



Rethinking the neurological basis of language

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Abstract

Functional neuroimaging, within 10 years, has produced evidence which leads us to question a number of the standard assumptions about the areas which are necessary and sufficient for language processing. Although neuroimaging evidence has corroborated much neuropsychological data, it forces a revision of a number of the standard interpretations of those data and some traditionally accepted notions must be totally discarded. We will provide an overview of some issues which have arisen in these years, giving examples from a number of laboratories and illustrating with experiments of our own. The circumstances under which the left posterior temporal lobe (Wernicke's area) and the left inferior frontal gyrus (Broca's area) are activated are reviewed, and several views of how they contribute to language processing are considered in the light of this evidence. Further evidence for the contribution of a number of other areas to language comprehension are reviewed, including the anterior temporal lobe, the cerebellum, the left superior median frontal lobe, the anterior insula and the left inferior temporal occipital junction. Further we discuss some of the conditions under which the right hemisphere contributes to language processing. We will conclude by discussing the implications of this research for the concept of modularity in the sense of Fodor [Modularity of Mind, MIT Press, Cambridge, 1983].

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1. Introduction

The classical theory of the neurological basis of language makes several basic assumptions. First, in most people the left hemisphere is dominant for language. Secondly,

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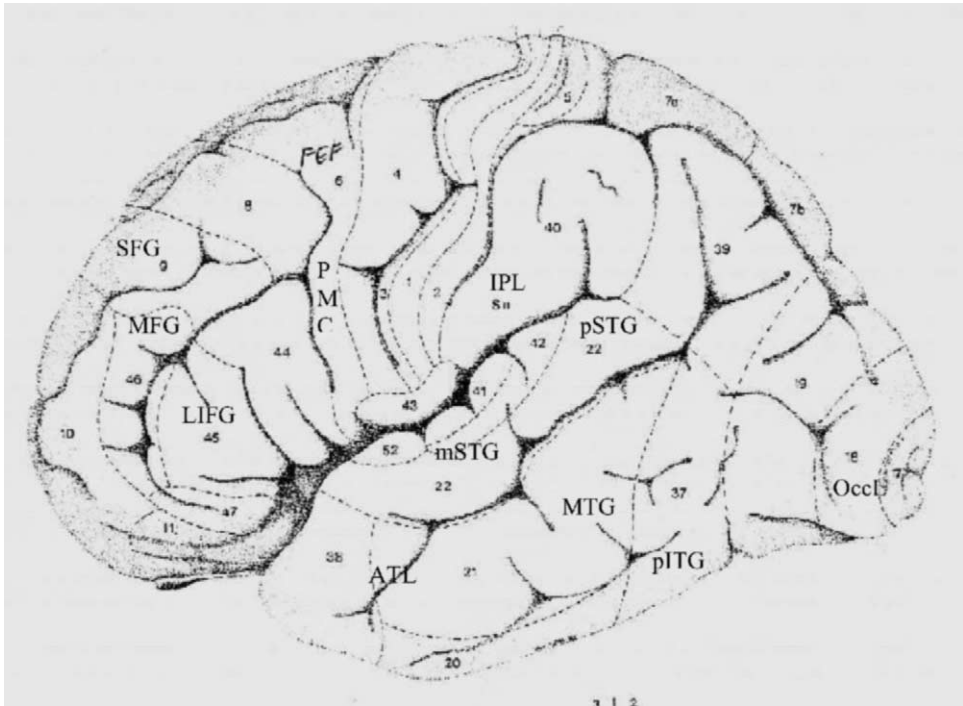


Fig. 1. Anatomical areas important for the following discussion. LIFG: left inferior frontal gyrus; pSTG and mSTG: posterior and middle superior temporal gyrus; MTG: middle temporal gyrus; ATL: anterior temporal lobe; Occl: occipital lobe; PMC: premotor cortex; MFG: middle frontal gyrus; SFG: superior frontal gyrus; IPL: inferior parietal lobe. Numbers indicate Brodmann's areas (different cytoarchitectural structures) which are discussed in the subsequent figures (adapted from Duvernoy, 1991).

there are at least two areas of the left hemisphere which are specialized for language functions: Broca's area, which is located in the inferior frontal gyrus, and Wernicke's area, which is located in the left posterior superior temporal gyrus (or sometimes more generally posterior temporal lobe). A third area in the inferior parietal lobe is considered to be important for some aspects of phonological storage and for reading. The locations of these regions and several others which will be discussed in this article are indicated in Fig. 1.

This characterization of the neurological basis of language is based primarily on lesion studies. Nearly 15 years ago, the first study using neuroimaging techniques to experimentally localize language in the brain in normal healthy volunteers was published (Petersen et al., 1989). Since then a plethora of studies have been carried out. Most of these studies support the facts of the classical model (left dominance, involvement of Broca's area, Wernicke's area, and the inferior parietal lobe in language); however, many of these studies have suggested that we need to rethink some of our assumptions about what these facts mean. We will briefly describe a wide range of studies, going into some more detail on some particular studies from our own laboratory, since these are the studies which led us to consider the issues we wish to discuss here.

In this article, we will discuss four claims which have generally been accepted in the classic neurological model of language processing:

- there are only two primary language areas, Broca's and Wernicke's,
- which are located in the left hemisphere,
- are dedicated to distinct aspects of language processing, and
- are specific to language.

We will present evidence from recent neuroimaging studies and supporting evidence from aphasiology studies which suggest that each of these claims is incorrect.

First, we will briefly describe the two neuroimaging methods which have provided most of the results with which we will be concerned, PET and fMRI. Then we will discuss the conditions which lead to activation of Wernicke's and Broca's areas, which turn out to be considerably more varied than expected under the classical model. We will discuss the impact of these results for three existing hypotheses on the roles of these areas in language processing and propose an alternative way of looking at the function of Broca's area. Second, we will show that there are a number of areas besides Broca's and Wernicke's that are involved in aspects of language comprehension and production, both in the left and the right hemisphere. This evidence leads to an alternative view of the language faculty, under which it consists of a network of anatomical areas which support specific component cognitive functions, which can be employed to support language, but which also support other cognitive processes with similar component cognitive demands. Third, we will show that the existence of such a complex network is not compatible with the classical theory and the assumption that the 'language faculty' is completely specialized or 'modular' in the sense of Fodor (1983). Neuroimaging results suggest that various cognitive tasks that make use of similar representations or processes frequently share component subfunctions with other tasks and that it is these component functions which tend to be anatomically localizable. Language processing shares components with several non-linguistic tasks in this way. Although a concept of modularity can be maintained under this view of language, it is rather different from the classical version.

1.1. Neuroimaging techniques

The major source of evidence that we will make use of in discussing these issues is functional neuroimaging using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI). Both of these methods can be used to measure changes in blood flow in various areas in the brain. PET does so by employing a very short-lived radioactive tracer injected into the blood. A "map" of the amount of blood flow in each region of the brain is made under different processing conditions. When a particular condition involves increased neuronal processing in one or more region of the brain, blood flow to that area increases. So for example, one can compare the conditions of seeing a word and recognizing it versus the condition of saying the word aloud (Petersen et al., 1989). The first task involves all the components of the second except those involved in articulatory production. Areas which show increased blood flow are assumed to be involved in production of the word. Or as another example, we can compare the comprehension of relatively simple sentences with the comprehension of relatively

complex sentences. The area(s) showing increases is again argued to be important for processing some aspect of sentence structure.

The basis of functional MRI is somewhat different. MRI uses rapid changes in magnetic fields to map the concentration of various magnetic protons in the body. When blood flow to an area increases due to neuronal activity, the amount of blood is greater than needed (that is, there is an overshoot), leading to a greater concentration of oxygenated hemoglobin, which differs in its magnetic characteristics from deoxygenated blood. The result is a local change in the MR signal in response to the condition that elicits increased neuronal activity. Again, by comparing the degree of blood flow change under different cognitive conditions, we can localize areas in which increased neuronal activity is apparent. To summarize, both of these methods measure changes in blood flow under different cognitive processing conditions, which can be used to determine the areas which are involved in carrying out a particular task, and thus, the particular cognitive function of the region.

2. The functions of Broca's and Wernicke's areas

In this section we will consider the functions of the two primary language areas, Broca's and Wernicke's areas, in the light of evidence from neuroimaging. However, what do we count as Broca's or Wernicke's area? Their exact locations are actually quite a vexed question, as can be seen by the variability in the way they are indicated in various articles and books. So what we consider to be evidence for the function of Broca's area or Wernicke's area depends on where we set our boundaries. We will begin by making the assumption that the left inferior frontal gyrus is the approximate location for Broca's and that the posterior superior temporal gyrus (and possibly posterior middle temporal gyrus) is the most likely for Wernicke's area.

We will start by giving an overview of some of the comparisons which lead to activation in Broca's area and Wernicke's area as defined above. [Table 1](#) summarizes the results of a number of studies in which quite diverse comparisons were made and indicates whether a significant activation was found in Broca's or Wernicke's area. One thing that becomes absolutely obvious from the variety of studies showing activation in these areas is that the ventral left inferior frontal gyrus and posterior superior temporal gyrus are indeed absolutely central for aspects of language production and comprehension. The variety of the comparisons involved, however, raises substantial issues about "the" function of these areas. Since the boundaries are indeed not clear, where an area contiguous to one or the other also showed activation or showed activation instead, that is indicated by giving the area in parentheses, generally middle frontal gyrus (MFG), (Pre)motor cortex (PMC) or middle temporal gyrus (MTG) or middle superior temporal gyrus (mSTG). Note that many of these comparisons show activation of both Broca's and Wernicke's areas.

We will use the data contained in [Table 1](#) as a basis for discussion of three existing hypotheses concerning the contribution of Broca's and Wernicke's areas to language processing. We will then address an alternative hypothesis for the function of Broca's area based on these data.

Table 1

Summary of selected studies showing activation in Broca's and Wernicke's areas, organized by the general cognitive nature of the comparison involved

Study	Comparison	Broca's	Wernicke's
Auditory, phonological and word perception tasks			
Fiez et al. (1996)	Pseudo words–words (with instruction to remember list)	+ (+PMC)	
Fiez et al. (1996)	Low frequency words–high frequency words	+	+
Keller et al. (2003)	Comprehending tongue twister sentences–normal sentences (no covert production required)	+ (+MFG, PMC)	+
Schubotz and von Cramon (2002)	Predict auditory pitch sequence; increase with sequence complexity	+ (+PMC)	
Zatorre et al. (1996)	Detect /b/ in two syllable sequences–passive listening	+ (+PMC)	
Zatorre et al. (1996)	Detect same final sound in two syllable sequences–passive listening	+	
Phonological and word production tasks			
Buckner et al. (1995)	Provide word from visual cue of first letters–fixation	+	
Buckner et al. (1995)	Verb generation–noun reading	+ (+MFG)	
Gelfand and Bookheimer (2003)	Manipulating syllable sequences–remembering syllable sequences	+ (+MFG, PMC)	
Heim et al. (2003)	Phonological identification first sound of picture's name–semantic category decision	+ (+MFG, PMC)	+ (+MTG)
Paulesu et al. (1997)	Generating words from initial letter–generating words from semantic category	+	
Paus et al. (1996)	Increase with ate of whispering ba-lu (white noise mask against auditory feedback)		+
Petersen et al. (1989)	Repeat word–hear/see it	+ (+PMC)	
Syntactic/sentential perception manipulations			
Caplan et al. (1999)	Object–subject relative clauses	+	
Cooke et al. (2002)	Long antecedent–gap relations (particularly for object relatives)–short antecedent gap relations	+	
Fiebach et al. (2001)	Unambiguous object relative clauses with long delay to gap vs. with short delay to gap	+	(Mid STG)
Friederici et al. (2003)	Syntactic anomalies–correct sentences		+ (+mid STG)
Grossman et al. (2002)	Long antecedent gap–short antecedent gap distance interacts with subject vs. object relative clause	+	
Homae et al. (2002)	Sentences–phrases	+ (+PMC)	MTG
Homae et al. (2003)	Sentences and phrases–non words	+ (+MFG, PMC)	+ (+MTG)
Inui et al. (1998)	Center-embedded–left branching	+	
Just et al. (1996)	Center-embedded object relatives–conjoined verb phrase active	+	+
Kuperberg et al. (2003)	Pragmatic violation > normal > agreement violation in sentences	+	+ (+MTG)
Meyer et al. (2000)	Syntactic anomalies–correct sentences		+ (+mSTG)
Michael et al. (2001)	Auditory syntactic complexity effect > visual complexity effect	+	
Moro et al. (2001)	Syntactic error detection–phonotactic error detection in pseudoword sentences	+	
Röder et al. (2002)	Increase with scrambled word order (German)	+	+ (+MTG)
Sakai et al. (2003)	Grammaticality decision–short-term verbal memory	+ (+MFG)	
Stowe et al. (1998)	Simple < complex < ambiguous sentences	+	+ (+MTG)
Suzuki and Sakai (2003)	Syntactic grammaticality decision–semantic, phonological decisions	+	

