

The Neural Correlates of Grammatical Gender: An fMRI Investigation

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Abstract

■ In an fMRI experiment, subjects saw a written noun and made three distinct decisions in separate sessions: Is its grammatical gender masculine or feminine (grammatical feature task)? Is it an animal or an artifact (semantic task)? Does it contain a /tch/ or a /k/ sound (phonological task)? Relative to the other experimental conditions, the grammatical feature task activated areas of the left middle and inferior frontal gyrus and of the left middle and inferior temporal gyrus. These activations fit in well with neuropsychological studies that document the correlation between left frontal lesions and

damage to morphological processes in agrammatism, and the correlation between left temporal lesions and failure to access lexical representations in anomia. Taken together, these data suggest that grammatical gender is processed in a left fronto-temporal network. In addition, the observation that the grammatical feature task and the phonology task activated neighboring but distinct regions of the left frontal lobe provides a plausible neuroanatomical basis for the systematic occurrence of phonological errors in aphasic subjects with morphological deficits. ■

INTRODUCTION

To know a word is to know three types of things: its meaning, its form, and its grammatical properties. How are these three types of information represented in the brain? More specifically, what relationship is there between a word's grammatical properties and its form and meaning? Here we present evidence that the grammatical properties of a word activate a neural circuit that is partially independent of the networks activated by that word's form and meaning.

Neuropsychological studies have shown that meaning and form are functionally dissociable, and that they are represented in distinct brain structures. Evidence to this effect comes from complementary patterns of performance in brain-damaged subjects, demonstrating the double dissociation of meaning and form. Thus, there have been reports of selective damage to meaning in the presence of spared lexical form in subjects with focal brain damage (e.g., Hillis, Rapp, Romani, & Caramazza, 1990) and in subjects with "semantic dementia" who suffer from a degenerative disease of the temporal lobes (e.g., Patterson & Hodges, 1992). The reverse dissociation has been documented in cases of selective damage in accessing lexical form in the face of spared meaning,

as a consequence of focal lesions of the left hemisphere (e.g., Caramazza & Hillis, 1990; Kay & Ellis, 1987). The dissociation of meaning and form is also supported by neuroimaging investigations. PET and fMRI studies have found that semantic processing involves activation of a neural network distributed over several lobes of the left hemisphere or both hemispheres (e.g., Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996). Other reports have found that phonological processing activates a more restricted network, including the posterior portions of the left superior and middle temporal gyri and the left inferior frontal gyrus (e.g., Xu et al., 2001; Hagoort et al., 1999; Fiez, 1997).

Neuropsychological observations have also provided evidence on the functional and neural organization of the grammatical properties of words. For example, there are many reports of aphasic patients with selective difficulties in processing either verbs or nouns (e.g., Berndt, Haendiges, Burton, & Mitchum, 2002; Tranel, Adolphs, Damasio, & Damasio, 2001; Bak, O'Donovan, Xuereb, Boniface, & Hodges, 2001; Cappa et al., 1998; Hillis & Caramazza, 1995; Daniele, Giustolisi, Silveri, Colosimo, & Gainotti, 1994; Caramazza & Hillis, 1991; Zingesser & Berndt, 1988; Miceli, Silveri, Villa, & Caramazza, 1984). These reports link the processing of nouns and verbs to distinct neural substrates—poor performance with verbs is frequently associated with damage to the left middle frontal gyrus, poor performance with nouns is most frequently linked to lesions of the temporal (and parietal) structures of the left hemisphere. The existence

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of separate neural networks in the processing of nouns and verbs is also supported by neuroimaging studies (e.g., Perani et al., 1999; Warburton et al., 1996; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Petersen, Fox, Posner, Mintun, & Raichle, 1988) and by electrophysiological investigations (Federmeier, Segal, Lombrozo, & Kutas, 2000; Dehaene, 1995). However, the interpretation of the noun/verb dissociation as a specifically grammatical effect remains controversial. This is because grammatical categories correlate with semantic properties (e.g., nouns typically denote objects, whereas verbs typically denote actions; nouns are usually more concrete, verbs usually more abstract, etc.). It is not implausible, therefore, to suppose that the observed dissociations reflect the organization of the semantic system rather than grammatical properties of words (e.g., Bird, Howard, & Franklin, 2000; Breedin, Saffran, & Schwartz, 1998; but see Berndt et al., 2002; Caramazza & Shapiro, in press, for arguments and evidence that challenge the strong version of this hypothesis).

