete content words. The combined data suggest that the activation pattern underlying word processing is predicted neither by syntactic class nor semantic concreteness but, rather, by task demands focusing either on semantic or syntactic aspects. Thus, our findings that semantic and syntactic aspects of processing are both functionally distinct and involve different subparts of the neuronal network underlying word processing support a domain-specific organization of the language system.

Introduction

The relation between language processing and its neurobiological basis has been investigated recently by means of electrophysiological and neuroimaging techniques. At a functional level, language production and language comprehension have been described as consisting of different, separable subprocesses [for reviews see (Levelt, 1989; Friederici, 1999)]. Most models assume that lexical-semantic processes and syntactic structure building processes are distinct. This separation has often been exemplified in the distinction between two word classes: namely, content words and function words. While the content words (nouns, verbs and adjectives) primarily carry semantic meaning and are members of the so-called open class, function words (articles, prepositions, conjunctions, etc.) together with other functional elements (inflections) primarily carry syntactic information and constitute the so-called closed class. The small set of closed class elements is critical for syntactic processes as these indicate the syntactic relations of the words in a sentence. Empirical studies with healthy and brain-damaged subjects have provided support for the view that lexical-semantic and syntactic elements are processed differently. The processing of function words is selectively impaired in patients with lesions in the anterior part of the left hemisphere, including Broca's area (Bradley et al., 1980; Friederici and Schönle, 1980). Open and closed class words are

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involved in different types of speech errors in normals (Garrett, 1980; Stemberger, 1982) and show differential sensitivity to context during sentence processing (Friederici, 1985). Moreover, studies in children suggest different templates for the acquisition of open and closed class words [for a review see (Gleitman and Wanner, 1982)].

This distinction between the two classes seems to be rather clear-cut at first sight; however, a closer inspection of the relevant data suggests that this is not the case. First, although prepositions belong to the closed class, some have a clear referential meaning, i.e. a location (in, on, under). On the basis of behavioral evidence, Friederici argued that a crucial distinction might lie in the amount of semantic information a particular element carries rather than its class membership (Friederici, 1985). Moreover, there is a long-standing discussion about whether the functional distinction between open and closed class elements is evident when they are presented as single words (Bradley et al., 1980; Gordon and Caramazza, 1982; Kolk and Blomert, 1985; Matthei and Kean, 1989) or only when function words are processed according to their syntactic function, i.e. in sentence context (Friederici, 1985; Rosenberg et al., 1985; Rosenthal and Goldblum, 1989). Irrespective of this discussion, the investigation of the distinction between function words and content words is of crucial interest as it maps onto the basic linguistic distinction between functional elements and major category items.

Although earlier neuropsychological studies of aphasic patients investigated the influence of syntactic structure on the processing of open and closed class elements (Andreewsky and Seron, 1975; Friederici and Schönle, 1980), as well as the influence of semantic referential meaning (Friederici, 1983), none of the more recent neurocognitive studies using electrophysiological or imaging methods has systematically taken these aspects into account. Rather, in neurophysiological studies at the word level the factors word class and concreteness are often confounded (Nobre and McCarthy, 1994; Pulvermüller et al., 1995), weakening the conclusions that can be drawn. Neurophysiological studies investigating the processing of open and closed class words at the sentence level usually average over all function words versus all content words, whereby nouns, verbs and adjectives are categorized as content words and the rest as function words. Applying this procedure, two different components for the two different word classes were found in some studies: a left-lateralized negativity (N280) for function words and a non-lateralized N400-like negativity for content words (Neville et al., 1992; ter Keurs et al., 1999). Others report an early effect for both word types (Brown et al., 1999) or an N400-like component for both word types (Garnsey, 1985; Van Petten and Kutas, 1991).