Table 1 (Continued)

Study	Comparison	Broca's	Wernicke's
Sentence production manipulations			
Indefrey et al. (2001)	Increase with increasing phrase structure complexity	+ (+PMC)	
Müller et al. (1997)	Generate sentence–repeat sentence	+ (+MYG)	+
Sentential or discourse semantic manipulations			
Baumgärtner et al. (2002)	Semantically unexpected–expected sentence ending	+	(MTG)
Ferstl and Von Cramon (2001)	Coreference without coherence in sentence pairs–with coherence	+ (+PMC)	
Friederici et al. (2003)	Semantic anomalies–correct sentences	+	(mid STG)
Kuperberg et al. (2003)	Semantic anomalies–correct sentences	+ (+MFG)	(mid STG)
Mazoyer et al. (1993)	Listening to stories–passive rest, but not activated by sentences alone	+	
Röder et al. (2002)	Scrambling complexity effects in sentences with real words > than pseudowords sentences?	+	
Suzuki and Sakai (2003)	Semantically anomalous sentences > normal sentences		+
Lexical semantics manipulations			
Fiez et al. (1996)	See noun: generate verb–produce noun	n.a.	(MTG)
Friederici et al. (2000)	Semantic categorization–physical judgment (space between letters)		(MTG)
Kotz et al. (2002)	Unrelated words–related words (priming)	+ (+MFG, PMC)	+
Noppeney and Price (2002)	Semantic category decision–reading of words	+	
Stebbins et al. (2002)	Abstract/concrete decision–uppercase/lowercase decision	+ (+MFG)	
Wagner et al. (2001)	Identifying weakly related word among many distractors–identifying strongly related word among distractors	+ (+MFG)	
Working memory manipulations			
Awh et al. (1996)	Match item n-back–plain match	+ (+PMC)	
Barde and Thompson-Schill (2002)	Manipulating verbal list order on alphabetic or semantic criteria–maintaining list in memory	+	
Burton et al. (2003)	Generate semantically related or rhyming word not contained on list	+ (+MFG, PMC)	+ (+MTG)
Fiez et al. (1996)	Word list maintain–fixation	+	
Paulesu et al. (1993)	Maintain letter lists–visual recognition	+	
Smith et al. (1996)	Verbal n-back–spatial memory control	+ (+PMC)	
Music and motor manipulations			
Binkofski et al. (2000)	Imagery of own motion–imagery of moving target	+	
Halpern and Zatorre (1999)	Imagine continuation of tune–control (not beginning of tune)	+ (+MFG)	
Hickok et al. (2003)	Covert rehearsal of music	+ (+MFG)	+
Gelfand and Bookheimer (2003)	Manipulating pitch sequences–remembering pitch sequences	+	
Koelsch et al. (2002)	Chord structure, deviant informations	+ (+PMC)	+
Lacquaniti et al. (1997)	Pointing to memorized location–visual detection (same stimuli)	+ (+PMC)	
Platel et al. (1997)	Rhythm judgments–pitch and timbre judgments on same input	+	
Platel et al. (1997)	Tune familiarity–pitch and rhythm judgments	+	+
Thomsen et al. (2000)	Three-dimensional mental rotation judgment similar shape–two-dimensional judgment	+	

Note. Most of these studies showed activations in other regions as well; these are not addressed here, since they are not relevant to the issue at hand. See the articles for further details. The comparison which produced the activation is briefly described for each study, along with whether Broca's area, Wernicke's area or contiguous areas were activated.

2.1. Production versus comprehension

The initial evidence about the relationship between the brain and language came from aphasia; a lesion in a certain area of the brain affected language production or comprehension afterwards. Broca (1861a,b) described a patient who could not produce language, although his comprehension was relatively good; Wernicke (1874) described a patient with comprehension problems, whose production was comparatively spared. The areas in which these patients had lesions are those which are now called Broca's and Wernicke's areas. Wernicke (1874) was the first to formulate a model of how different areas in the brain supporting language use are related to each other. Wernicke's model was extended by Lichtheim (1884), who proposed that auditory input is related to a higher level linguistic (full word auditory images) representation in Wernicke's area, through which the meaning of the word can be accessed. Broca's area stores motor representations of words (motor instructions) on which motor output is based. This model also included writing and reading, two modalities that we will not discuss here in any detail. In some guise, the classical model as worked out by Lichtheim has survived into the latter part of the twentieth century, for instance in the influential work of Norman Geschwind (1970).

The results of a number of neuroimaging studies show that production and comprehension cannot be split up in this way. Let us take the theory very literally, for the minute, and make the prediction that if subjects are required to produce language, the frontal areas will be activated, but not posterior areas. Comprehension tasks or tasks which require only perception, on the other hand, should primarily activate posterior areas. This initially appeared to be true. Petersen et al. (1989) showed that hearing a word activated posterior temporal areas while repeating that word aloud produced only frontal activation.

However, when we examine the experiments summarized in Table 1, we find that many experiments show activations in both Broca's area and in the posterior superior temporal gyrus and middle temporal gyrus. Let us first consider the phonological aspects of production and comprehension. Listening to two syllable sequences and deciding if they end with the same sound does not, in principle, require that subjects produce the sequences, only that they be perceived. Nevertheless, both Broca's and Wernicke's areas are activated relative to passively listening to similar sequences (e.g. Zatorre et al., 1996). Similarly, simply reading sentences containing words with similar sounds (tongue twisters) in order to answer a comprehension question does not require that they be produced; nevertheless, both Broca's and Wernicke's are more activated while reading tongue twisters than sentences containing words with less phonological similarity (Keller et al., 2003). Tasks which require overt or covert production show a similar pattern of co-activation. Paus et al. (1996) asked people to say two syllable sequences which were masked with white noise to prevent auditory feedback. Activation in both frontal and Wernicke's areas increased as the rate of production increased. Heim et al. (2003) asked subjects to perform a semantic categorization task or a phonological categorization task on pictures. The phonological task requires covert production of the picture's name, while the semantic categorization task does not. The phonological task led to increased activation in both Broca's and Wernicke's areas. Taken together these results demonstrate that it is not possible to make a simple distinction between perception and production as in the classical model (see Hickok

and Poeple, 2000 for a much more extensive discussion of the evidence against this distinction).

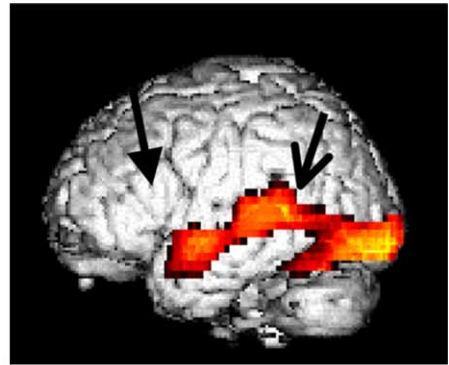
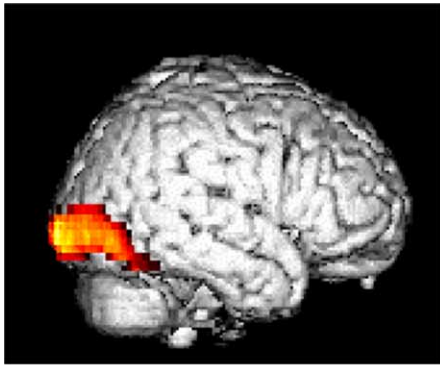
From a linguist's viewpoint, the least part of language comprehension and production concerns single sounds and single words; the combination of words into sentences, using syntactic structure to indicate the relations between entities, is what gives us flexibility in creating new expressions to convey novel ideas. Not surprisingly, the single study of production which manipulated structural complexity of which we are aware (Indefrey et al., 2001) showed activity in Broca's area. This might suggest that syntactic production is solely a matter for Broca's area, as predicted by the hypothesis. However, another study which compared the activation when subjects generate sentences with the activation evoked by repeating sentences have shown posterior superior and middle temporal gyrus activation as well as frontal activation (Müller et al., 1997).

Studies of sentence comprehension frequently show frontal activation as well as posterior activation. When sentence comprehension is compared with a resting control, cf. Fig. 2A and B, or sensory control condition, cf. Fig. 2C, posterior superior temporal gyrus is consistently activated (e.g. Bavelier et al., 1997; Mazoyer et al., 1993; Stowe et al., 1999).¹ The left frontal lobe is sometimes also activated, particularly when the sentences are complex (Fig. 2B and C). Activation of the inferior frontal gyrus is also seen when comprehension of syntactically complex sentences is compared with comprehension of syntactically simpler sentences (Caplan et al., 1998, 1999; Stowe et al., 1998; Stromswold et al., 1996). Many of these studies show a temporal activation as well as the frontal activation (Homaie et al., 2002; Just et al., 1996; Röder et al., 2002; Stowe et al., 1998). We will return to these experiments below.

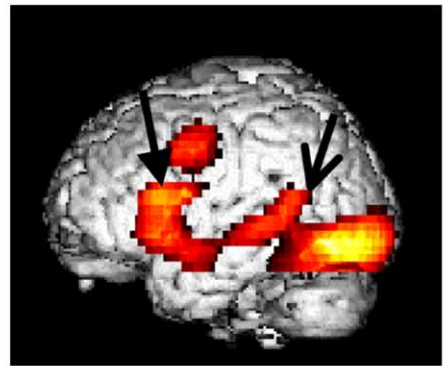
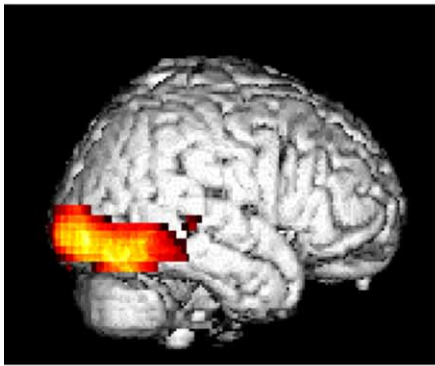
Although we have presented a fairly crude version of the predictions of the production versus comprehension theory, these results are difficult to explain even in a much more fine-grained version of the theory. Rather the combination of results suggests that Broca's and Wernicke's areas contribute in some way to both comprehension and production. If we want to maintain a model of brain function which is organized around perception versus production, we need to explain these co-activations in some way. Some authors have attempted to do so for particular comparisons; Wernicke's activation during production tasks can be attributed to a covert monitoring procedure (McGuire et al., 1996). Activation of Broca's during perceptual tasks can be attributed to covert production or to the use of working memory resources (i.e. articulatory rehearsal) to aid in task demands. However, the prevalence of these co-activations as seen in Table 1 suggests that, even if only in a supportive role, both areas are probably necessary to normal function.

This conclusion is possibly rather surprising for phonological processes since it has been claimed that there is a clear dissociation between production and perceptual processes in this domain. A recent discussion by Hickok and Poeple (2000) re-examines lesion and neuroimaging evidence and concludes that the dissociation in this domain is not as clear as has been claimed. The neuroimaging evidence is not particularly surprising for syntactic

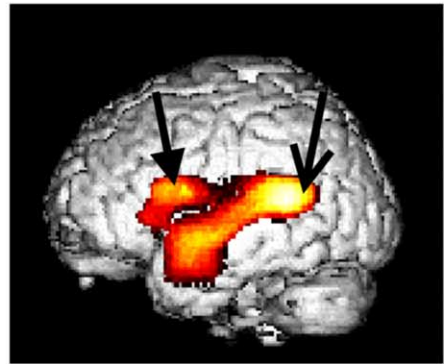
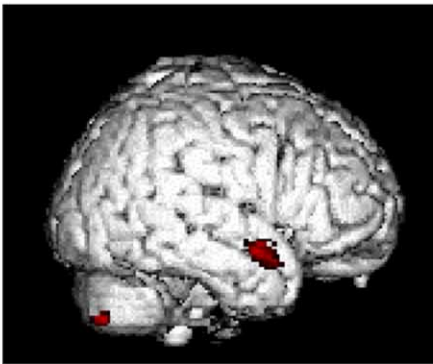
¹ The major difference between these two types of experiments is that when a sensory control is used, for example, the visual control of Fig. 2C, the increased blood flow for sentences consists of activation above and beyond that necessary for pure visual processing. In this case, the occipital lobe shows no activation, since this area supports sensory processing, but apparently not higher-level linguistic processing.



(A) Simple sentences vs. passive fixation



(B) Complex sentences – passive fixation control



(C) Complex sentences – non-linguistic visual control

Fig. 2. Activation for reading sentences projected onto lateral brain surfaces; the areas activated differ somewhat depending on whether simple sentences (A) or complex sentences (B) are compared with a passive fixation control condition or complex sentences are compared with a visual control (C). Activation in the left inferior frontal lobe is indicated with a closed arrow; activation in the posterior temporal lobe is indicated with an open arrow. As can be seen in each comparison several other areas are also activated.

processing, given the usual assumption that linguistic knowledge in the different sub-modules of syntax is neutral vis-à-vis production and perception processes. Lesion studies have also demonstrated that most aphasics exhibit a mixed behavior with both comprehension and production deficits in sentence processing and are not easily classified unambiguously in one of the groups. This evidence led to a revised, sentence-oriented model which we will discuss in the next section.