One way to study the neural representation of the grammatical properties of words is to focus on a lexical feature that is independent from meaning. The grammatical feature gender meets this requirement in many languages (Corbett, 1991). This property of nouns plays an important role in determining agreement among words in noun phrases, in the selection of pronominal forms, and even in subject–verb agreement (e.g., specifying agreement between the subject of a sentence and the past-participle form of the verb in Italian). For example, in Italian, all the words in a noun phrase—determiners, adjectives, and nouns—must agree in number and gender.¹ Consider the case of the phrases (masc = masculine; fem = feminine; sg = singular; pl = plural): “*il*_{masc sg} *piccolo*_{masc sg} *ponte*_{masc sg}” (the small bridge), “*i*_{masc pl} *piccoli*_{masc pl} *ponti*_{masc pl}” (the small bridges), “*la*_{fem sg} *piccola*_{fem sg} *nave*_{fem sg}” (the small ship), and “*le*_{fem pl} *piccole*_{fem pl} *navi*_{fem pl}” (the small ships). As may be seen, the definite determiner takes different forms depending on the gender and the number of the noun—*il* and *i* for masculine singular and plural nouns, respectively, and *la* and *le* for feminine singular and plural nouns, respectively. Similarly, the adjective “small” is inflected appropriately for number and gender: *-o* or *-i* for masculine singular and plural, respectively, and *-a* and *-e* for feminine singular and plural, respectively. As another example, consider the case of clitics. In Italian, the sentence “give it to me” is produced with cliticized forms in which both the dative pronoun (“to me”) and the direct object pronoun “it” are cliticized onto the verb. However, the specific form of the clitic for the direct object depends on the grammatical gender and number of the noun for which the pronoun stands. If the noun is singular masculine the clitic would be *-lo*, as in *dammelo* (literally, give-me-it) and it would be, respectively, *-li*, *-la*, and *-le* for masculine plural, feminine singular, and feminine plural nouns.

As these examples illustrate, the retrieval of a noun’s grammatical gender is an essential part of the sentence production process.

Crucially for our purposes, a noun’s semantic content and grammatical gender have only an arbitrary relationship. This can be readily appreciated by considering the fact that closely related semantic coordinates have different grammatical genders. For example, the Italian translation of the first member of each of the following pairs of words is masculine while the second is feminine: lemon/orange, grapefruit/apple, table/chair, sheet/blanket, plate/cup, glass/bottle, spoon/fork, train/car, elephant/giraffe, lion/tiger, sun/moon, and so on. Furthermore, the grammatical gender of a word is language specific. While the Italian and French translations of pencil, desk, carriage, summer, and flag are feminine and masculine, respectively; the opposite is true for sea, table, limit, river and, tomato. If grammatical genders were determined by a noun’s semantic properties, we would expect semantically related words to have the same gender, and that words would have the same gender across languages. Neither condition holds. Thus, the results of investigations of the neural mechanisms involved in processing grammatical gender can be interpreted to reflect grammatical as opposed to semantic aspects of language processing.

Although grammatical gender and meaning are related only arbitrarily, the same is not true for the relation between gender and form. In many languages, including Italian, Russian, and Hebrew, for example, words of the same grammatical gender tend to share specific phonological properties. In the case of Italian, a majority of masculine singular nouns end in the vowel /o/ (plural /i/) and a majority of feminine singular nouns end in the vowel /a/ (plural /e/). However, the correlation is far from perfect. Thus, among the 3000 most frequent words in Italian, only 66% of nouns have a “regular ending” (De Mauro, Mancini, Vedovelli, & Voghera, 1993). The nonregular nouns consist either of words ending in /e/ (and a few in /i/), which are associated equally frequently with masculine and feminine nouns, or masculine nouns that end in /a/ and feminine nouns that end in /o/. Thus, although it has been shown that subjects are sensitive to the correlation between gender and word ending in word recognition tasks (e.g., Bates, Devescovi, Pizzamiglio, D’Amico, & Hernandez, 1995), a definitive decision about a word’s grammatical gender can only be taken after lexical access has occurred.

The independence of grammatical gender from meaning and the fact that lexical access is necessary in order to determine the gender of a noun has made this grammatical feature an appropriate tool for investigating the process of lexical access in normal language production (see Caramazza, Miozzo, Costa, Schiller, & Alario, in press; Schriefers, 1993). These same properties of grammatical gender make it suitable for the study of the representation of grammatical word properties in the

brain. As already noted, the crucial aspect of this grammatical feature is that it is independent of meaning and therefore any effect of grammatical gender cannot be ascribed to the organization of conceptual knowledge in the brain.

It is possible to formulate plausible expectations about the areas of the left hemisphere that are likely to be involved in processing grammatical gender. Since grammatical gender is a property of nouns and since there is considerable evidence that damage to the left temporal lobe results in the impairment of lexical access of nouns, we might expect the temporal lobe to be implicated in processing grammatical gender. Another area that is likely to be involved in processing grammatical gender is the left inferior frontal lobe. It is well established that lesions in this area result in difficulties in morphological processing in sentence production (agrammatism; Goodglass, 1976; Tissot, Mounin, & Lhermitte, 1973). Since morphological processing is controlled by information about grammatical category and the various grammatical features associated with nouns and verbs, we would expect the left frontal cortex to play a crucial role in processing this type of information. In short, the expectation is that the processing of grammatical features of nouns will implicate a left fronto-temporal network (Shapiro & Caramazza, submitted).