Recent functional magnetic resonance imaging (fMRI) studies which try to define the brain areas involved in word processing

have focused mainly on the processing of concrete nouns. These studies indicate that passive listening or silent reading of words evokes major activation in Brodmann's areas (BA) 22/42 in the left temporal cortex (Petersen et al., 1989, 1990; Frith et al., 1991; Howard et al., 1992; Price et al., 1997), although sometimes this activation is bilateral. Left inferior frontal activation is reported during word perception when strategic semantic processes come into play (Fiez, 1997). Bilateral inferior frontal activation with a dominance of the left hemisphere was observed for verbal-semantic memory (Wagner et al., 1998). Kiehl and colleagues (Kiehl et al., 1999) tried to define the neural pathways involved in the processing of concrete and abstract words (presumably nouns) in an fMRI study applying a lexical decision task. They specify the neural network of word processing to involve the bilateral fusiform gyrus, anterior cingulate, left middle temporal gyrus, right posterior superior temporal gyrus, and left and right inferior frontal gyrus, and claim that the right anterior temporal cortex particularly supports the processing of abstract representations of language. Nobre et al., using a semantic judgement task, found the left inferior frontal gyrus (BA 47), superior frontal gyrus/sulcus (BA 9), angular gyrus (BA 39) and left anterior temporal region to be activated during processing concrete content words, whereas the superior part of Broca's area (BA 44/6), the inferior frontal gyrus (BA 45) and temporal areas (BA 21, BA 40) were active during the processing of function words (Nobre et al., 1997). Thus, it appears that different inferior frontal and temporal areas are activated by different conditions, i.e. stimulus types as well as task demands.

The Present Study

The present study set out to disentangle the effect of class membership (open class/closed class) and the effect of concreteness (concrete word/abstract word) on word processing as well as the effect of task (semantic task/syntactic task) in a systematic way. We report an event-related fMRI experiment in which open and closed class words, varying in their meaning content, were presented visually. Subjects performed either a syntactic or a semantic categorization task and a physical categorization task. Results indicated that activation in the left inferior frontal and temporal areas varied systematically as a function of word class, concreteness and task. The major effect observed, however, was a function of the task demands. The inferior part of the left fronto-opercular cortex (BA 44) and the inferior part of the precentral gyrus (BA 44/6) were predominantly activated during the syntactic task, whereas left BA 45 and the posterior part of the left superior and middle temporal gyrus (BA 21/22/37) were selectively activated during the semantic task.

Materials and Methods

Participants

Fourteen right-handed subjects (age 22–31 years, six female) participated in the experiment. They all had normal or corrected to normal vision. Informed consent was obtained from all participants. One participant was excluded from all analysis due to coarse motion artifacts.

Materials

The material for the semantic and syntactic task consisted of 80 nouns and 80 function words. Note that none of the items was word form and thereby category ambiguous. Half of the nouns were concrete nouns, half abstract nouns. The mean frequency of occurrence was 115 for abstract nouns and 110 for concrete nouns. The function word set consisted of 20 locative prepositions (*auf/on*) and 20 adverbs of location (*oben/above*), representing the concrete items, and 40 abstract items, i.e. 20 conjunctions (*weil/because*) and 20 adverbs (*falls/if*). Mean frequency was 413 for abstract function words and 533 for concrete function words. The mean word length for function words was 5.8 and for content words 5.0. Though the mean frequency within each word class (noun and function words) was comparable, the frequency between the two classes could not be held constant. Thus, if only word class effects were to occur, these might be difficult to interpret. However, possible effects between concrete and abstract words would not be, as words of equal frequency are compared. Moreover, possible main effects of task are also independent of the frequency issue. The material for the physical task consisted of consonant letter strings (1.3° vertical visual angle). The spacing between the letters was normal, i.e. identical to that of the words in half of the items, and larger than normal between the individual letters in the rest of the items (25 versus 5% of the height of a single letter).

Procedure

In an event-related design stimuli were presented visually for a period of 500 ms with an inter-stimulus interval of 10 s, during which a fixation cross was presented. This interval allowed the fMRI signal to return to the baseline level.

Participants were required to look at and classify the presented stimulus item. Due to the extensive recording time in event-related fMRI studies, subjects performed either a syntactic or a semantic categorization task. A physical categorization task served as a baseline task in both groups. The syntactic task required participants to indicate whether the stimulus seen was a noun or a function word. The semantic task required participants to judge whether the stimulus was a concrete or an abstract word. Word stimuli were written in upper case with normal spacing between the letters. The physical task required participants to decide whether the items were written normally or with an enlarged space between each letter. Participants had to indicate their decision by pressing a button. One second before each stimulus a visual cue (500 ms duration) indicated which task was required. To ensure subjects were attentive during fixation, in 10% of the trials, evenly distributed across items and tasks, the fixation cross changed its color randomly in the time interval between two stimuli. Participants were instructed to respond as quickly as possible to these changes. These trials were excluded from all analyses.