Taken together the evidence from aphasia and neuroimaging shows that the production versus comprehension model is wrong about the functions of Broca's and Wernicke's areas. However, there are also other problems with the classical model. The model was cast in terms of storing knowledge about auditory representations or motor representations; when damage to one of the centers occurs, the information (e.g. auditory images or motor instructions) that is stored there is lost. In the behavior of aphasics, however, information that is not accessible at one moment may be accessible in the future. A number of careful case studies by Kolk and Heeschen (1990, 1992) have shown that, depending on the experimental conditions under which data are collected, patients can show marked differences in how much linguistic knowledge they make use of. This suggests that the *use* of information is damaged rather than the information itself. We will return to this point below.

2.2. *Syntax versus semantics*

As we pointed out above, the sentence is a much more important level of linguistic representation than the word, while Lichtheim's model is concerned only with information at the word level. Neurolinguists in the 1970s began to address this issue. On the basis of the production/comprehension model, one would have predicted that Wernicke's area would support sentence comprehension. However, a number of seminal studies showed that Broca's aphasics, as well as showing clear production problems, were less able to use syntactic information in understanding sentences than normal controls. Zurif et al. (1972) showed that Broca's aphasics, unlike normal controls, did not use syntactic information when they sorted words from sentences to indicate how closely they were related. Caramazza and Zurif (1976) tested comprehension of sentences under several different circumstances: sentences in which semantic information provided a clue to the syntactic relations, sentences with no semantic information to help identify the syntactic relations, and sentences which were relatively implausible given the syntactic relations. Broca's aphasics were unable to understand sentences if the syntactic structure could not be inferred on the basis of lexical semantics. This suggested that Broca's patients' apparent ability to comprehend sentences is due to use of lexical semantics, world knowledge, and heuristic strategies in the absence of syntactic processing.

Studies like these led to the development of an alternative theory, according to which Broca's area supports syntactic processing in both production and comprehension, while Wernicke's area supports lexical semantic processing. If Broca's area supports syntactic processing in both comprehension and production, that explains the co-occurrence of production of unstructured sequences of words on the one hand with the inability to use syntactic structure to combine lexical semantics into a representation of prepositional meaning on the other.

However, the recent neuroimaging evidence presented in [Table 1](#) casts doubts on the function of Broca's area suggested by this model as well as on the neurological model. First, let us consider the issue of lexical semantics, which are normally considered to be the realm of Wernicke's area. It is clear that both Wernicke's and Broca's areas can be activated by certain aspects of semantic processing. A number of studies have reported greater activation of Broca's area when a semantic categorization decision has to be made than when a perceptual decision has to be made (e.g. [Friederici et al., 2000](#); [Stebbins et al., 2002](#)). A related task, covert generation of words belonging to a given semantic category, has also been shown to activate Broca's area. In these tasks where semantic category is consciously manipulated, frontal activations seem to be more prominent than temporal activations ([Noppeney and Price, 2002](#)). On the other hand, studies which have manipulated semantic priming (i.e. a word is processed more easily when it appears after a semantically related word), have shown that priming leads to decreased activation in both Broca's and Wernicke's areas ([Kotz et al., 2002](#)).

Even if we limit ourselves to sentential semantic manipulations, it seems that the frontal area is as likely to be activated as the posterior temporal area when complexity increases. [Röder et al. \(2002\)](#) looked at sentences containing real words and sentences containing pseudowords in order to investigate the effects of scrambling NPs in German. They found clear effects of scrambling in the left inferior frontal gyrus, but these were much more pronounced for sentences containing real words. Their results are difficult to explain under the syntax/semantics dichotomy. If Broca's area is concerned only with syntax and not with semantic integration, there is no reason why the effects of scrambling for sentences containing real words should be significantly larger than for sentences containing pseudowords. A number of other studies have shown that sentences containing semantic anomalies evoke more activation in the posterior or middle temporal lobe than sentences which do not contain anomalies, which is consistent with the syntax/semantics hypothesis if the boundaries of Wernicke's area are somewhat extended ([Baumgärtner et al., 2002](#); [Friederici et al., 2000](#); [Kuperberg et al., 2003](#)); [Baumgärtner et al. \(2002\)](#) and [Kuperberg et al. \(2003\)](#), at least, report an inferior frontal activation as well, which is not expected.

When we consider the role of Broca's area in syntactic processing, the results do not support the hypothesis any more straightforwardly. As we pointed out above, in many studies, both Broca's and Wernicke's show increasing activation in response to increasing sentential complexity; however, processing simple sentences (simplex clauses or sentences containing right-embedded subject relatives) causes extensive temporal activation relative to a passive fixation condition, but it does not reliably cause activation in the left inferior frontal gyrus. When simple sentences are compared with a resting condition, as in [Fig. 2A](#) (data from [Stowe et al., 1998](#)), no frontal activation is seen. This result is very difficult to explain if syntactic processing actually occurs in the left inferior frontal gyrus; although they require less syntactic processing than complex sentences, even simple, semantically reversible sentences require some syntactic processing and should have shown activation relative to non-syntactic controls. Other studies have also failed to find any Broca's activation for simple sentences relative to baseline as well (e.g. [Mazoyer et al., 1993](#); [Meyer et al., 2000](#)).

Complex sentences (containing center-embedded adverbial or object relative clauses), on the other hand, do elicit a frontal activation as well as a temporal activation; this can

be seen in Fig. 2B (data from Stowe et al., 1998), where complex sentences are compared with a passive fixation condition and in Fig. 2C (data from Stowe et al., 2001), in which complex sentences are compared with a non-linguistic visual control. When subjects read syntactically ambiguous simplex sentences, frontal activation also becomes apparent relative to unambiguous simplex sentences as discussed below (cf. Fig. 4; data from Stowe et al., 1998). These results show that the left inferior frontal gyrus plays some role in comprehending sentences when processing is more difficult, but combined with the simple sentence results, they suggest that its role is not syntactic processing per se.

The conclusion that syntactic processing does not necessarily depend on the left inferior frontal gyrus is also supported by evidence from aphasia, as pointed out in a recent review by Grodzinsky (2000). Agrammatic aphasics (patients who are unable to produce a syntactically complete structure) frequently can give fairly reliable grammaticality judgments, even when they perform at chance level in a sentence-picture matching task with similar structures (Linebarger et al., 1983). Slowed responses are normally observed to words which do not fit the syntactic structure of a sentence (syntactic “priming”), due to their ungrammaticality. This effect has also been observed experimentally in agrammatic patients (Hofstede, 1992), which cannot be explained if these patients are not able to recognize the relevant aspects of sentence structure. Further, agrammatics typically produce phrases which are locally grammatical, although they do not form complete sentences (Bastiaanse and van Zonneveld, 1998; Kolk and Heeschen, 1990).

These observations all suggest that grammatical knowledge, as it is organized in different sub-modules of syntax, needs to be distinguished from the ability to make use of that knowledge during language processing (see Sabourin and Haverkort, 2003 for an overview). Further, they suggest that it is the ability to process syntactic structure or to make use of syntactic structure in interpretation which is in some way impaired in agrammatic aphasics. Lastly, they imply that the impairment severely limits the complexity of the syntactic representation which can be constructed. This view of agrammatism is supported by the observation that patients who produce agrammatic spontaneous speech may produce much less agrammatic symptoms in a picture description task (Kolk and Heeschen, 1992). Agrammatics’ syntactic deficits are thus more limited than would be expected if the ‘syntax’ area had been significantly damaged.

2.3. *Alternative hypotheses about the function of Broca’s area*

So far we have discussed evidence that neither the production/comprehension or syntax/semantics dichotomy can adequately explain the activations seen in neuroimaging studies. Rather, activation of both areas during both types of tasks occurs quite frequently. This does not mean that there is no distinction in their contribution to the tasks. If this were the case, local lesions should affect all functions equally; this is clearly not the case. This suggests that we need to consider alternative hypotheses about the functions of these areas. For the minute, let us concentrate on the function of Broca’s area in syntactic processing. We will return below to the phonological and semantic processes that seem to be subserved by Broca’s area.

Although it does not appear that the left inferior frontal gyrus is involved in all conditions which require syntactic processing, it clearly supports sentence comprehension in some way. As we noted above, a number of PET and fMRI studies have found activation in this region during the processing of complex or syntactically ambiguous sentences. This difference relative to simpler sentences has been confirmed in a number of studies (Caplan et al., 1998, 1999; Stowe et al., 1994, 1995, 1998; Stromswold et al., 1996). Most of these experiments have compared object relative clauses with subject relative clauses and have found that object relatives lead to increased Broca's activation (Caplan et al., 1998, experiment 1; Caplan et al., 1999; Just et al., 1996; Stowe et al., 1995; Stromswold et al., 1996). An additional two studies show that sentences containing syntactic ambiguities dependent on a categorically ambiguous word, as in the following sentence, are also associated with increased activation in the frontal lobe (Stowe et al., 1994, 1998).

Zij kunnen bakken met zulk deeg niet verplaatsen
 they can bake(V)/containers(N) with such dough not move

In this sentence, the preferred interpretation of *bakken* after the modal verb *kunnen* is the verb interpretation, not the noun interpretation; as soon as the negation *niet* is encountered, it is clear that *bakken* cannot be interpreted as a verb, but must be a noun; if it were a verb, the negation would have to precede it: *zij kunnen niet bakken met zulk deeg* (lit. they can not bake with such dough).

We have already argued that it is unlikely that Broca's area is responsible for syntactic processing in general. If it is not responsible for syntactic processing, what function does it carry out? One possibility is that the area is responsible for a limited aspect of syntactic processing. A theory of this sort has been proposed by Grodzinsky (2000). A second possibility, which we will argue is better supported by the data at hand, is that it has a more general role related to working memory or storage of information. This function supports syntactic processing, although it is probably not specifically syntactic in nature and may indeed not even be specifically linguistic. We will consider both of these possibilities below.

2.3.1. A single aspect of syntactic processing

Grodzinsky (2000) pointed out that the constructions which cause difficulty for agrammatic aphasics generally contain syntactic dependencies between a moved XP and a trace (e.g. WH-questions, relative clauses and passives). Grodzinsky hypothesized that agrammatic aphasics have a deficit in a specific aspect of syntactic computation, with the consequence that they are unable to establish an XP/trace dependency. However, Grodzinsky's reinterpretation of the left inferior frontal gyrus' function does not mesh with some of the neuroimaging results which we just summarized. His hypothesis predicts that the left inferior frontal gyrus should be activated only by XP/trace dependencies. Stowe et al. (1998) showed that blood flow in the left inferior frontal gyrus was least for simple sentences, increased for complex sentences containing center-embedded clauses (some of which but not all of which contained XP/trace dependencies), and was highest for syntactically temporarily ambiguous sentences as can be seen in Fig. 4. The syntactically

ambiguous sentences contained only the XP/trace dependencies found in the simple condition.² These results show that the function of the left inferior frontal gyrus in sentence comprehension are not limited to establishing XP/trace dependencies. Results for center-embedded structures relative to non-center-embedded clauses (e.g. Inui et al., 1998) present the same problem for Grodzinsky's theory, since these do not contain increased XP/trace relationships either.

Another line of evidence that tends in the same direction comes from experiments by Cooke et al. (2002), Fiebach et al. (2001), and Grossman et al. (2002). In each of these studies, it appears that the left inferior frontal gyrus is not necessarily activated by WH-trace relations at all; for example, a WH phrase linked to a subject gap does not seem to reliably cause any activation; under Grodzinsky's account it should do so. In fact, activation generally only appears when there is a relatively long period between the antecedent and the gap (e.g. The *man* (in the long black coat) *who* Susan noticed *t* was very tall); lengthening the sentence in this fashion does not increase the length between WH-phrase and gap, only between the antecedent head noun and the gap). Grossman notes that this difference between short and long antecedent sentences is much more significant for object relative clauses than for subject relative clauses. Again, the effect of distance suggests that establishing a WH-trace relationship is not the major function of the left inferior frontal gyrus, but rather that reactivating the antecedent with significant amounts of intervening material is costly.

Another problem for both the view that syntactic computation occurs in the frontal lobe and for Grodzinsky's reinterpretation is that word lists presented with no task other than comprehension of the individual words activate the left inferior frontal gyrus more than simple sentences (Mazoyer et al., 1993; Stowe et al., 1998, 1999). The activation found for this condition by Stowe et al. (1999) is shown in Fig. 3. If we compare Fig. 3 with Fig. 2A, it is clear that the presentation of a word list causes more activation in Broca's area than simple sentences do; this impression is supported statistically by Stowe et al. (1998). This result is difficult to explain under the hypothesis that the function of this area in language is syntactic in nature.