In the neuroimaging investigation reported here, we asked normal subjects to process isolated nouns in contexts that accentuated distinct properties of each noun—meaning, form, or grammatical gender. The patterns of activation observed in the three experimental tasks were compared to those observed in a baseline task, during which subjects were asked to silently read pseudowords while alternately pressing response buttons. The pseudowords were matched to words in length and consonant–vowel structure. Performance on each experimental condition was also compared to performance on the other two experimental conditions. We were interested in seeing how the processing of a specific lexical property influenced the activation of different neural structures during fMRI scanning, and we specifically focused on grammatical gender. Based on available neuropsychological and neuroimaging observations, we expected relatively distributed (possibly bilateral) activation in response to semantic features and left frontal activation in response to segmental phonological properties of lexical representations. More importantly, we expected activation of a fronto-temporal network in processing grammatical gender.

RESULTS

Behavioral Results

The experimental stimuli were administered to eight volunteers, in the context of a reaction time task. For each condition (semantic, syntactic, and phonological),

Table 1. Behavioral Results: Average Reaction Times (msec) and Response Accuracy (Correct Responses) and Standard Deviations in the Three Experimental Conditions

	<i>Reaction Time (Average – SD)</i>	<i>Response Accuracy (Average – SD)</i>
Semantic condition	682.6 ± 38.1	36.2 ± 2.0
Syntactic condition	669.0 ± 64.6	37.0 ± 2.5
Phonological condition	709.8 ± 62.4	36.6 ± 2.8

subjects were asked to press a button as soon as they had made their decision. Reaction time and response accuracy were comparable across conditions (Table 1). The average reaction time was 669 ± 64.6 msec for the grammatical gender condition, 709.8 ± 62.4 msec for the phonological condition, and 682.6 ± 38.1 msec for the semantic condition, $F(2,14) = 1.89, p = .188$. On average, control subjects produced 36.2 ± 2 correct responses for the semantic condition, 36.6 ± 2.8 for the phonological condition, and 37 ± 2.4 for the grammatical condition, $F(2,14) = .59, p = .569$.

Activation Results

Experimental Conditions Versus Baseline

When compared to silent reading of pseudowords while alternately pressing buttons placed in the left and in the right hand, all experimental conditions yielded significant activations ($p < .001$) at the highest threshold level (voxel correction $< .01$; cluster correction $< .001$) (Table 2). In the grammatical gender condition, there was significant activation in the left frontal lobe, involving BA 9 and BA 45. The left BA 7 was also activated. The phonological task resulted in significant activation of the left inferior frontal gyrus, involving the frontal operculum (BA 44) and extending inferiorly to BA 47 and posteriorly to the precentral gyrus (BA 6). There was also bilateral activation of the superior parietal lobule (BA 7), extending into the uppermost portion of BA 40 in the left hemisphere. The semantic task activated bilaterally the frontal and parietal structures and the cerebellum. Frontal activation involved the middle and inferior frontal gyri on the left (BA 9, BA 9/46, and BA 47), and the middle frontal gyrus on the right (BA 45/46, BA 9, and BA 6/8); symmetrical activation was observed in the superior parietal lobule (BA 7).

Thus, all experimental conditions resulted in significant activation of the frontal lobe. Activation was bilateral in the semantic condition and was restricted to the left hemisphere in both the gender and the phonology conditions. Gender processing activated the more inferior portions of the inferior frontal gyrus to a lesser extent than did the phonological processing task.

Significant activation of the superior parietal lobule (BA 7) was observed in all experimental conditions when

Table 2. Stereotactic Coordinates (Talairach & Tournoux, 1988) of the Foci of Activation for the Comparisons Between Each Experimental Condition and the Baseline Task ($p < .001$)

		x, y, z	Z
<i>Gender > pseudowords (voxel correction <.01; cluster correction <.001)</i>			
L inferior frontal gyrus	BA 9	-40, 16, 26	4.54
L inferior frontal gyrus	BA 9	-48, 26, 26	4.11
L inferior frontal gyrus	BA 45	-44, 24, 18	4.03
L superior parietal lobule	BA 7	-30, -56, 48	4.71
L superior parietal lobule	BA 7	-20, -54, 48	4.07
L inferior parietal lobule	BA 7	-38, -42, 36	3.58
<i>Phonology > pseudowords (voxel correction <.01; cluster correction <.001)</i>			
L inferior frontal gyrus	BA 44	-44, 10, 22	4.32
L inferior frontal gyrus	BA 47	-34, 26, -8	3.60
L prefrontal gyrus	BA 6	-34, 2, 28	4.24
L superior parietal lobule	BA 7	-32, -56, 50	4.01
L superior parietal lobule	BA 7	-32, -52, 42	3.57
L supramarginal gyrus	BA 40	-44, -40, 40	3.69
R superior parietal lobule	BA 7	24, -50, 44	4.00
R superior parietal lobule	BA 7	30, -66, 52	3.12
R inferior parietal lobule	BA 7	32, -60, 46	3.54
<i>Semantics > pseudowords (voxel correction <.01; cluster correction <.001)</i>			
L middle frontal gyrus	BA 9	-44, -32, 66	4.77
L middle frontal gyrus	BA 9/46	-36, 26, 26	4.38
L inferior frontal gyrus	BA 47	-34, 26, -10	4.28
L superior/inferior parietal lobule	BA 7	-22, -62, 36	3.92
L superior parietal lobule	BA 7	-30, -56, 50	3.62
L superior parietal lobule	BA 7	-32, -64, 52	3.56
R middle frontal gyrus	BA 45/46	38, 32, 12	4.71
R middle frontal gyrus	BA 9	44, 16, 32	3.68
R middle frontal gyrus	BA 6/8	40, 12, 38	3.62
R superior parietal lobule	BA 7	16, -52, 58	3.96
R precuneus	BA 7	12, -70, 50	3.34
L cerebellum		6, -66, -18	4.60
R cerebellum		-6, -54, -8	4.41