Data Acquisition and Analysis

Echo planar and conventional imaging was performed on a 3 T Bruker Medspec 30/100 scanner. A standard birdcage head coil was used. Visual stimuli were presented on a screen positioned at the head end of the magnet bore. Subjects viewed the screen through mirror glasses. Cushions were used to reduce head motion. Imaging procedures included the collection of structural images (IR-RARE sequence, TE = 20 ms, TR = 3750 ms, matrix = 512 × 512) and gradient echo planar imaging (EPI) (TE = 40 ms, TR = 2 s, 3.0 mm^2 in plane resolution) from 10 axial slices (5 mm thickness, 2 mm skip) parallel to the AC-PC line. Prior to any statistical analysis, low-frequency signal fluctuations were removed on a voxel-by-voxel basis (Kruggel et al., 1998). Second, a spatial smoothing with a Gaussian kernel of FWHM = 2.35 was applied to individual datasets. For each participant functional images were analyzed by computing a voxelwise Pearson correlation of the MR signal with a reference wave form. This reference function represented the time course of the alternating task conditions (semantic/syntactic task versus physical baseline task). To account for the physiological delay in the hemodynamic response, the reference function was delayed by 4 s relative to the onset of a particular stimulus (Buckner et al., 1998). The correlation coefficient for each single voxel was normalized to Z-scores. Data evaluation on a trial-by-trial basis provided the flexibility to compute the hemodynamic response separately for each single stimulus within each condition. High-resolution brain images, acquired in a separate session using a T1-weighted 3-D MDEFT sequence, were used to assist localization of activation foci. Prior to multisubject averaging [under H_0 (a given region is not activated) the Z-scores across subjects have a normal distribution. In this case, the mean is a proven estimate of the expected value of the distribution of Z-scores across subjects] the registration of individual Z-maps was completed by correlating the anatomical slices with the individual high-resolution whole brain dataset (Friston et

al., 1995; Kruggel, 1995). Spatial linear normalization of registered individual data to the stereotactic coordinate system (Talairach and Tournoux, 1988) was carried out, to allow for superimposition of statistical maps across participants. The averaged activation maps were thresholded at P < 0.001 to assess significant activation foci.

To analyze differences of significant hemodynamic responses across subjects, the center of fMRI activation foci were identified within consistently activated regions. Spherical regions (3 mm radius) were defined around each of these peak activations, and mean Z-scores were subjected to a repeated-measure analysis of variance (ANOVA) with the task as a between-subject factor and word class and concreteness as within-subject factors [cf. (Bosch, 2000)].

Results

Behavioral Data

As shown in Table 1, performance in the syntactic task was faster and less error prone than the performance in the semantic task. An ANOVA on the number of correct responses confirmed the accuracy differences with a significant main effect of task [F(1,11) = 73.11, P < 0.001].

The ANOVA for the reaction times revealed a significant main effect of task [F(1,11) = 2.10, P < 0.05] and word class × concreteness interaction [F(1,11) = 99.05, P < 0.001], as well as a three-way interaction of word class × concreteness × task [F(1,11) = 50.63, P < 0.001]. Separate analyses were conducted for the two task conditions. For the *semantic task* there was a significant main effect of word class [F(1,5) = 9.9, P < 0.05], with faster reactions to content words than function words, and a significant word class × concreteness interaction [F(1,5) = 85.6, P < 0.001], reflecting the relatively fast responses to the concrete content words as compared with the other conditions. For the *syntactic task*, there was a significant main effect of concrete than for abstract words, and a word class × concreteness interaction times for concrete than for abstract words, and a word class × concreteness interaction [F(1,6) = 7.16, P < 0.05], which was

Table 1

Mean reaction times in ms, percent correct and SD (in parentheses) as a function of condition

	Reaction times		Percent correct			
	Semantic task	Syntactic task	Semantic task	Syntactic task		
Abstract function words Abstract content words Concrete function words Concrete content words	1043 (110) 1075 (104) 1131 (104) 927 (111)	753 (72) 724 (79) 740 (64) 671 (74)	85.5 (2.3) 82.5 (4.1) 87.5 (4.4) 91.0 (1.7)	97.9 (1.4) 97.9 (0.7) 95.7 (1.4) 97.5 (1.6)		

Table 2

Significantly activated brain regions (Z-scores) for the semantic task per word condition

due again to the relatively fast responses to concrete content words.