One suggestion is that the subjects are trying very hard to treat the word lists as sentences, trying to establish syntactic relations between the words, leading to more syntactic processing than in simple sentences. However, the left inferior frontal gyrus is activated by word lists under a number of circumstances: when word lists are presented with no further task as in the Stowe et al. (1999) study; when subjects memorize a list during the scan (e.g. Grasby et al., 1994); when subjects maintain a short list presented before the scan (e.g. Fiez et al., 1996); when subjects continuously update a short list for comparison with new input (n-back task; e.g. Awh et al., 1996; Smith et al., 1996); and when subjects recall or recognize words out of a short study list presented before the scan (e.g. Awh et al., 1996; Buckner et al., 1996; Paulesu et al., 1993; Smith et al., 1996). In many of these studies, although there is a very noticeable memory component to the task, there is no great likelihood that the subjects will attempt to construct a syntactic structure.

² Depending on the syntactic theory, virtually any sentence can contain syntactic dependencies. Therefore the same structures were used in the simple sentence condition as the structure to which the ambiguous sentence was eventually disambiguated, so that the number of dependencies were equivalent.

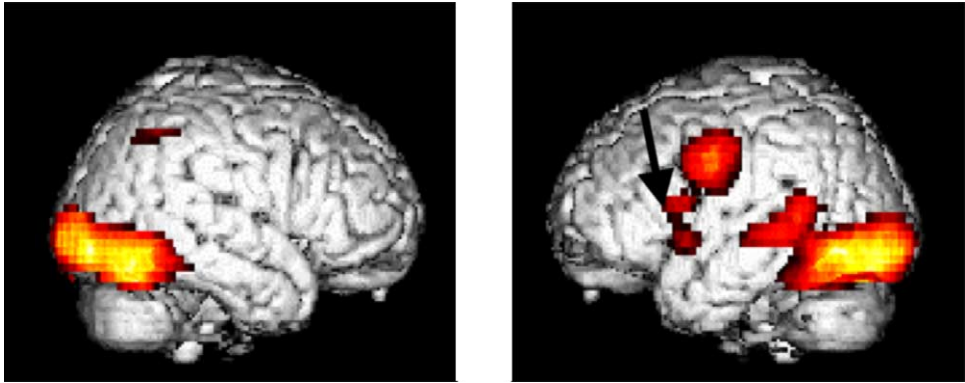


Fig. 3. Activation for word lists relative to passive fixation. The arrow indicates Broca's area.

Is this word list activation really problematic for the syntactic hypothesis? It could be that word lists activate Broca's area for a different reason than sentences do. It could be that there are two distinct cognitive functions which are located in adjacent regions of the brain. However, the locations of the activations appear to be pretty comparable. In this sort of research, the center of the activation is normally described in terms of a stereotactic coordinate system which designates the anatomical location of the activation (Talairach and Tournoux, 1988). Thus we can determine where, on average, the maximum of the activation is located for those studies which are concerned with syntactic complexity and for those studies which looked at word lists. In fact, the average maximum is virtually identical in a set of studies examined by Stowe et al. (2002); it does not vary by more than three millimeters in any dimension. This is very close for blood flow changes, which are generally not small. The variances around average centers were also fairly comparable. This strongly suggests that the neuronal networks activated in both of these sets of experiments are located in the same anatomical structure in the brain rather than in adjoining regions. We thus consider it likely that the overlap between activations for verbal short-term memory and for sentential complexity is not accidental, and, until other evidence proves the assumption wrong, we will assume that the area supports a single function which is employed in both tasks, viz. supporting temporary storage of verbal information during short-term verbal memory tasks and during sentence processing, maintaining phrasal as well as lexical information.

2.3.2. A memory or storage function

Most of the word list tasks we just reported were carried out as studies of short-term verbal memory. The researchers who found frontal activations (e.g. Fiez et al., 1996; Paulesu et al., 1993) generally assume that the left inferior frontal gyrus makes up part of an articulatory rehearsal mechanism (Baddeley, 1986; Baddeley and Hitch, 1994). One possibility is that the area maintains fairly unstructured information such as words or articulatory patterns. Stowe et al. (1998) pointed out that if lexical items (or articulatory patterns) are simply temporarily stored in the left inferior frontal gyrus with no reference to sentence structure, then the length of the maintenance and thus the storage load would be

the same for scans containing an equal number of words, and therefore provide no explanation of the complexity effects found in the sentential complexity experiments discussed above. Therefore, it seems possible that words or sounds are only maintained until a syntactic structure has been built or interpreted.³ There are earlier experimental results which also support this conclusion (Jarvella, 1971; Lombardi and Potter, 1992; McElree and Bever, 1989).

This characterization of the function of the area also does not seem to make the correct predictions, however. If words are maintained until a phrase is formed (after which they do not need to be maintained any longer), then word lists would typically be associated with a higher load than even the most complex sentences, while the storage load associated with sentences would depend on how long the words had to be maintained before a phrase was formed (Stowe et al., 1998). This would typically be least for simple sentences, and increase for more complex sentences with more complex phrases and filler-gap relations. In the experiment reported by Stowe et al. (1998), blood flow was compared for word lists (=W), simple sentences with no sentential embeddings and minimal XP/trace dependencies (=S), complex sentences with multiple sentential embeddings and XP/trace dependencies (=C), and syntactically ambiguous sentences (=A) with two possible structures, although no more XP/trace relations in the correct structure than the simple sentences. They failed to find any region in the brain for which the word lists showed a greater activation than the other three conditions. These results suggest that the left inferior frontal gyrus does not just support simple lexical storage. It suggests even more strongly that the function cannot be explained as purely a lower level representation, such as an articulatory representation.

However, a second important sort of information that needs to be kept available during sentence comprehension concerns structures which are not yet complete (e.g. Gibson, 1998; Just and Carpenter, 1992). An alternative hypothesis is thus that the left inferior frontal gyrus temporarily maintains lexical information until a phrase can be constructed and then information relevant to phrase structure is kept available until higher level phrases can be constructed. Under this hypothesis, blood flow in the left inferior frontal gyrus would be predicted by the combination of lexical load and phrasal load. Thus word lists have a high lexical load but a low phrasal load and should exhibit more blood flow than simple sentences (which have low loads for both), but less than the most complex sentences (which are high in both phrasal load and lexical load due to longer incomplete phrases). The left inferior frontal gyrus exhibited this pattern, as shown in Fig. 4; the location of the activation is shown in the left panel, and the relative level of blood flow over the four conditions is shown in the right panel. Furthermore this hypothesis is consistent with the distance effects for WH clauses discussed in the preceding section (Cooke et al., 2002; Fiebach et al., 2001; Grossman et al., 2002). If WH phrases and their antecedents must be kept available until a trace location is identified, the length between antecedent and gap is an important variable. These results are thus consistent with the hypothesis that both lexical load and phrasal storage load affect the blood flow in Broca's area.

³ This is similar to the assumption that the articulatory rehearsal mechanism is only used until the task at hand has been completed during verbal short-term memory tasks.

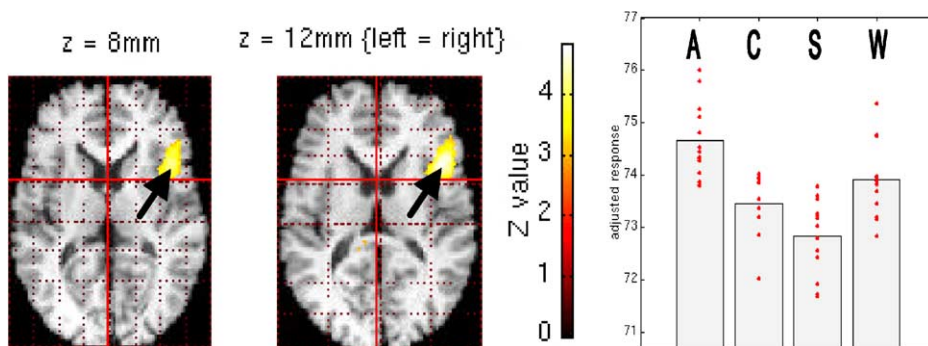


Fig. 4. Area in left inferior frontal gyrus activated by the combination of lexical and phrasal memory load. The activations are shown in the left panel projected onto anatomical MRI slices to give an indication of their anatomical location; each slice is viewed as if from below, so that the left hemisphere appears on the right side of the image. In the right panel, the relative regional blood flow (in ml of blood per min per dl brain volume) is shown for the four conditions included in the comparison: A: ambiguous sentences, C: complex sentences, S: simple sentences, W: word lists.

The hypothesis that the left inferior frontal gyrus supports temporary access to lexical and phrasal information can explain data from aphasia as well. First, it can explain apparent knowledge of syntactic structure, combined with the inability to construct complete structures in production (Bastiaanse and van Zonneveld, 1998) or to construct complete syntactico-semantic representations in comprehension (Grodzinsky, 2000). Second, it can explain on-line experimental results which indicate that semantic priming from words earlier in the sentence is not present for agrammatic aphasics, although it is found for Wernicke's aphasics (Swinney et al., 1996); we will discuss these experiments further below.

We argue that in simple structures, the memory resources of the frontal lobe are not central for comprehension or maybe even for production. In production, it is clear that for longer range production plans, the structure to be produced later must be stored temporarily, and it appears that agrammatics do not have sufficient resources to do so. In comprehension, maintenance is apparently also only necessary when longer sequences must be simultaneously available to support comprehension. Thus, it is in general those aspects of comprehension which require longer availability of lexical or syntactic information which cause comprehension problems in agrammatic aphasics. Under this view, agrammatic symptoms in production are not a direct consequence of loss of grammatical information, as in the classical model. Rather, they are due to a problem with on-line information maintenance, which necessitates simplification of the syntactic representation by optionally leaving out (a subset of) functional categories (cf. Haverkort and Kolk, in preparation).

The theory we have just sketched is similar in spirit to a proposal of Kolk and Heeschen (1990, 1992), who proposed that agrammatic aphasic production is limited by their computational resources. Limited computational resources can be attributed to a number of factors. Quick decay in particular would imply that computation has to occur immediately (Haarmann and Kolk, 1991). Evidence for quick decay has in fact been

found for agrammatic aphasics under several circumstances. In normals, semantic priming from a WH-filler is normally found at the location of a syntactic gap; a word which is semantically related in meaning to the antecedent is recognized more quickly than a semantically unrelated word, which indicates that the meaning of the word is reactivated in this syntactic position so that semantic interpretation can take place. Agrammatic aphasics do not show this pattern of reactivation (Swinney et al., 1996). The model which we just sketched suggests that this is because the lexical and phrasal information which guides semantic reactivation in normals is not available to these patients. A second experiment which supports this picture was reported by Haarmann and Kolk (1994), who observed that agrammatic aphasics' behavior was affected by a subject verb agreement violation just as strongly as that of normals when the words were adjacent; however when there is a longer delay and more structure intervening between the subject and the verb, the mismatch does not have any apparent effects on their behavior, unlike normal controls. These results can be accounted for if the primary deficit is considered to be one of keeping available lexical and phrasal information.

2.3.3. Evidence against two separate functions

We suggested above that verbal short-term memory and complexity effects overlap so strongly that it is likely that the same anatomical structure is involved. Furthermore, we assumed a single function for that area, given that a single cognitive function can be defined which can plausibly be involved in both comprehension and verbal memory tasks. However, despite Occam's razor, it is also possible that two functionally separate networks (e.g. lexical memory and phrasal memory or computation) are located in the same anatomical structure but are supported by overlapping but independent neural subsystems within it. This sort of neural organization is not uncommon in the brain; for example, within the primary visual area, a cortical area receiving information from a particular part of the retina is organized into columns which respond to different aspects of visual information.⁴ The possibility of overlapping neuronal networks in the left inferior frontal gyrus therefore deserves closer investigation.

Any hypothesis that postulates separate networks predicts that effects of syntactic complexity and a non-sentential verbal memory load should be independent of each other. The single storage function hypothesis, on the other hand, predicts that as phrasal storage demands increase during sentence processing, the amount of resources available for a non-sentential verbal memory task should decrease. A PET study which investigated this prediction was reported by Stowe et al. (2002). They asked subjects to read sentences containing center-embedded clauses and sentences with only one clause (sentential complexity manipulation) while monitoring for words out of a list containing one or five words presented before the beginning of the scan (verbal memory load manipulation). A highly significant interaction between the two variables was found in the left inferior frontal gyrus, centering in the same location as the complexity effects which we discussed earlier, cf. Fig. 5.

⁴ It is probably worth pointing out that these columns interact with each other very heavily, rather than consisting of totally separate systems.