compared to the baseline task. This pattern of activation most likely results from the different demands of the experimental and baseline conditions in terms of both attention and memory. The control task required the silent reading of pseudowords and alternately pressing response buttons, with no need to maintain the stimuli active in working memory. The experimental tasks involved a binary decision to items presented in random

sequence, requiring the subject to attend carefully to each stimulus and to keep active a representation of the stimulus until a decision could be made. This interpretation is supported by neuroimaging studies showing increased activation in the inferior and superior parietal lobules in tasks involving selective and divided attention and working memory (for a review, see Cabeza & Nyberg, 2000). Since this activation appears to be

unrelated to the linguistic dimensions under scrutiny, it will not be discussed further.

Comparisons Between Experimental Conditions

The activation observed in each experimental condition was also compared with the activation observed in each

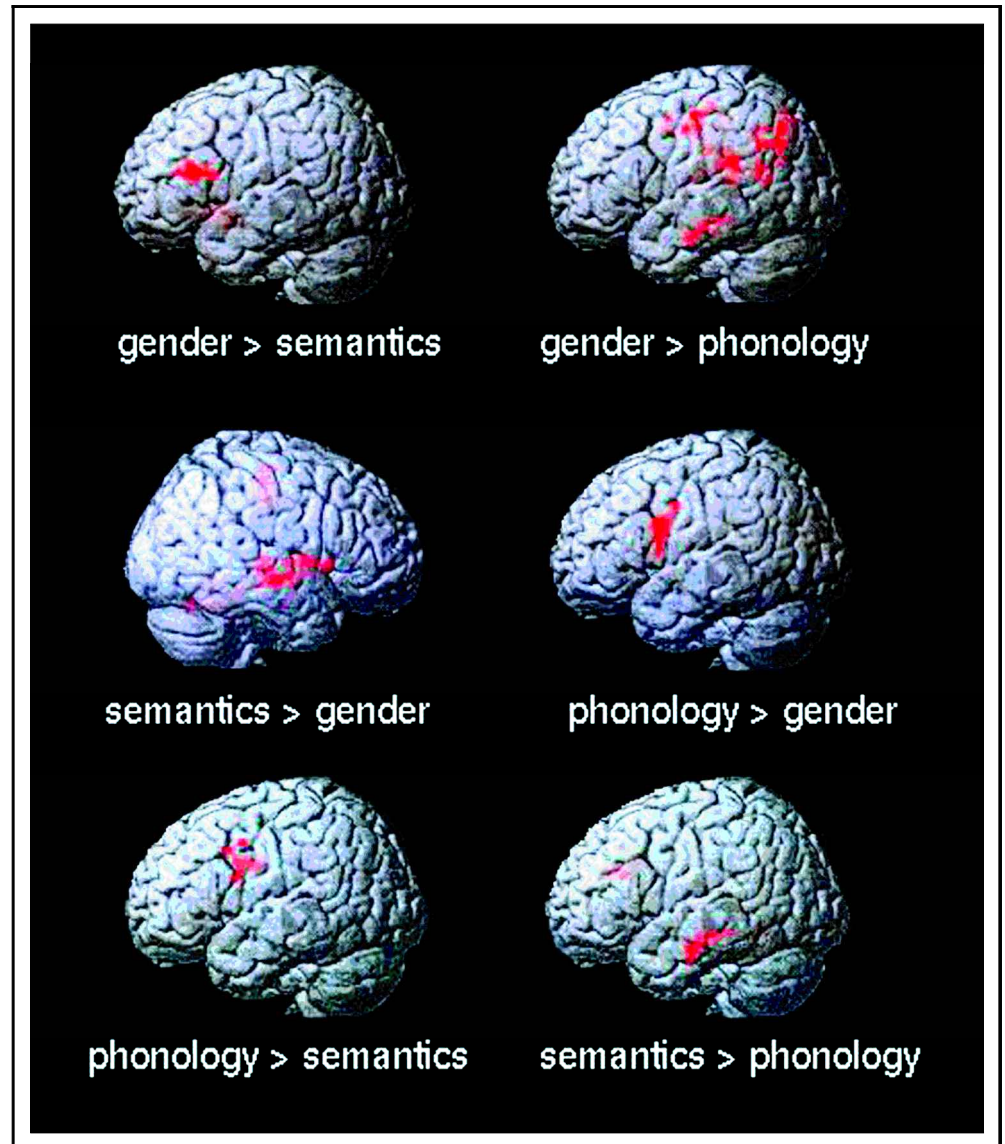
of the other two experimental conditions (Table 3 and Figure 1).