The observed main effects of task in both analyses indicate that it is easier to perform judgements if they are clearly categorical. It is the nature of syntactic categories that they have clear boundaries (allowing a clear classification judgement), and it is the nature of the semantic dimension of concreteness that it is continuous (a word refers to something which is more or less concrete, thereby requiring a relative classification judgement). The three-way interaction found in the reaction time data suggests that the three factors, i.e. task, word class and concreteness, are intimately related. It appears that an item's concreteness even plays a role when a syntactic judgement is required, and that an item's word class plays a role when a concreteness judgement is required.

Imaging Data

Activations of different brain regions during the semantic task and the syntactic task for the different word conditions, significant at the alpha level of P < 0.001, are presented in Tables 2 and 3, respectively. The mean *Z*-scores for each region of interest showing a significant activation in at least one condition are presented in Tables 4 and 5. These mean *Z*-scores entered the statistical analysis. Statistical maps for the semantic and the syntactic task are displayed in Figure 1.

From these tables it appears that there is a main effect of task for some regions, a main effect of concreteness for others and that word class interacts with the factor task as well as with the factor concreteness in specific regions.

The presentation of the data will be structured as follows: in the Results section we present the activation of the different conditions and the statistical analyses for each region of interest (ROI) separately. In the Discussion, however, we present the particular activation pattern as a function of a particular task and/or item type. The analysis for each ROI includes the factors task (semantic/syntactic), concreteness (abstract/concrete) and word class (function word/content word). The different regions in which significant activation was found in at least one of the conditions are (i) left inferior frontal regions: the inferior tip of the left fronto-opercular cortex (BA 44), the cortex at the junction of the inferior frontal and the precentral sulcus (BA 44/6), and the pars triangularis (BA 45); (ii) left temporo-parietal regions: the posterior part of the middle temporal gyrus (BA 21/37), the superior temporal gyrus (BA 22) and the parietal operculum (BA 43); (iii) additional left cortical regions; (iv) right cortical regions; and (v) subcortical regions.

	Coordinates				Abstract content		Concrete content
	X	Y	Ζ	words	words	words	words
L frontal operculum (BA 44)	-45	12	6	_	3.21	_	_
L cortex lining inferior precentral/inferior frontal sulcus (BA 44/6)	-54	2	25	4.29	4.47	4.68	3.20
L inferior frontal gyrus, pars triangularis (BA 45)	-46	21	25	-	6.16	-	-
L superior temporal gyrus, posterior portion (BA 22)	-56	-48	19	6.53	-	3.56	-
L middle temporal gyrus, posterior portion (BA 21/37)	-52	59	14	8.42	6.92	8.30	6.34
L parietal operculum (BA 43)	-50	-23	24	6.79	6.29	5.36	5.52
L cortex lining postcentral sulcus (BA 40/2)	-52	-14	38	3.46	3.17	-	-
L cortex lining intraparietal sulcus	-50	-24	47	7.30	5.98	6.92	5.98
L thalamus	-10	-19	14	4.86	5.90	4.99	5.62
R thalamus	4	-18	15	5.46	6.50	4.73	4.78
R inferior frontal gyrus	38	23	23	5.20	4.37	5.72	4.91
Posterior precuneus	1	-65	16	8.32	9.36	7.10	7.96

Table 3

Significantly activated brain regions (Z-scores) for the syntactic task per word condition

	Coordinates			Abstract function		Concrete function	
	X	Y	Ζ		words	words	words
L frontal operculum (BA 44)	-45	12	6	3.48	6.03	3.51	_
L cortex lining inferior precentral/inferior frontal sulcus (BA 44/6)	54	2	25	-	5.12	4.26	-
L parietal operculum (BA 43)	-50	-23	24	6.11	6.21	5.88	5.20
L cortex lining postcentral sulcus (BA 40/2)	-52	-14	38	3.56	-	4.68	4.97
L thalamus	-10	-19	14	6.21	4.76	5.12	3.77
R thalamus	4	-18	15	5.85	4.60	4.58	3.38
R medial temporal gyrus	49	-57	14	5.01	3.20	4.89	4.29
Posterior precuneus	1	-65	16	3.34	-	-	-