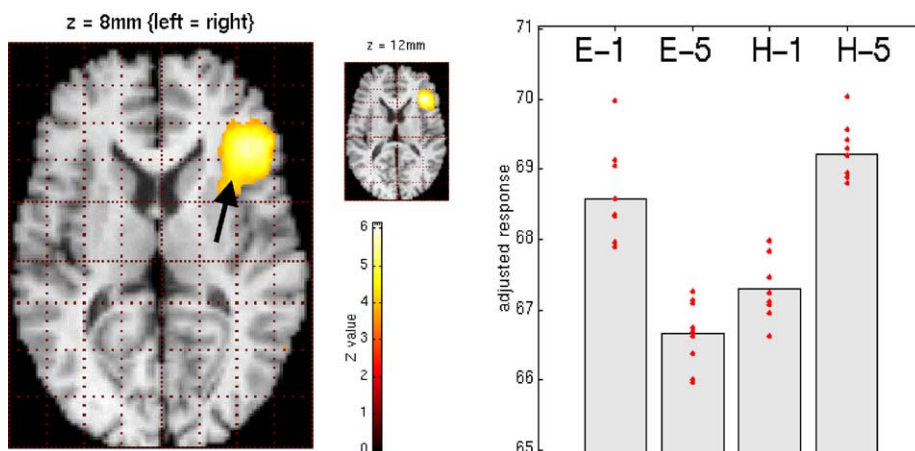


Fig. 5. Area in left inferior frontal gyrus in which complexity and memory load interact is shown in the left panel (left hemisphere appears on the right, cf. Fig. 4). The amount of activation for each condition is shown in the right panel (E-1: easy sentences/low load; E-5: easy/high; H-1: hard/low; H-5: hard/high).

While monitoring for a single word the left inferior frontal gyrus was more activated when subjects read easy sentences than while reading complex sentences. This suggests that subjects did not have the resources available to maintain even a single word in this system when they had to deal with a complex sentence, and therefore they carried out the task in a different system, insofar as possible. The verbal memory load manipulation in this experiment produced primarily an activation in the occipital lobe; this is the area in which visual processing occurs and which has also been implicated in visual memory processes, supporting this explanation of the results (Fiez et al., 1996). The most important implication of these results, then, is that phrasal complexity affects the availability of resources for word memory. Such a result is difficult to explain for any hypothesis postulating two separate networks within a single area.

Taken together, these experiments lead us to the hypothesis that a single cognitive function in the left inferior frontal gyrus supports temporary storage of verbal information during short-term verbal memory tasks and during sentence processing, maintaining structural as well as lexical information. It seems likely that the mechanism used for maintenance of lexical and phrasal information in comprehension is related (or identical) to that used for storing production plans, as suggested by the 1970s linguistic model of agrammatism.

The hypothesis that the main function of the left inferior frontal gyrus is to keep information available accounts for more data than the hypothesis that the left inferior frontal gyrus directly carries out (aspects of) syntactic computation, as proposed by both the 1970s syntax versus semantics model or Grodzinsky's reinterpretation of it, which we discussed above. The storage hypothesis is capable of explaining the agrammatic data presented by Grodzinsky as well, since the aspects of syntactic processing which are disturbed under his hypothesis are those that require the longer maintenance of phrasal information. Under the storage hypothesis, it is not coincidental that particularly long

XP/trace dependencies, the paradigmatic case of storage of unintegrated structural information, are problematic for these patients. The syntactic dependency hypotheses, on the other hand, cannot readily explain the activation evoked by syntactically ambiguous sentences, nor the interaction between verbal memory load and syntactic complexity. Additionally the storage hypothesis is consistent with the evidence that agrammatic aphasics retain grammatical knowledge but are unable to use that knowledge effectively in on-line production or comprehension.

2.4. *Linguistic specificity*

In the last section we concentrated on the issue of how Broca's area contributes to syntactic processing. However, it is clear that Broca's area contributes to other language related functions as well as to syntactic processing. The studies summarized in [Table 1](#) make it clear that Broca's area can be activated during phonological tasks and semantic tasks as well as during sentence processing. Are all these aspects of processing supported by a single area or are there distinct areas within Broca's which support different aspects of linguistic processing?

According to a number of researchers the answer to this question should be the latter. One sort of evidence advanced to support this idea is that the three sorts of processes appear to have activations with different centers. The inferior frontal gyrus can be divided into more or less three sections according to cytoarchitectural structure (the distribution of various cell types in the layers of the cortex), using systems like that developed by [Brodmann \(1909\)](#). The most inferior part of the inferior frontal gyrus is in Brodmann's area 47; the area somewhat higher is Brodmann's area 45 (which also extends somewhat into the middle frontal gyrus); the most superior area is Brodmann's area 44, adjoining (pre)motor cortex, which includes BA 6 and 4. These can be seen on [Fig. 1](#) above. It has been claimed that studies which use semantic tasks such as category membership judgments ([Noppeney and Price, 2002](#)) and semantic fluency tasks such as generation of words belonging to a certain category ([Phelps et al., 1997](#)), tend to activate Brodmann's area 47, while syntactic manipulations tend to activate Brodmann's area 45 and phonological tasks activate Brodmann's area 44. Others claim that Broca's area can be divided into anterior and posterior areas, with semantic and syntactic functions more anterior (BA 45) and phonological tasks more posterior (BA 44). Under this view, although the inferior frontal gyrus carries out processing at several different linguistic levels, each linguistic process has a specific cortical area dedicated to it.

To examine this issue in more detail, several studies have examined the differences between tasks which manipulate phonological, semantic and syntactic tasks in single subjects. [Paulesu et al. \(1997\)](#) examined differences between phonological and semantic processing, contrasting tasks in which subjects were required to generate words according to a semantic cue or to the initial sound (verbal fluency tasks). These tasks tend to be differentially impaired depending on the form of aphasia exhibited by a patient. Both tasks activated anterior Broca's area (BA 45), the phonological task more so in the posterior and superior part (BA 44). Semantic fluency activated other areas selectively, but no part of Broca's area. [Phelps et al. \(1997\)](#) found that phonological fluency task activated BA 45 more than either producing a presented word or producing its opposite. The task where

subjects generated opposites did not, on the other hand, elicit a semantic activation like Paulesu et al.'s task, possibly because it was easier and had less memory demands.

Burton et al. (2003) also compared semantic and phonological processing, using a different task. Subjects saw lists of words and had to generate either a semantically related (word under which the presented words fall and which is also not included on the list) or a phonologically related word (rhyme that is not contained in the list). Obviously both of these tasks have a considerable memory component as well as semantic and phonological criteria for generating a response. They found that the meaning task elicited stronger activation in the anterior area of the left inferior frontal gyrus (BA 45 and 47), while the phonological task elicited stronger activation in the posterior area (including BA 44). McDermott et al. (2003) found a similar dissociation. Barde and Thompson-Schill (2002) compared processing (order manipulations: reorder on semantic criteria (size) versus reorder on phonological criteria (alphabetical order) with subsequent sequential position decisions) with simple maintenance (sequential position decisions).⁵ They found no difference between the semantic and alphabetical tasks, but they did find a dissociation of the anterior and posterior areas, with greater activation in the posterior areas (BA 44 and posterior 45) when manipulation of the sequence was required.

Newman et al. (2001) attempted to distinguish semantic and syntactic processing by examining those areas which showed effects of syntactic complexity, and those which showed differences between ungrammaticalities caused either by verb agreement or by inserting an extra verb. They argued that the latter leads to more difficulties of semantic integration than the former. They found that a more anterior and inferior part of the left inferior frontal gyrus (BA 45) showed effects of the type of grammaticality, but only for syntactically simpler conjoined active sentences, not for sentences containing center-embedded object relative clauses. A more superior portion showed effects of syntactic complexity (BA 44). Kuperberg et al. (2003) took an alternative approach to this issue. They compared the response to sentences containing a violation of the pragmatic interpretation of the sentences, which presumably elicit more effortful semantic integration, with the response to sentences containing agreement violations. They found that BA 44, 45 and 47 all showed a pattern in which pragmatic violations elicited the most activation and syntactic violations the least activity. They suggest that the amount of activity is related to how difficult the subjects found it to decide whether the sentences were plausible. Dapretto and Bookheimer (1999) addressed the same issue by asking subjects to decide whether sentences had the same meaning when their form was varied by syntactic means (e.g. active versus passive) or by lexical means (using synonymous words). They found that both tasks activated the inferior frontal gyri bilaterally; the syntactic manipulation produced a greater activation than the semantic manipulation in the superior part of the left inferior frontal gyrus (BA 44), but there was no area showing a greater semantic activation in the left inferior frontal gyrus. The right frontal lobe, on the other hand, did show greater activation for the semantic task in BA 47, the most inferior part of the inferior frontal gyrus.

⁵ One obvious problem with this contrast is whether alphabetization should be regarded as a phonological task. This may explain why no difference between manipulation tasks was found.

Last, Miceli et al. (2002) attempted to dissociate semantic, syntactic and phonological processing by asking subjects to decide if a word has masculine or feminine grammatical gender (syntactic categorization) or is living or man-made (semantic categorization) versus whether it contains a *č* or /k/ sound (phonological categorization). Gender categorization activated BA 45 more than semantic categorization, but not more than phonological categorization. Phonology activated BA 44 more than gender or semantic categorization. Semantic categorization did not activate left inferior frontal gyrus more than either of the other tasks.

When we consider these studies, the most striking point is the diversity of the tasks which were used to investigate processing of phonological, semantic and syntactic processing. Semantic manipulations vary from lexical semantics such as categorization or generating antonyms or noun–verb relationships or establishing a semantic relationship among a set of words, to judgments of sentence synonymy. Syntactic processing ranged from grammaticality violations to complexity manipulation to comparison of different syntactic structures. Phonological processing tasks ranged from detecting rhymes to using phonological criteria to retrieve words from the lexicon for production. In general, the tasks vary considerably in complexity, but share the characteristic that they require conscious processing or conscious decision making. Despite this variability, it seems that tasks which require manipulation of language materials generally activate the left inferior frontal gyrus. Since this is regarded to be one of the primary language areas, this suggests that all of these tasks make use, in some sense, of the language relevant abilities of this area.

Further it seems clear that a distinction can be made between a more posterior and superior region (BA 44) and a more inferior and anterior area (BA 45), but the actual functionality of the distinction is considerably less clear. In many cases the degree of activation in the posterior region particularly seems to have more to do with the complexity of the task being carried out than with the nature of the task or of the level of language representation which is manipulated. In fact, an additional study by Michael et al. (2001) which investigated a completely different distinction, auditory versus visual modality, found that the location of the effect of syntactic complexity (center-embedded relative clauses versus conjoined verb phrases) was more anterior and inferior within the left inferior frontal gyrus than for the visual modality. This dissociation cannot easily be explained as a difference in linguistic level of processing.

The last issue we wish to bring up in this section is whether the cognitive function supported by Broca's area should be regarded as specifically linguistic in nature. As can be seen in Table 1, several recent experiments have shown that various aspects of music perception such as perception of rhythm or imagining the completion of a tune also activate the left inferior frontal gyrus in an area close to that activated by sentences (Platel et al., 1997; Halpern and Zatorre, 1999). Listening to complex music and mentally rehearsing music activate much the same areas as language, both Broca's and Wernicke's (Hickok et al., 2003; Koelsch et al., 2002). Hickok et al.'s (2003) subjects showed virtually identical activations for language and music stimuli. Music and rhythm both necessarily make use of a representation of an incremental hierarchical relationship between elements in the sequence (cf. Bernstein, 1976; Lerdahl and Jackendoff, 1983; Staal, 1989; Gilbers and Schreuder, 2000 for structural parallelism between language and music) Non-verbal and non-musical motor planning or imagery can also activate Broca's area (Binkofski et al.,

2000; Lacquaniti et al., 1997; Thomsen et al., 2000). Again relatively fine-grained sequential processing is involved in these tasks.

Following the same logic as in the studies which attempted to dissociate phonology, semantics and syntax described above, Gelfand and Bookheimer (2003) compared within the same subject group tasks involving three syllable sequences and sequences of three hummed notes in which subjects had to remember the sequence for a match decision, reverse the sequence for a match decision or delete the middle element for a match decision. Like Barde and Thompson-Schill (2002), they found that the sequence manipulations activated BA 44 more than simply maintaining the sequence. This was not specific to the language materials; in fact, the hummed sequence deletion task produced greater left inferior frontal gyrus BA 44 activation than the linguistic task. There were no activations specific to language in the left inferior frontal gyrus in this experiment. Given the preceding discussion, it seems quite likely that this is because the task demands in the two domains were so carefully matched. Thus, it is not inconceivable that a very general cognitive component supported by the left inferior frontal gyrus is involved in the representation of various sorts of incremental, hierarchically organized (motor or auditory) sequences, which can be used to support a large number of tasks; the more complex the tasks demands, the more activation will appear.