The gender-versus-semantics comparison yielded significant values at low thresholds (voxel correction <.05; cluster correction <.05). Significant left-sided activation was observed in the inferior frontal gyrus (BA 45) and in

Table 3. Stereotactic Coordinates (Talairach & Tournoux, 1988) of the Foci of Activation for the Comparison Between Pairs of Experimental Tasks ($p < .001$)

		<i>x, y, z</i>	<i>Z</i>
<i>Gender > phonology (voxel correction <.05; cluster correction <.001)</i>			
L inferior temporal gyrus	BA 21	-42, -10, -22	4.68
L middle temporal gyrus	BA 20/21	-52, -32, -12	3.97
L middle temporal gyrus	BA 21	-48, -22, -14	3.75
L inferior parietal lobule	BA 40	-52, -38, 24	3.80
L cingulate gyrus	BA 31	-6, -32, 42	3.58
<i>Phonology > gender (voxel correction <.05; cluster correction <.05)</i>			
L inferior frontal gyrus	BA 44	-44, 6, 26	3.09
<i>Gender > semantics (voxel correction <.05; cluster correction <.001)</i>			
L inferior frontal gyrus	BA 45	-52, 22, 16	3.37
Lenticular nucleus		-14, 6, -8	4.30
<i>Semantics > gender (voxel correction <.05; cluster correction <.001)</i>			
R Heschl's gyrus	BA 41	42, -20, 4	3.97
R cingulate gyrus	BA 31	16, -24, 40	3.60
R cerebellum		20, -66, -22	3.85
<i>Semantics > phonology (voxel correction <.01; cluster correction <.001)</i>			
R inferior frontal gyrus	BA 8	28, 10, 30	3.86
L middle/superior frontal gyrus	BA 9	-18, 34, 26	3.66
L inferior temporal gyrus	BA 20	-40, -10, -20	3.74
L inferior temporal gyrus	BA 20	-48, -26, -16	3.70
L fusiform gyrus	BA 20	-40, -12, -30	3.70
L cingular gyrus	BA 32	12, 14, 30	3.68
L cerebellum		-10, -54, -8	4.66
R cerebellum		10, -50, -18	3.90
R thalamus		10, -40, 10	4.03
R thalamus		8, -30, 12	3.82
<i>Phonology > semantics (voxel correction <.01; cluster correction <.001)</i>			
L middle frontal gyrus	BA 8	-50, 12, 38	3.60
L inferior frontal gyrus	BA 44/6	-42, 6, 32	3.19
L precentral gyrus	BA 6	-50, 2, 42	3.19

Figure 1. Lateral see-through of the activations observed when comparing pairs of experimental conditions.



the lenticular nucleus. The reverse comparison (semantics vs. gender) yielded significant activation at an intermediate threshold (voxel correction = .05; cluster correction = .001) in the right hemisphere structures that are outside of the typical language areas (Heschl's gyrus, cingulate gyrus, and the cerebellum).²

The gender-versus-phonology comparison yielded significant activations at an intermediate threshold (voxel correction <.05; cluster correction <.001), in the left inferior and middle temporal gyrus (BA 20/21 and BA 21). Patchy activation was observed also in a large region that includes the left supramarginal gyrus (BA 40) and the left posterior cingulate gyrus (BA 31). At a lower threshold (voxel correction <.05; cluster correction <.05), the phonology-versus-gender comparison yielded significant activation in the left inferior frontal gyrus (BA 44).

Comparisons between semantics and phonology yielded significant differences at high threshold (voxel correction <.01; cluster correction <.001). The semantics-versus-phonology comparison yielded significant left

hemisphere activation in the inferior temporal gyrus and in the fusiform gyrus (BA 20); small areas of activation were also observed in almost symmetrical structures of the left (BA 9) and right (BA 8) frontal lobe and in the left anterior paracingulate cortex (BA 32). Additional small activations of unclear significance involved the right thalamus and the cerebellum. The phonology-versus-semantics comparison yielded significant activation of the left middle (BA 8) and inferior (BA 44/6) frontal gyrus, extending posteriorly to the precentral gyrus (BA 6).

DISCUSSION

We had predicted that processing of grammatical gender would activate structures in the left frontal and temporal lobes. Both predictions were borne out. Deciding whether a noun is masculine or feminine resulted in the significant activation of (1) the left inferior frontal gyrus (BA 45) relative to the baseline condition and

to the semantic task, (2) the left middle frontal gyrus (BA 9) relative to the baseline, and (3) the left middle and inferior temporal gyrus (BA 20/21 and BA 21) relative to the phonological condition. In addition to the predicted areas, the gender decision task also resulted in the significant activation of the left parietal lobe (BA 40) and of the left posterior cingulate gyrus (BA 31), when compared to the phonological task.