Table 4

Mean Z-scores (\pm SEM) of regions of interest for the semantic task per word condition

	Coordinates			Abstract function		Concrete function	
	X	Y	Ζ	words	words	words	words
L frontal operculum (BA 44)	-45	12	6	0.81 (0.55)	1.18 (0.78)	1.04 (0.65)	0.71 (0.43)
L cortex lining inferior precentral/inferior frontal sulcus (BA 44/6)	-54	2	25	1.65 (0.77)	1.72 (0.96)	1.80 (0.32)	1.23 (0.89)
L inferior frontal gyrus, pars triangularis (BA 45)	-46	21	25	1.09 (0.39)	2.37 (0.60)	0.65 (0.32)	0.93 (0.49)
L superior temporal gyrus, posterior portion (BA 22)	-56	-48	19	2.51 (0.53)	1.06 (0.38)	1.37 (0.45)	1.09 (0.53)
L middle temporal gyrus, posterior portion (BA 21/37)	-52	-59	14	3.24 (0.79)	2.66 (0.59)	3.19 (0.63)	2.44 (0.70)
L parietal operculum (BA 43)	-50	-23	24	2.61 (0.78)	2.42 (0.66)	2.06 (0.80)	2.08 (0.62)
L cortex lining postcentral sulcus (BA 40/2)	-52	-14	38	1.33 (0.67)	1.22 (0.71)	0.87 (0.85)	0.91 (0.66)
L cortex lining intraparietal sulcus	-50	-24	47	2.81 (0.57)	2.30 (0.61)	2.66 (0.62)	2.30 (0.61)
L thalamus	-10	-19	14	1.87 (0.66)	2.27 (0.68)	1.92 (0.82)	2.16 (0.66)
R thalamus	4	-18	15	2.10 (0.52)	2.50 (0.52)	1.82 (0.70)	1.84 (0.51)
R inferior frontal gyrus	38	23	23	2.00 (0.45)	1.68 (0.54)	2.20 (0.30)	1.89 (0.47)
R medial temporal gyrus	49	-57	14	0.24 (0.74)	0.58 (0.83)	0.78 (0.76)	1.03 (0.63)
Posterior precuneus	1	-65	16	3.42 (2.27)	3.60 (1.77)	2.73 (1.97)	3.06 (2.78)

Table 5

Mean Z-scores (\pm SEM) of regions of interest for the syntactic task per word condition

	Coordinates			Abstract function			
	X	Y	Ζ	words	words	words	words
L frontal operculum (BA 44)	-45	12	6	1.34 (0.78)	2.32 (0.71)	1.35 (0.23)	0.74 (0.50)
L cortex lining inferior precentral/inferior frontal sulcus (BA 44/6)	-54	2	25	1.14 (0.47)	1.97 (0.53)	1.64 (0.49)	0.98 (0.56)
L inferior frontal gyrus, pars triangularis (BA 45)	-46	21	25	0.34 (0.31)	0.30 (0.61)	0.04 (0.31)	0.51 (0.48)
L superior temporal gyrus, posterior portion (BA 22)	-56	-48	19	-0.06 (0.31)	0.25 (0.35)	0.14 (0.32)	-0.06 (0.32)
L middle temporal gyrus, posterior portion (BA 21/37)	-52	-59	14	0.84 (0.38)	0.52 (0.48)	0.83 (0.46)	0.39 (0.41)
L parietal operculum (BA 43)	-50	-23	24	2.35 (0.68)	2.39 (0.52)	2.26 (0.65)	2.00 (0.41)
L cortex lining postcentral sulcus (BA 40/2)	-52	-14	38	1.37 (0.48)	1.01 (0.47)	1.80 (0.44)	1.92 (0.48)
L cortex lining intraparietal sulcus	-50	-24	47	0.57 (0.40)	0.40 (0.40)	0.62 (0.44)	0.34 (0.37)
L thalamus	-10	-19	14	2.39 (0.45)	1.83 (0.30)	1.97 (0.41)	1.45 (0.24)
R thalamus	4	-18	15	2.25 (0.30)	1.77 (0.35)	1.76 (0.46)	1.30 (0.24)
R inferior frontal gyrus	38	23	23	0.59 (0.44)	0.51 (0.35)	0.81 (0.34)	0.08 (0.36)
R medial temporal gyrus	49	-57	14	1.93 (0.33)	1.23 (0.36)	1.88 (0.31)	1.65 (0.24)
Posterior precuneus	1	-65	16	0.80 (0.45)	0.80 (0.45)	0.96 (0.58)	0.36 (0.51)