3. Additional “language” areas

As we pointed out in the introduction, it was formerly commonly accepted that only a limited number of areas are involved in language processing (primarily Broca’s and Wernicke’s) and that normally these are located in the left hemisphere. As we have already seen, there is considerable evidence from neuroimaging that Broca’s and Wernicke’s areas are indeed essential for normal language processing. Although we have not gone into this evidence, there is also considerable evidence that the left inferior parietal lobe is important for some aspects of phonological processing. The goal of this section is to examine evidence that a number of less traditional areas in the left hemisphere contribute in important ways to language processing and additionally that the right hemisphere is not nearly as non-linguistic as was once assumed. We will end with a preliminary attempt to provide a revised model of language comprehension which takes account of the new evidence which has become available through neuroimaging.

3.1. Additional left hemisphere activations

It is not in fact surprising to anyone who has read about aphasia beyond introductory linguistics textbooks that there are additional areas which are important for normal language function. For example, Caplan et al. (1996) showed that lesions anywhere around the Sylvian fissure, which forms the border between the temporal lobe and the frontal and parietal lobes, are likely to have some impact on sentence comprehension. However, it is difficult to use lesion data to address the question of the exact functional contribution of any given area within the cortex to a complex task such as language comprehension. Lesions tend to be quite large and they are not anatomically or functionally

well-circumscribed; moreover, patients with clearly dissociable functional damage are difficult to find. Neuroimaging evidence, in principle, can be combined with lesion data to specify the function of a given area more clearly. The questions to be addressed are what the contribution of each of the extra “language” areas is and to what extent these areas are necessary for language comprehension and production.

3.1.1. Anterior temporal lobe

The lateral anterior temporal lobe is one of the areas which have been activated in a number of sentence processing studies, sometimes only in the left hemisphere as in Fig. 6 (see the boxed area), sometimes bilaterally as in Figs. 2C and 7 below. This area is quite reliably activated when sentences (presented either auditorily or visually) are compared to a sensory or passive baseline (Bavelier et al., 1997; Mazoyer et al., 1993; Rumsey et al., 1994; Stowe et al., 1999, 2001; Tzourio et al., 1998). Additionally, it is more activated by auditory or visual sentences (cf Fig. 2A and B) than by word lists (cf. Fig. 3) as demonstrated by Mazoyer et al. (1993), Stowe et al. (1998, 1999), and Vandenberghe et al. (2002). Stowe et al. (1998, 1999) showed that the difference between sentences and word lists is statistically significant, as shown in Fig. 7 (data from Stowe et al., 1998).

The anterior temporal lobe, however, is not one of the classic language areas, since lesions of the anterior temporal lobe are not strongly associated with aphasia. For example, anterior temporal lobectomies, which are frequently performed on epileptics, do not generally produce obvious language disorders or increase a pre-existing disorder (Hermann et al., 1991). However, as we have already noted, lesions anywhere around the sylvian fissure are likely to cause some problems with language comprehension (Caplan et al., 1996). Additionally, Grossman et al. (1998) showed that decreased metabolism in this area of the brain correlates with deficits of sentence processing in patients suffering from fronto-temporal dementia. If the anterior temporal lobe contributes to sentence comprehension, how does it do so? Does it contribute to syntactic processing or to semantic

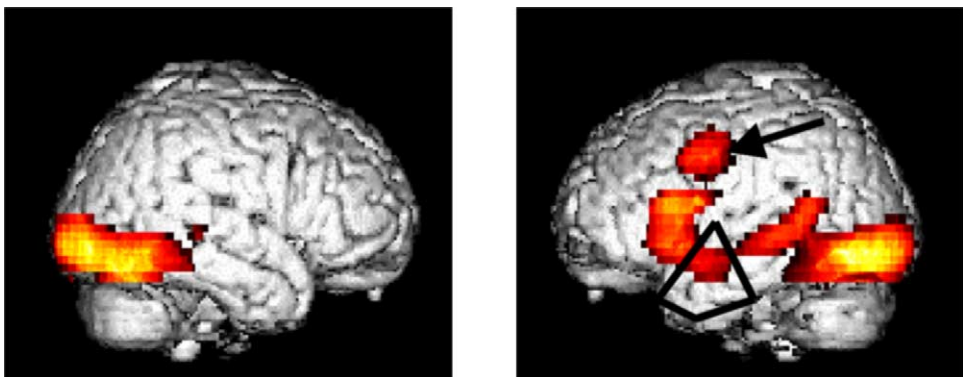


Fig. 6. Additional left hemisphere activations during the reading of difficult (syntactically ambiguous) sentences. The temporal activation seen during the reading of sentences includes the anterior temporal lobe (indicated by the boxed area) as well as the posterior temporal lobe. Frontal motor cortex (indicated by an arrow) is activated as well as Broca's area.

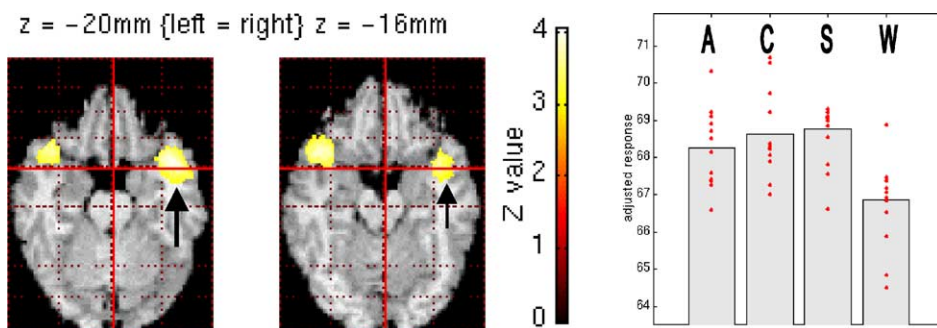


Fig. 7. Localization of anterior temporal areas which are more activated bilaterally during the reading of sentences than word lists.

processing directly or does it carry out a third function which is important for one of these aspects of processing?

Dronkers et al. (1994) found that the lesions of a number of patients with morpho-syntactic processing deficits overlapped in this area. However, the epilepsy evidence suggests that a lesion of this area in the left hemisphere does not necessarily produce such a deficit. The evidence from brain dysfunction suggesting a specific role for the anterior temporal lobe in syntactic processing is thus rather limited. The neuroimaging evidence does not necessarily implicate this area in syntactic processing either. Stowe et al. (1998) showed that the anterior temporal lobe is not sensitive to structural complexity, as one would expect if it played a major role in sentence level semantic processing. In this experiment, as we have already noted, three sorts of sentences were used, viz. simple sentences, complex sentences containing center-embedded clauses, and syntactically ambiguous sentences, as well as word lists. The structural complexity manipulation did not correlate with increasing blood flow in the left anterior temporal lobe; as can be seen in the right panel of Fig. 7, all three sentence types (A = Ambiguous, C = Complex and S = Simple) had approximately equivalent activation in the left anterior temporal lobe, and all three were more activated than word lists (W = word lists). This study thus supports the suggestion from aphasia that the left anterior temporal lobe is not directly involved in processing the syntactic structure of the sentence.

Nevertheless, the anterior temporal lobe is consistently activated during sentence processing, and in the deficit literature some correlations with sentence comprehension do exist. Recently, Kotz and Friederici (2003) and Kotz et al. (2003) have shown that after anterior temporal lobe damage, there are some signs of semantic processing difficulty. Normally, when a word occurs in a sensible sentence context or follows a related word (e.g. doctor–nurse) the EEG wave form is different from the response to an anomalous or unrelated word. This can be seen when a number of instances of EEG responses to words are averaged (event related potentials or ERPs). The component of the wave form which is affected is called the N400 because it is a negative response that reaches its maximum about 400 ms after the presentation of the word; this component is more negative when a word does not fit the preceding context semantically, more positive when it does. Kotz and Friederici (2003) and Kotz et al. (2003) showed that this response is delayed and

diminished in patients with anterior temporal lesions; in a single patient with bilateral damage, the N400 distinction was missing entirely. This effect suggests that the anterior temporal lobes bilaterally are important for some aspect of semantic processing.

Further evidence suggests that the more material which must be (semantically) integrated, the greater the activation in the anterior temporal lobe. Stories consisting of several connected sentences activate this area more strongly than unconnected sentences (Fletcher et al., 1995; Maguire et al., 1999). Single sentences containing real words activate the anterior temporal lobes more strongly than sentences of the same structure containing pseudowords (Baumgärtner et al., 2002; Ferstl and Von Cramon, 2001; Röder et al., 2002), but pseudoword sentences activate the area more than word lists (Mazoyer et al., 1993). Sentences containing semantically unrelated words also activate this area more strongly than word lists, but less than sentences containing related words (Vandenberghe et al., 2002). If we think of word lists as having the least (semantic) coherence, sentences containing pseudowords and unrelated words as having somewhat more, but less than unconnected sentences containing related words, and unconnected lists of sentences having less coherence than stories, this total pattern of activations can be accounted for. Notice that the pattern does not correspond to syntactic coherence, as we have already noted, but neither does it correspond to purely sentential semantics. Rather a more general coherence, perhaps discourse coherence, seems to be involved.

It thus seems that there is considerable evidence that the anterior temporal lobe(s) support some aspects of semantic integration over sentences and texts. It is not necessarily the case, however, that this area carries out the integration itself. There is some evidence about the function of the anterior temporal lobe which suggests one possible role which may support semantic integration. Preoperative electrical stimulus mapping studies on epileptic patients (e.g. Ojemann and Dodrill, 1985) have been used to identify the functions of various areas of cortex. Electrical stimulation of an area of cortex disrupts the neuronal function of the area, which shows up as a disruption of sensory or behavioral function. Ojemann and Dodrill showed that the anterior temporal lobe is involved in encoding verbal information for delayed retrieval tasks. Stimulation in this area during the presentation of a word does not affect immediate production of the word, so it is clear that recognition and output functions are not affected, but stimulation interferes with later (delayed) production of the word.

The role of the anterior temporal lobe in encoding verbal information into memory has been confirmed by tests of epileptics from whom the anterior temporal lobe has been removed. Although the patients were quite good at recognizing words out of a list presented earlier for study, they did not show some of the normal ERP effects of repetition after study (Rugg et al., 1991). The N400 described above is normally less negative for words that have been previously studied; this appears to be due to increased ease of accessing the word or of accessing its semantic representation. This pattern of results suggests that there are several routes by which lexical information can be encoded during study. One, which is unimpaired in these patients, is sufficient to support recognition. Another, which is impaired after anterior temporal lobe lesions, keeps relevant aspects of the word accessible, including at least semantic information; it is the lack of this latter maintenance which affects the N400 seen in these patients in response to words which are repeated later.

Encoding some aspects of lexical semantic information so that they remain readily available is clearly important for establishing coherence across texts. It may not always be necessary for sentence comprehension, but it may be necessary under some circumstances. Therefore, it is possible that an encoding function of the anterior temporal lobe indirectly supports sentence processing. Particularly, it may be necessary for the comprehension of complex or ambiguous sentences. If information about a particular lexical item early in the sentence is critical for the parsing or interpretation of a phrase late in the sentence, damage to this area of the brain may cause problems, as the information is not initially encoded and hence not readily available for integration later. Later availability is particularly likely to be necessary for ambiguous sentences which must be reinterpreted. At the time of the reinterpretation, it is essential to be able to easily access information about the words earlier in the sentence. Zaidel et al. (1995) suggested that left anterior temporal lobectomy led to a deficit in the comprehension of the second meaning of syntactically and lexically semantically ambiguous sentences. Right anterior temporal lobectomy affected interpretation of semantically ambiguous sentences only. Thus, even though anterior temporal lobe patients are not normally classified as aphasic, it is clear that they may suffer from more subtle comprehension deficits.

3.1.2. Motor activations: articulatory rehearsal and error detection

One of our attempts to address syntactic complexity (briefly discussed above) was to manipulate syntactic complexity (Stowe et al., 1998, *in press*). Stowe et al. (*in press*) discuss an experiment in which syntactically unambiguous sentences were contrasted with ambiguous sentences which were disambiguated to the less preferred syntactic structure after a delay. This ensured that subjects had to process both structures, either in parallel or by revising to the correct structure when the first parse proved to be untenable.