Our reason for expecting left frontal activation is that grammatical gender is involved in the control of morphological processes, which are known to be impaired in agrammatism and that lesion analysis in agrammatic speakers has frequently demonstrated damage involving (but, often not limited to) the left frontal lobe (e.g., Vanier & Caplan, 1991; Miceli, Silveri, Romani, & Caramazza, 1989). Another reason to expect left frontal lobe activation is that recent neuroimaging studies have found activation of these structures during tasks requiring the ability to process sentences that violate morphological constraints (Moro et al., 2001; Ni et al., 2000).

Activation of the left inferior (BA 45) and middle (BA 9) frontal gyrus during the gender decision task is intriguing also in the light of recent studies that implicate these regions in processing grammatical category information. Results consistent with this possibility have been reported in studies of aphasics (Bak et al., 2001; Shapiro, Shelton, & Caramazza, 2000; Cappa et al., 1998; Daniele et al., 1994), in neurophysiological investigations (Shapiro, Pascual-Leone, Mottaghy, Gangitano, & Caramazza, 2002; Federmeier et al., 2000; Dehaene, 1995), and in neuroimaging studies (Friederici, Oppitz, & von Cramon, 2000).

The gender decision task resulted also in the significant activation of portions of the left middle and inferior temporal gyrus (BA 20/21 and BA 21), when compared to the phonological condition. Our reason for expecting activation in the left temporal lobe was based in part on reports of aphasic subjects with "pure anomia." These patients typically present with selective difficulty in accessing lexical information about nouns despite preserved ability to process the meaning of nouns. The lesion site most often associated with this pattern of performance is the left temporal lobe (Lambon Ralph, Sage, & Roberts, 2000; Miceli, Giustolisi, & Caramazza, 1991; Kay & Ellis, 1987; Gainotti, Silveri, Villa, & Miceli, 1986), suggesting that the left temporal lobe is a crucial component in accessing nouns. Since grammatical gender is a property of nouns, its retrieval presupposes access to the lexical node of the to-be-produced word. The findings of left temporal lobe activation in normal subjects engaged in performing a gender decision task and of left temporal damage in pure anomia provide evidence for the role of these left hemispheric structures in lexical access of nouns.

The remaining two foci of activation, in the left parietal lobe (BA 40) and in the left cingulate gyrus

(BA 31), cannot be related straightforwardly to the processing of grammatical gender, either as a property of lexical representations or as a feature involved in morphological processes. This is because deficits of lexical access or morphological processing are not associated with damage (exclusively) to these regions. A more likely basis for the observed foci of activation is the metalinguistic nature of the gender decision task. When debriefed after scanning, most participants reported solving the gender task by silently generating the determiner of the noun. For example, when deciding the gender of, say, "falce_{fem}" (sickle), they would silently say to themselves "la_{fem} falce_{fem}" This strategy may have resulted in the involvement of working memory, which has often been associated with left or bilateral activation of the supramarginal gyrus in PET and fMRI studies (e.g., Paulesu, Frith, & Frackowiack, 1993; for an exhaustive review, see Cabeza & Nyberg, 2000). The activation of BA 31 has been documented in other metalinguistic language tasks, such as fluency tasks (e.g., Frith, Friston, Liddle, & Frackowiack, 1991), and is also probably aspecific. Consistent with these possibilities, the activation of the left BA 40 and BA 31 was observed in the comparison between the grammatical gender task and the phonological task. In the gender task, the decision must be made on a feature (grammatical gender) that cannot be predicted by the written word; whereas the decision required by the phonological task can be reached on the basis of the segmental information provided in the written stimulus.

In short, the results of our neuroimaging experiment converge with evidence from neuropsychological, neurophysiological, and neuroimaging studies in suggesting that the grammatical features of nouns are represented in a network that includes frontal (BA 45 and BA 9) and temporal (BA 20/21 and BA 21) structures of the left hemisphere. The same results, in association with neuropsychological studies of agrammatism and with neuroimaging studies of sentence processing in cognitively unimpaired subjects confirm the critical role of the left frontal lobe in morphological processes (and in representing grammatical category information).

The close proximity of the areas activated by the phonological task and by the gender task is also worth stressing. BA 44 was activated by the phonological task more than the baseline condition, the gender task, and the semantic task, and BA 45 was activated more by the gender task than the baseline and the semantic tasks. This pattern of activation is intriguing in the light of the clinical observation that subjects who make morphological errors in single-word processing tasks almost invariably also make phonological errors in the same tasks (e.g., Miceli & Caramazza, 1988). The reasons for this seemingly systematic co-occurrence are unclear. The results reported here suggest that it might be due to the proximity (or even the partial overlap) of the neural

substrates involved in processing the morphophonological (e.g., the computation of the gender and number agreement inflections in adjectives) and phonological properties of words. In particular, our results are consistent with the hypothesis that the left inferior frontal gyrus participates in distinct but at least partially intertwined neural networks, involved in phonological and morphophonological processing. On this view, the adjacent but separate foci of activation observed in the present study would indicate a higher density of neural tissue representing phonological processing in BA 44, and higher density of neural tissue representing morphophonological processing in BA 45. The fact that contiguous brain regions are involved in processing the morphology and the phonological properties of a word does not necessarily lead to the conclusion that these two types of information are functionally inseparable. It is possible that morphophonological processes (i.e., those processes involved in specifying the phonological form of polymorphemic words) are inextricably intertwined with lexical phonological information, whereas morphosyntactic processes (i.e., those processes that manipulate inflectional morphology at the sentence level) may be clearly separable from phonological processes.