Left Inferior Frontal Regions

Activations in regions in the inferior frontal cortex did not vary as a function of word class as such (no main effect of word class); however, there were clear word class × concreteness interactions in frontolateral cortex. For the inferior tip of the fronto-opercular cortex (BA 44) a significant word class × concreteness interaction [F(1,11) = 5.78, P < 0.05] was found, which was due mainly to differences in the syntactic task in which activation was largest for abstract content words. The word class × concreteness interaction was significant for the syntactic task [F(1,6) = 6.26, P < 0.05] but not for the semantic task. The cortex at the junction between the inferior frontal and the inferior precentral sulcus (BA 44/6) also showed a significant word class × concreteness interaction [F(1,11) = 11.4, P < 0.01]. This interaction was due to less activation for the prototypical members of a word class (i.e. abstract function words and concrete content words) compared with the non-prototypical members of a word class (i.e. concrete function words and abstract content words). Again, this effect was significant only for the syntactic task [F(1,6) = 10.52, P < 0.05]. Activation of the

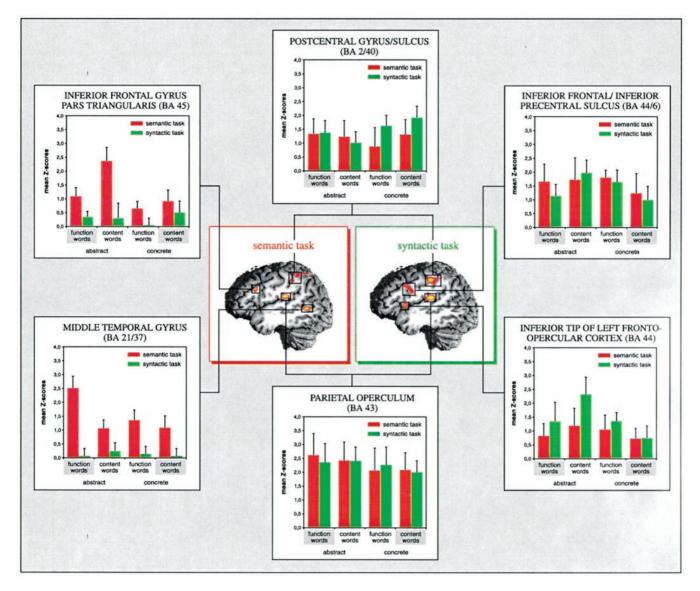


Figure 1. Activation clusters in the semantic task (red box) and the syntactic task (green box). Statistical maps are superimposed on an average structural MRI in Talairach space. Bright colors represent more significant activation. Activation strength is presented as mean Z-scores for different brain areas. Activations for the semantic task are color-coded in red, those for the syntactic task in green.

pars triangularis (BA 45) varied as a function of task [F(1,11) = 4.95, P < 0.05] and concreteness [F(1,11) = 5.8, P < 0.05], and of a concreteness × task interaction [F(1,11) = 4.7, P < 0.053]. Separate analyses for the two tasks indicate no effects for the syntactic task but a marginal significant main effect of concreteness for the semantic task [F(1,5) = 5.44, P < 0.067], indicating larger activation for abstract than for concrete words.

Left Temporo-parietal Regions

The posterior portion of the middle temporal gyrus (BA 21/37) showed a significant main effect of task [F(1,11) = 11.65, P < 0.01], with larger activation for the semantic compared with the syntactic task. The activation of the posterior portion of the superior temporal gyrus (BA 22) varied as a function of task [F(1,11) = 10.25, P < 0.01], with an increase for the semantic task compared with the syntactic task. The three-way interaction task × word class × concreteness was also significant [F(1,11) = 7.53, P < 0.05]. This effect was due mainly to the elevated activation for abstract function words in the semantic task, as confirmed by

a significant main effect of word class [F(1,5) = 7.35, P < 0.05]and a concreteness × word class interaction [F(1,5) = 6.85, P < 0.05] in the semantic task but no significant effects in the syntactic task. In addition, the parietal operculum (BA 43) was found to be active in all conditions, showing no systematic differences between them.