Several unexpected areas are activated by syntactically ambiguous sentences. We will discuss three areas that were found to be significantly activated in this comparison; they are shown in Fig. 8. The first was an area of left inferior frontal gyrus. However, this area extended somewhat higher than the localization generally found for syntactic complexity,

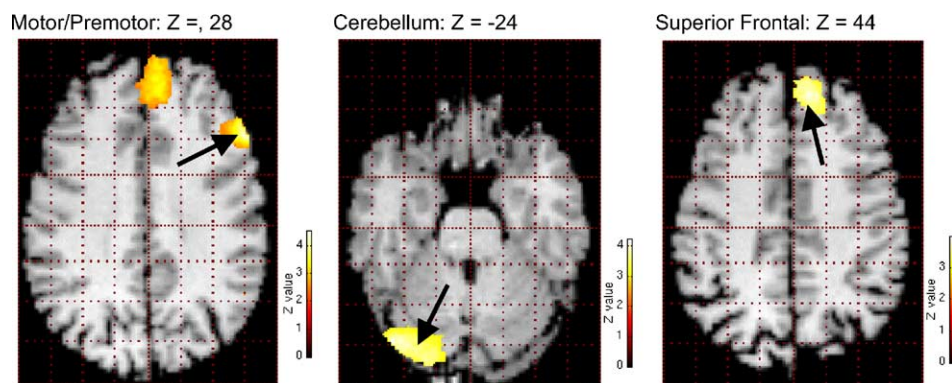


Fig. 8. Areas found to be activated by syntactically ambiguous sentences relative to unambiguous sentences. The left hemisphere appears on the right side of the slice, cf. Fig. 4.

and included motor cortex as well as the more traditional location of Broca's area. The second activation was located in the right cerebellum; the third was in the medial left superior frontal gyrus. These activations suggest that sentence comprehension, when it becomes particularly difficult, may appeal to a network of brain areas which together support resolution of the ambiguity. Each area potentially makes a completely separate contribution to the task.

The first two areas can be characterized as motor areas, as far as their basic function goes. The left motor area was also seen in another experiment which we discussed earlier (cf. Fig. 6), where we compared syntactically ambiguous sentences with a passive control; see also results in Table 1, which show that activations frequently extend into the left Premotor cortex. Although this area would normally be characterized as controlling facial movements, no movements occurred during this experiment, since the right hemisphere homologue shows no activation. Similarly, no right hemisphere difference is seen in the current experiment (cf. left panel, Fig. 8). The right cerebellum is connected to left motor areas, so that its co-activation with left motor areas is anatomically reasonable. We shall thus first consider whether an abstract "motor" function can explain the results in the current experiment. Then we will consider another possible cognitive function of the cerebellum which provides an alternative explanation of its role in this experiment.

The cerebellum and motor cortex have been co-activated in a number of short-term verbal working memory experiments (e.g. Awh et al., 1996; Fiez et al., 1996; Paulesu et al., 1993; Smith et al., 1996). In these experiments it has been assumed that the cerebellum forms part of an articulatory rehearsal mechanism (Baddeley, 1986; Baddeley and Hitch, 1994). It is thus possible that the right cerebellum provides an 'articulatory rehearsal'-like form of memory which aids in the retention of sufficient information to parse the second structure of an ambiguous sentence. However, one difference between our syntactic ambiguity experiment and the articulatory rehearsal experiments just mentioned is that in the working memory experiments, the cerebellar activation is typically bilateral rather than only in the right cerebellum and there is an additional medial activation, as would be expected if a detailed motor plan were being maintained. The cerebellar activation seen in the syntactic ambiguity experiment, on the other hand, was clearly right lateralized. Additionally the cerebellar activation was located nearly 2 cm posterior to the mean center of the working memory activations. It is thus possible that the right cerebellum plays another role in language.

Recently, it has been shown that the cerebellum plays a role in cognitive aspects of motor learning and planning as well as more basic motor functions. In motor learning, the cerebellum is essential for error detection which is needed when a previously learned response is inappropriate under new circumstances (Bloedel and Bracha, 1997). This may apply to higher forms of cognition as well as to overt motor behavior. A set of overlapping activations from one line of experiments suggest that this may be the case for language production tasks. The right posterior cerebellum has frequently been activated during various verbal fluency tasks, cf. the summary by Fiez and Raichle (1997). Verbal fluency tasks require that subjects choose words based on given criteria, such as the initial letter or sound or semantic class, rather than responding reflexively. Fiez et al. (1992) examined the performance of a patient with a right cerebellar lesion on a number of verbal fluency tasks. This patient was prone to making mistakes in all of the verbal fluency tasks; the errors frequently involved production of highly associated words that did not fit the criteria of the

task. The patient's performance did not improve to semi-automatic nearly perfect performance with experience on the task, as normal control subjects did. This data suggests that the right cerebellum may be involved in error detection at a higher level of representation in verbal production, as well as in motor execution.

This hypothesis raises the possibility that a similar error detection procedure may be important for the resolution of syntactic ambiguities, just as it is for motor planning and appears to be for verbal production. The initial response to a syntactically ambiguous sentence normally is to choose the most likely alternative, but when the first analysis proves to be incorrect, the error must be detected and corrected. Whether an articulatory memory-based explanation of this activation or an error-detection explanation is preferable must wait on further experimentation; both show that under complex conditions sentence comprehension invokes the use of additional cognitive functions and the neural networks that support those functions.

3.1.3. Superior frontal gyrus: semantic evaluation

As we have already seen, syntactically ambiguous sentences also caused an activation in the left superior frontal gyrus relative to unambiguous sentences. Again this is not an area which is by any means normally thought of as a 'language area'. Activation in this area has, however, been found in several other language studies: primarily for theory of mind tasks and for probabilistic reasoning tasks. For example, [Goel et al. \(1997\)](#) showed an activation in this area when subjects were required to make an inductive inference about the plausibility of a last sentence in a short paragraph versus reading similar paragraphs for comprehension. [Gallagher et al. \(2000\)](#) showed that when subjects are required to make sense of theory of mind stories, which involve inferences about the reasons for behavior, there was increased activation relative to non-theory of mind stories. Both of these sorts of study definitely suggest that the area is activated by some aspect of processing of meaning.

The hypothesis that this area supports some aspect of semantic processing is supported by another result. In an unpublished study from our laboratory, activation was found in this area in a comparison of two different tasks. Given highly similar input sentences, making a plausibility judgment activated this area more than making a grammaticality judgment. This activation is shown in [Fig. 9](#). In this experiment, subjects read sentences which were equivalent except that a relatively small subset of the sentences (4 out of 14) contained an semantically anomalous word in one task or a semantically appropriate but ungrammatical word in the other task (i.e. determiner gender agreement and verb agreement). Thus, it is not likely that the activation was due to other differences between the input, rather it appears to be due to making a decision about the plausibility of the sentences.

All of the tasks mentioned above have two things in common: they contain an overt decision component and that decision becomes more difficult for one type of input than another (theory of mind inference versus physical inference, probabilistic reasoning judgment versus deductive inference). Although syntactically ambiguous sentences do not require an overt decision about plausibility or any other aspect of semantics, they may well involve a covert decision between the two possible meanings of the sentence at the point of ambiguity. The syntactically ambiguous sentences included sentences with a word which was ambiguous between two syntactic categories. A decision as to which of these is most likely may be based on the relative frequency of the meanings ([Burgess and Simpson,](#)

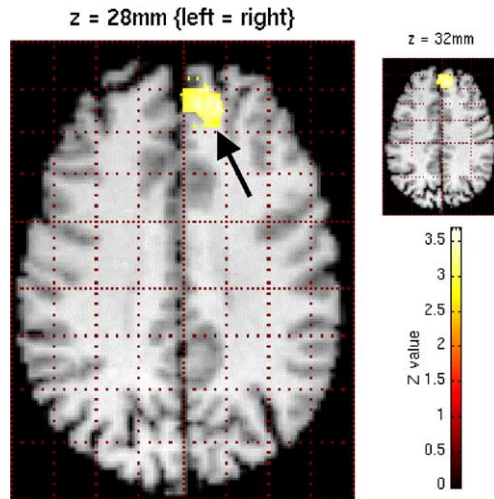


Fig. 9. Left superior frontal gyrus activation found for plausibility judgment relative to grammaticality judgment. The left hemisphere appears on the right side of the slice, cf. Fig. 4.

1988); alternatively, it may be based on the plausibility of the two meanings within the sentence context (Swinney, 1979). The second procedure for making a decision requires semantic evaluation of the two meanings. If this is the correct explanation of this activation, it is interesting that the area can be activated by a conscious decision procedure initiated as part of the experimental task, but can also be initiated as a probably unconscious part of sentence comprehension. To sum up, the hypothesis that the region supports semantic evaluation can explain all of these results.

More research will be necessary to determine whether this is the correct characterization of the function of this area. Caplan et al. (1998) found a similar activation when comparing simple and complex sentences. They have made an alternative suggestion that the activation seen in their experiment consists of activation of the supplementary eye fields. This is possible. At least one experiment (O'Driscoll et al., 1998) which investigated the control of eye movements found more activation in this general area for smooth pursuit of a moving point than for making movements in a jump to a given point (saccades). However, eye movement experiments have more generally found activations in posterior medial superior frontal gyrus rather than the more anterior locations discussed here (Dejardin et al., 1998; O'Driscoll et al., 1998; Petit et al., 1997). These activations were centered several centimeters posterior to the center of the average maximum for the language experiments just described. Further, Caplan et al.'s results are compatible with the suggestion made here. They required their subjects to make a plausibility judgment to each sentence and half of the sentences in each condition were anomalous, due to reversal of the noun phrases involved (e.g. *It was the man that the book read*). Making a plausibility decision to reversed sentences (i.e. rejecting the a priori plausible relationship) is more difficult for complex sentences than for simple sentences (Saffran et al., 1998); therefore, the hypothesized decision component could differ between the two conditions, producing the increased activation which Caplan et al. report.

3.1.4. Other areas which are important for language processing

It should be clear by now that the major focus of this article is on sentence comprehension; nevertheless we would like to briefly mention that a number of areas may be relevant for other aspects of normal language function.

The first of these is the anterior insula, which appears to be important for articulation. The area has been shown to be activated in many studies in which production is overtly carried out, for example, Riecker et al. (2002) showed that both singing and speaking, which are presumably equally complex at a motor planning level, both activate motor cortex, anterior insula and cerebellum. Speech, however, evokes greater left hemisphere activation in the anterior insula, while singing elicits greater right-sided activation. This result suggests that the activation of the left anterior insula is not due to motor aspects per se, but to motor processes which are important in speech. Dronkers (1996) used a technique in which they carefully overlaid the extent of lesions from a wide pool of patients and correlated lesion sites with the exact set of symptoms which each patient exhibited. This method showed that articulatory production problems were associated with a lesion in this area. The exact function of this area is not yet clear, however. It has been posited that the area is important for prearticulatory planning. However, Ackermann and Riecker (in press) demonstrated that the area is only activated in covert speech, while motor cortex is activated by covert speech as well. Since pre-articulatory planning is required by both covert and overt speech, they suggest that the left anterior insula is important for fine motor coordination in speech.

Last, it appears that the posterior inferior temporal and fusiform gyrus may be important for various aspects of language processing. It was first suggested that this area might be important primarily for accessing semantic information from visual input, as in reading and naming of pictures (Usui et al., 2003; Vandenberghe et al., 1996). Since this area forms part of the “what” system, which allows animals and humans to recognize objects in the world, this use is not unexpected. However, it appears that the function may be more general, since this area also shows increased activation when people process sentences with greater semantic complexity; Caplan et al. (1998) showed that active sentences containing a relative clause activate this area more than clefts, which contain only one full proposition, in the terms of Caplan et al. (1998). Furthermore, two studies have shown that this area is activated when subjects generate their own content relative to a baseline in which they must repeat an auditory sentence or produce motor output (Braun et al., 2001; Müller et al., 1999). In neither of these cases was there any visual input, so it appears that the function is not dependent on modality specific input, but probably rather on certain aspects of recruitment of semantic representations.

There is no reason to hypothesize that either of these areas is dedicated to language; the inferior temporal lobe certainly has other functions. However, it appears that they contribute in important ways to normal language use, one at the motor level, the other more probably at the conceptual level. As such they make up part of the language system as a whole.

3.2. Right hemisphere and language

One of the prime tenets of classical neurological models of language is that language functions are normally located primarily in the left hemisphere, except for rare cases of

reversed lateralization, although some aspects of language processing such as prosodic processing may be supported by the right hemisphere. Evidence from neuroimaging supports this conclusion to a certain extent, but suggests some substantial reservations as well.

If we consider global patterns of activation during sentence comprehension, the outcome is clearly left lateralized. For production, both left and right hemisphere are activated by both singing and language, but singing more strongly activates the right hemisphere, while speaking is lateralized to the left (Riecker et al., 2000). For comprehension, in Fig. 2A and B, reading sentences appears to activate an extensive area of the posterior right hemisphere relative to a passive control; however, in Fig. 2C, we can see that reading sentences activates primarily the left hemisphere when compared to a visual control. This implies that the right hemisphere does not contribute to any great extent after the level of visual processing. Auditory sentence processing and language production activate both hemispheres, but the left hemisphere is typically more activated (e.g. Friederici et al., 2003; Riecker et al., 2000). Hickok and Poeppel (2000) discuss the interpretation of this data in the light of results from aphasia which suggest that both hemispheres play an important role in auditory comprehension at the word level.