In conclusion, grammatical gender (and probably other properties of the lexical representations of nouns) appears to be represented in the left hemisphere, in a neural network that includes the inferior and middle frontal gyri and the inferior and middle temporal gyri. In addition, the results obtained for gender converge with other neuropsychological and neuroimaging investigations in showing that the left inferior and middle frontal gyri play a critical role in the representation of grammatical category information and in the processing of morphological information. The contiguity of the structures activated by the phonological and the grammatical gender condition indicates both functional overlap and functional specialization within the left inferior frontal gyrus.

METHODS

Subjects

Nine right-handed (based on the Edinburgh Handedness Inventory; Oldfield, 1971) participants, 6 men and 3 women, aged 23–29, native speakers of Italian, gave informed consent to participate in the study. All subjects had normal or corrected-to-normal vision. Exclusion criteria included a history of prolonged use of prescription or recreational drugs, a neurological or psychiatric condition, claustrophobia, and significant prior radiation exposure. Subjects were advised not to use alcohol within 24 hr and tobacco within 3 hr prior to the scan. The Ethics Committee of Fondazione Santa Lucia approved the experimental protocol. Subjects were paid for their participation in the study.

Materials

The experimental stimuli consisted of 40 concrete nouns and of 40 pseudowords. Word stimuli were counterbalanced for grammatical gender, semantic category, and phonological content. There were 20 masculine nouns (15 ending in *-o* and 5 ending in *-e*) and 20 feminine nouns (15 ending in *-a* and 5 ending in *-e*), 20 animal names and 20 artifact names, and 20 nouns containing a /tch/ sound (e.g., *uncino*, /un'tchino/, hook) and 20 nouns containing a /k/ sound (e.g., *capra*, /'kapra/, goat). The position of the target sound was balanced across stimuli. Regardless of the parameter over which nouns were counterbalanced (meaning, grammatical gender, phonology), the frequency of usage was comparable in the two 20-item subsets. The 40 nouns selected as experimental stimuli were used to construct six 20-word lists. Each list contained equal numbers of masculine and feminine nouns, of animal and artifact names, and of words containing the /tch/ or the /k/ phoneme ($n = 10$ each). Each word was included in three sublists. In one sublist, participants were asked to decide whether the word was of masculine or feminine gender, in another sublist, they were asked to decide whether the word was the name of an animal or of an artifact, and in the other sublist, they were asked to decide whether the word contained a /tch/ or a /k/ sound. In this last condition, the phonological contrast corresponds to a difference between the orthographic contexts for the letter ⟨c⟩ in the written string. In Italian, the letter ⟨c⟩ is pronounced as /k/ when followed by the vowel ⟨o⟩, ⟨a⟩, or ⟨u⟩ or by the sequence ⟨hi⟩ or ⟨he⟩ and it is pronounced /tch/ when followed by the vowel ⟨i⟩ or ⟨e⟩. The fact that the phonological task could be performed accurately simply by inspecting the written stimulus may have allowed subjects to base their responses in this condition on the segmental features of the stimulus, and not on the retrieval of the corresponding lexical form, as was necessary in the grammatical gender and in the semantic conditions. The putative effects of this difference across tasks are considered in the Discussion.

Pseudowords consisted of pronounceable letter strings. They were identical to the 40 experimental words in number of letters and syllables, and in consonant/vowel structure. For each pseudoword, the n count corresponded to 0 (in other words, changing one letter at a time did not result in a word). Pseudowords were divided in two lists that were alternately repeated during the experiment.

Procedure for the Behavioral Task

This task was administered to eight subjects (5 men, 3 women), comparable in age to those who participated in the fMRI experiment. A practice session was run to acquaint subjects with the experimental tasks. Each

subject was presented with the six sublists of words. For each sublist, subjects were given explicit information about the dimension they were going to be asked to evaluate (grammatical gender, semantic category, phonological content) and were instructed to press one of two computer keys, as soon as they decided whether the stimulus was of masculine or feminine gender, an animal or an artifact, or whether it contained a /tch/ or a /k/ sound. A fixation point appeared at the center of the computer monitor for 400 msec, followed by the stimulus, which remained on the screen for 1200 msec.