Additional Left Cortical Regions

The cortex lining the left intraparietal sulcus was activated significantly more in the syntactic task than in the semantic task condition [F(1,11) = 9.62, P < 0.01]. Significant activation was observed for the cortex lining the left postcentral sulcus (BA 40/2). The main effect of word class [F(1,11) = 15.19, P < 0.01], the word class × task [F(1,11) = 12.85, P < 0.01] and the word class × concreteness interactions [F(1,11) = 5.73, P < 0.05] were all significant. Separate analyses for the two tasks revealed significant effects for the syntactic task only: a main effect of word class × concreteness interaction [F(1,6) = 23.83, P < 0.01] and a word class × concreteness interaction [F(1,6) = 7.42, P < 0.05]. This inter-

action reflects higher activation for the non-prototypical word class conditions compared with their prototypical counterparts.

Right Cortical Regions

Right hemispheric activations were found in the middle temporal gyrus, in the inferior frontal gyrus and in the right posterior precuneus in the vicinity of the parieto-occipital fissure. For the middle temporal gyrus no significant effect was found. The activation in the right inferior frontal gyrus revealed a significant main effect of task [F(1,11) = 9.23, P < 0.05], with greater activation for the semantic than for the syntactic task. There was also a significant main effect of task in the right precuneus, reflecting more activation in the semantic than in the syntactic task [F(1,11) = 6.97, P < 0.05].

Subcortical Regions

Significant activation was found for the left and the right thalamus. The left thalamus showed a word class × task interaction [F(1,11) = 7.51, P < 0.05]. Separate analyses, however, revealed no significant effects. The activation in the right thalamus varied as a function of concreteness [F(1,11) = 14.18, P < 0.01], with an increase for the abstract compared with the concrete words. Moreover, there was a significant word class × task interaction [F(1,11) = 5.44, P < 0.05]. Separate analyses for the two tasks revealed main effects of concreteness [F(1,6) = 13.77, P < 0.01] and word class [F(1,6) = 5.36, P < 0.06] for the syntactic task only.

Discussion

The present data on the processing of open and closed class words suggest a systematic interaction between word class, concreteness and linguistic task. There are a number of activations in the underlying neuronal network which are present in all eight subconditions. These are the activations in the left parietal operculum (BA 43), the postcentral sulcus (BA 40/2) and both thalami (except for content words in the syntactic condition). The additional activations in the left superior and middle temporal gyrus (BA 21/22/37) appear to be modulated to a large extent by the demands in the semantic task, whereas the cortex lining the junction of the inferior frontal and the inferior precentral sulcus (BA 44/6) and the left fronto-opercular cortex (BA 44) were modulated by the demands in the syntactic task.

Semantic Aspects of Processing

A specific increase of activation for the semantic judgement task was observed in the posterior part of the left superior and middle temporal gyrus (BA 21/22/37) and in the left pars triangularis (BA 45). Moreover, an increase of activation for the semantic task was found for the left intraparietal sulcus and the right inferior frontal gyrus, as well as the right posterior precuneus.

The present data suggest that earlier reports of activation in the left inferior frontal gyrus and in the superior and middle temporal gyrus reported for the processing of concrete content words may be a function of the nature of the semantic task rather than of the item's word class or concreteness. This conclusion is in line with the view that involvement of the left inferior frontal cortex in semantic processes is dependent on whether semantic processing (induced by the task) is strategic or not (Fiez *et al.*, 1995; Thompson-Schill *et al.*, 1997).

The selective activation in the right inferior frontal cortex in the semantic task is compatible with earlier findings. Activation in this brain area was reported for semantic memory processes (Rugg *et al.*, 1996) [for an overview see (Nyberg *et al.*, 1996)]. The increased activation in the inferior frontal and the temporal cortices during the processing of semantic aspects of language is in general agreement with findings from a number of earlier imaging studies [for an overview see (Gabrieli *et al.*, 1998); for further discussion see below].