Procedure for the fMRI Task

The study consisted of three experimental tasks and a control task. All tasks involved the presentation of a written word, at the center of the subject's field of vision, with the same timing as in the behavioral task. The gender task required subjects to indicate whether the stimulus was masculine or feminine. The semantic task required participants to judge whether the stimulus word corresponded to an animal or an artifact. The phonological task required participants to decide whether the stimulus contained, when pronounced, a /tch/ or /k/ sound. Subjects responded by pressing buttons held in the right and left hand. The control task consisted of alternately pressing buttons while silently reading pseudowords. This task was clearly less demanding than the experimental tasks in terms of processing (attention and memory) resources. However, the stimuli were closely matched in visual complexity to the experimental noun lists and the task provides a good control for the motor component of the response in the experimental tasks. Prior to scanning, each participant was acquainted with the experimental tasks during a practice session, during which different sets of words from those included in the experimental conditions were presented.

The four experimental tasks were organized in a block design, administered in one scanning session lasting approximately 15 min. Each experimental condition was presented in alternation with the control task (c.t.)—A-c.t.—B-c.t.—C-c.t. During the scanning session, this block was repeated four times. The order of task presentation (A-c.t.—B-c.t.—C-c.t.) was fixed for each subject, but counterbalanced across subjects (e.g., C-c.t.—B-c.t.—A-c.t.). Each experimental block began with a slide showing instructions about the dimension of the judgment (gender, semantic category, phonology) to be performed in that block of trials and which key had to be pressed for each judgment (e.g., masculine gender: left key; feminine gender: right key).

The stimuli were projected via mirroring to a back projection screen using an LCD video projector (Model VPL-351QM, Sony, Tokyo) located inside the MRI room and connected to a Macintosh computer (G3/266, Apple Computer, Cupertino, CA) located outside the MRI

room. Images were obtained by using MATLAB 5.3 (MathWorks, Natick, MA) and the MATLAB stats toolbox running on UNIX workstations (O2, Silicon Graphics, Mountain View, CA).

fMRI Procedures and Data Analysis

A Siemens Vision Magnetom MR system (Siemens Medical Systems, Erlangen, Germany) operating at 1.5 T and equipped for echo-planar imaging was employed in order to acquire functional MR images. Head movement was minimized by mild restraint, and cushioning. Using an EPI gradient-echo sequence (TR = 3200 msec; TE = 40 msec), 240 functional images were collected for each data acquisition run. Thirty-four adjacent oblique-axial slices, starting from the superior convexity so as to cover the whole brain, were acquired in an interleaved sequence, with 3-mm slice thickness, an FOV = 192 × 192 mm, and a 64 × 64 matrix size, resulting in in-plane resolution of 3 × 3 × 3 mm.

Functional data were analyzed using the SPM99 (Wellcome Department of Cognitive Neurology, London, England). Prior to any statistical analysis, all volumes for each subject were realigned using the first volume as reference and resliced using sinc interpolation. In order to perform intersubject averaging, all images were transformed into a standard space (Talairach & Tournoux, 1988) matching to a template image. As a final preprocessing step, functional data were smoothed using a 6-mm FWHM isotropic Gaussian kernel to compensate for residual variability after spatial normalization and to permit application of Gaussian random field theory to provide for correct statistical inference (Friston et al., 1995). Tasks were modeled as boxcar functions and convolved with a synthetic hemodynamic response function. Head motion parameters were added as regressors (Friston et al., 1995; Worsley & Friston, 1995).

The contrast between each activation condition versus rest was examined first. Each experimental task was also directly compared with each of the other two. Random-effects analyses were performed on the group data. Foci of activation were characterized in terms of spatial extent (k) and peak height (u). The correct significance of each region was estimated in terms of the probability that a region of the observed number of voxels could have occurred by chance and that the observed peak height could have occurred by chance over the entire volume analyzed.

Different thresholds were retained for the various analyses. The t statistic images for each contrast were created first by retaining regions surviving a threshold of $p < .01$ at the voxel level, with a cluster-level correction corresponding to $p < .001$. In the absence of significant activations, images were created by retaining regions that survived a higher threshold ($p < .05$ at voxel level). In this case, the significance of each region was estimated in terms of spatial extent (cluster-level) applying a

threshold of $p < .001$ or $p < .05$. This strategy was preferred to the selection of a uniformly low significance level, so that, for each contrast, we could evaluate the regions showing the greatest activation.

Acknowledgments

This project was supported in part by grants from MURST and from Fondazione Santa Lucia to G. M. and by NIH Grant No. DC 04542 to A. C.

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The data reported in this experiment have been deposited in The fMRI Data Center (<http://www/fmridc.org>). The accession number is 2-2002-112NH.

Notes

1. In Italian, most adjectives occur postnominally: “il leone feroce” literally means “the lion ferocious.” For expository purposes, we have used an adjective that can be used prenominal as in English.
2. Failure to demonstrate significantly different activation of the language areas of the left hemisphere in this comparison may reflect the fact that, since access to grammatical gender presupposes lexical access, which in turn requires the retrieval of meaning, the gender and the meaning condition activated overlapping structures. Greater activation of right hemisphere structures in the semantic condition may result from the fact that grammatical gender information is lateralized to the left hemisphere, whereas semantic information is represented more bilaterally.

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