Syntactic Aspects of Processing

Activation specific for the syntactic judgement task was found in the inferior tip of the left fronto-opercular cortex (BA 44) and the cortex lining the junction of the inferior frontal and the inferior precentral sulcus (BA 44/6). This activation pattern is due to an interaction of word class and concreteness, reflecting that nonprototypical word class members, i.e. abstract content words (open class) and concrete function words (closed class), showed an increased activation compared with prototypical members of the respective word class, i.e. abstract function words and concrete content words.

Concerning the functional specification of BA 44 in language processing, the present data seem to indicate that the inferior tip of this area supports syntactic processes such as word category classification independent of a word's class membership. Nobre and colleagues (Nobre et al., 1997) argued, based on data from a semantic task, that the involvement of BA 44 in processing abstract function words may be due to the fact that these elements do not carry semantic information and are thus more reliant on phonological processes. On the basis of a literature review it has recently been proposed that Broca's area (BA 44) may be functionally separated into a superior and an inferior part, with the superior part involved in phonological processing and the inferior part involved in syntactic processing (Friederici, 1999). This proposal receives tentative support from the present finding that an increase of activation in the inferior tip of BA 44 was found for non-prototypical members of their category when a judgement about their syntactic word category was required. The view that a subpart of BA 44 is involved in syntactic processes is also compatible with recent imaging studies on syntactic aspects of processing during sentence comprehension. It has been shown that during sentence reading activation in BA 44 varies as a function of syntactic complexity (Stromswold et al., 1996; Just et al., 1996).

The finding that activation in BA 44, although larger for both types of function words than for concrete content words, was largest for abstract content words deserves some discussion. Under the hypothesis that the inferior tip of BA 44 subserves syntactic processes, one would have expected function words to evoke the largest activation in this area. Although this pattern was only partially observed, the following arguments may be brought forward in support of this hypothesis. As the particular increase for abstract content words was only present in the syntactic task, it can be attributed to syntactic aspects of processing. It appears that the syntactic classification of an abstract noun as a non-prototypical member of its class requires more neuronal resources than a prototypical member. This interpretation in terms of a prototypicality effect gains some support from a study by Raichle and colleagues (Raichle et al., 1994) that demonstrated that the activation of a particular brain area decreased as the familiarity of items increased.

This notion of familiarity or prototypicality can be applied to the present data and to the related data in the literature. Assume that a portion of BA 44 is indeed the area that subserves syntactic processes. This area has been shown to support structuring processes involved in syntactically complex sentences (Just et al., 1996; Stromswold et al., 1996). As syntactic structure building is necessarily based on word category information, this brain area may also be involved in syntactic word category judgements. For both functions it appears that more difficult processes lead to an increase in activation, be it the processing of complex sentences in the sentence reading studies (Just et al., 1996; Stromswold et al., 1996) or the processing of nonprototypical word class members (present study). Moreover, differential activation for typical and non-typical syntactic input was observed in a recent study by Friederici et al. (Friederici et al., 2000) in that more activation was found in the deep frontal operculum near Broca's area for so-called jabberwocky sentences (which are syntactically correct but in which content words are replaced by pseudowords) as compared with normal sentences (which are syntactically correct and contain real content words). Thus it appears that activation decreases when the processes under investigation deal with more familiar or prototypical input, because these processing procedures may require less neural resources.

This latter interpretation receives further support from a recent study by Petersen and colleagues (Petersen *et al.*, 1998), who found a change in the relative activation of different brain areas in a given neural network as a function of practice.

The present findings are in general agreement with a recent hypothesis on the functional domain-specificity of the left prefrontal cortex. Gabrieli and colleagues (Gabrieli *et al.*, 1998) proposed that BA 45 and BA 47 support semantic processes (Petersen *et al.*, 1989; Kapur *et al.*, 1994), and that phonological processes 'occur more posteriorly, near Broca's area, in left inferior frontal cortex' (Démonet *et al.*, 1992; Zatorre *et al.*, 1992; Fiez *et al.*, 1995; Gabrieli *et al.*, 1998). The present data further specify this claim as they suggest that the inferior tip of BA 44 (rather than its superior portion) subserves syntactic aspects of language processing in particular. Given that attention allocation can enhance activation of the specific areas engaged either in semantic or syntactic aspects of processing, it appears that attentional processing induces activations in a domain specific fashion.

Notes

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