Reading sentences nevertheless sometimes activate other parts of the right hemisphere, even relative to a visual control, suggesting that the role of the right hemisphere is not limited to auditory processing. In Fig. 2C at least one area of the right hemisphere, the right anterior temporal lobe, is clearly and significantly activated, although the activation is less extensive than in the left hemisphere. In Fig. 7 we also saw that the anterior temporal lobe is more activated for sentences than for word lists in both hemispheres, although the left hemisphere counterpart is activated at a higher level of significance and more extensively. Individual subjects also show right superior temporal gyrus activations during sentence reading, as in Fig. 10. These areas may not be totally necessary for language processing, but they are clearly involved under normal conditions.

We have already noted some evidence that effective use of lexical semantics in sentence comprehension may be partially dependent on the right hemisphere, in particular the right

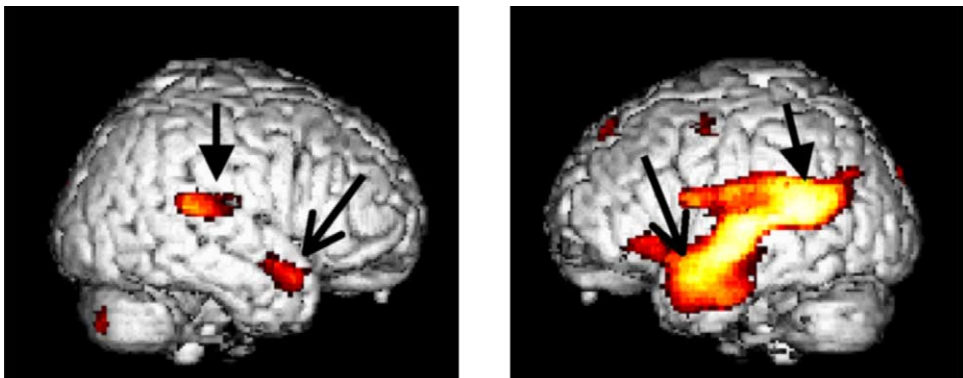


Fig. 10. Minor right hemisphere activations seen in an individual subject for sentences relative to visual control. The closed arrow indicates posterior temporal lobe, the open arrow anterior temporal lobe in both hemispheres.

anterior temporal lobe. Zaidel et al. (1995) showed that right anterior temporal lobectomy patients had more difficulty finding the second meaning of a lexically semantically ambiguous sentence, while Kotz and Friederici (2003) and Kotz et al. (2003) showed that damage to either anterior temporal lobe delays or diminishes the N400 response to incongruent words. This suggests that the right anterior temporal lobe has access to lexical semantic information which may not be available to the left hemisphere, otherwise the intact left hemisphere would be able to process the meaning on its own and no deficit would be seen. The hypothesis that the hemispheres have differential access to different meanings of an ambiguous word is supported by experimental evidence as well. Divided visual field studies have suggested that the right hemisphere is capable of responding independently to aspects of word meaning. The lexical semantic representation that is available to the right hemisphere appears to be somewhat different than that used by the left hemisphere, which may be important for certain aspects of comprehension (Beeman, 1998; Chiarello, 1991). Particularly, it appears that the right hemisphere maintains a second meaning of an ambiguous word at a later stage of processing than the left hemisphere does (Burgess and Simpson, 1988; Koivisto, 1997; Faust and Gernsbacher, 1996). For a recent review of language processing, particularly processing of lexical semantics, in the right hemisphere, see Chiarello (2003).

The frontal lobe of the right hemisphere also appeared to play a role in the comprehension of lexical semantic ambiguities. Stowe et al. (submitted) compared lexically unambiguous sentences with ambiguous sentences which were disambiguated to the less likely meaning, as the following sentence illustrates:

De ezel stond in de schuur al lang te rotten
the donkey/easel stood in the shed already a long time to rot (rotting)

The dominant meaning (donkey) is selected initially over the non-dominant meaning (easel) and can be maintained in the sentence context until the last word (rot) is encountered and forces selection of the non-dominant meaning (easel), as the meaning ‘donkey’ is incompatible with rotting (while still standing).

Stowe et al. found that an area of the right frontal lobe was activated by such sentences, as shown in Fig. 11. This suggests that the right frontal lobe may be involved in construction of a secondary interpretation of the sentence or revision of the initial interpretation. This function is likely to underlie the contribution of the right frontal lobe to humor comprehension; much humor relies on unexpected revisions of the initial assumptions about the meaning of words and situations. Furthermore, the right frontal lobe also plays a role in constructing other kinds of alternative interpretations. Bottini et al. (1994) demonstrated that part of the right frontal lobe is more activated during the processing of sentences which had to be interpreted metaphorically (e.g. *The investors were squirrels gathering nuts*). Other studies have shown right frontal activation due to increased cohesion between sentences (Robertson et al., 2000) and to inferring topic shifts in text (Caplan and Dapretto, 2001). These studies converge on the conclusion that the right frontal lobe is involved in some, broadly speaking semantic, aspects of sentence comprehension.

This conclusion is in line with results from studies of brain damage; several facets of comprehension can be damaged due to right hemisphere lesions. These include lexical

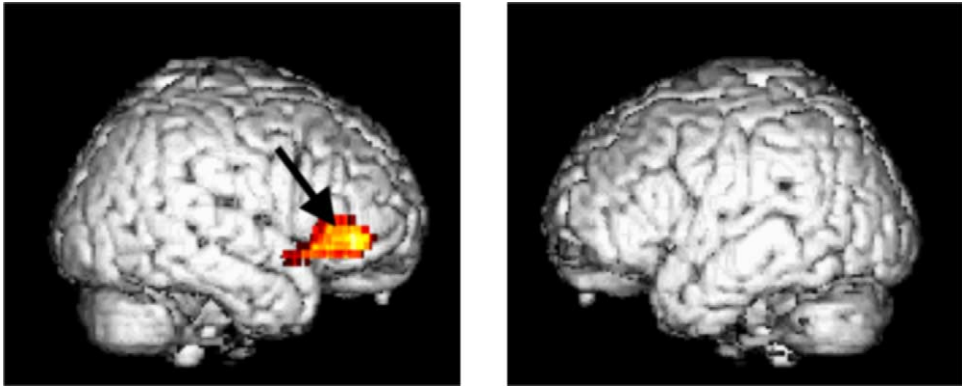


Fig. 11. Right hemisphere activation for sentences containing lexical semantic ambiguities relative to unambiguous control sentences.

semantics (Chiarello and Church, 1986) and non-literal meanings such as metaphoric processing (Brownell et al., 1990), indirect speech acts (Hirst et al., 1984) and making or revising discourse inferences (Brownell et al., 1986; McDonald and Wales, 1986). Taken together, it appears that the right hemisphere plays a role in providing a secondary or non-literal meaning if the initially constructed meaning turns out to be incompatible with the end of the sentence or the discourse. The source of the alternatives appears to be quite general, ranging from lexical ambiguity, to literal versus metaphorical readings or the possibility of an incorrect inference. The contribution of the right frontal lobe in providing an alternative interpretation may well be related to its use in the manipulation of information retrieved out of episodic memory (see Buckner, 1996, for an overview of memory-related activations in this area). That is, the role of this area in sentence comprehension does not necessarily imply that the cognitive function of the area is specifically linguistic.

A number of studies suggest that the right hemisphere may be quite generally important for language comprehension, however, even aside from these relatively limited functions. A number of studies in different domains have suggested that when linguistic complexity increases, the resources of the right hemisphere are recruited for processing; increased activation in both the homologue of Wernicke's and the homologue of Broca's has been reported. Cooke et al. (2002), Meyer et al. (2000), Moro et al. (2001) and Röder et al. (2002) among others have reported that one or both of these areas show increased activation as linguistic sentential complexity and task demands increase. When the demands of sentence verification are increased by compressing speech, right frontal lobe activation increases (Poldrack et al., 2001); right temporal lobe is activated by anomaly, possibly in search of alternative interpretations (Kuperberg et al., 2001) and by the need to generate a plausible final word as well (Kirchner et al., 2001). Even for a simple lexical relatedness judgment, increasing the complexity by needing to find a related item among distractors or decreasing the degree of relationship appears to increase the activation of the right hemisphere homologues of the areas involved in the simpler task (Wagner et al., 2001). These results suggest a general pattern in which when processing demands increase,

activation in the right hemisphere increases. This is in line with the interpretation of the results we just discussed, but is considerably broader in scope.

This general approach is consistent with the fact that bilateral activation is apparent in a number of subject groups who may be expected for a variety of reasons to have insufficient resources for some aspect of language processing. These include second language users (Ding et al., 2003), healthy elderly subjects, particularly those with good comprehension (Grossman et al., 2002), stutterers (Braun et al., 1997; De Nil et al., 2000), autistics (Müller et al., 1999), and schizophrenics (Artiges et al., 2000; Sommer et al., 2001). With those patient groups who show decreased lateralization during language tasks, it has been common to regard this as a causal factor in their language-related symptoms, but the generality of the pattern suggests rather that it may be a strategic attempt to deal with the limitations imposed by the impact on language processing of the cognitive deficits seen in the group.

3.3. Language comprehension as a complex network of interacting components

The upshot of the preceding sections is that the neurological basis of language comprehension is more complex than has generally been assumed. As we have noted several times, aphasia and other forms of language disturbance too are far more complex than would be expected if the traditional, fairly simple models were correct. It is probable that yet other areas will turn out to play a role in language comprehension and production when specific processing conditions are examined. The classical model in any case needs to be extended to deal with the contribution from motor areas (face area and cerebellum), the anterior temporal lobes, the superior frontal gyrus and right frontal lobe, as discussed above.

We have seen that the anterior temporal lobes shows increasing activation as the distance over which coherence must be established increases. A review of the literature suggests that the anterior temporal lobe(s) may contribute to sentence and text comprehension by carrying out a form of encoding which ensures that certain sorts of lexical information remain available to the language processor later. Broca's area appears to be important in maintaining information about both lexical items and phrases; thus this area is important for maintaining word lists as well as for processing complex and ambiguous sentences. As we have seen, sentential complexity, in particular syntactic ambiguity, also activates left motor cortex and the right cerebellum. This suggests that motor areas are recruited during the processing of syntactically more demanding sentences. They may function to provide extra storage capacity via an articulatory rehearsal mechanism, but possibly they also support error detection. Lastly, when semantic processing becomes more difficult, we see additional left and right frontal lobe activation. The right frontal lobe is activated in both metaphor processing and disambiguation of lexical semantic ambiguities; this area appears to be recruited to support processing of alternative meanings of a sentence or discourse. The left superior frontal gyrus appears to play a role in evaluating semantic plausibility, both during conscious decision making and as a part of sentence comprehension when a choice between potential interpretations becomes necessary. More research will be necessary to understand the roles of these areas completely, but it is clear that normal language comprehension involves a much wider network of brain areas carrying out

different components of processing than was assumed in the models introduced at the beginning of this article.

A last point is that when we attempted to determine what contribution each of these areas makes to sentence comprehension, we needed to look at a wide variety of evidence as to their probable function. Looking solely at language comprehension experiments gave us evidence in many cases (e.g. the superior frontal gyrus), but in other cases, other cognitive domains also have to be considered (e.g. music perception and the left inferior frontal gyrus). The possibility that the cerebellum is involved in identifying errors, for example, was initially posited and corroborated in the motor domain, using animals. The extension to higher cognitive functions, including language, suggests that areas which carry out a particular task in the motor domain may also be capable of carrying out a similar task sub-component in another cognitive domain. This leads us to our final topic: the relationship between the neurological components of language, and the relationship between the components of language and other cognitive functions.

4. Language and modularity

The assumption that the language faculty is a module of the mind separate from other cognitive functions has been widely accepted in mainstream linguistics and psychology over the past few decades (Chomsky, 1987, and references cited therein). It is worth considering the extent to which neuroimaging data is easily reconcilable with this viewpoint, since some authors have claimed that much of the early evidence was clearly in favor of linguistic modularity (Fromkin, 1997). Historically, this viewpoint arose as a reaction to the viewpoint that the brain is an all-purpose machine, in which a very general capacity can be applied to a number of different cognitive functions. Clearly, the sort of functional specializations of various anatomical structures which we have discussed in this article argues against this view of the brain and is consistent with the existence of modules, one of which might be language-specific. Under the language module hypothesis, language is a specific ability (or set of abilities) which can be damaged without obvious damage to other cognitive functions, and which can be maintained even when other cognitive functions are damaged. This view of linguistic modularity has been supported by identification of a population with normal intelligence and impaired language learning (specific language impairment), and a population with medium low intelligence and relatively normal language use (Williams syndrome).

We have already mentioned some evidence that other functions such as music make use of both Broca's and Wernicke's areas, and that complex motor operations also seem to utilize Broca's area. This evidence raises questions about whether the brain is organized according to this notion of modularity, with specific regions dedicated to a specific cognitive task such as language (i.e. domain-specific in the terms of Fodor, 1983). Further, the evidence which we have presented in this article suggests that even if there are some areas which are specific to language in this sense, language comprehension makes use of, and thus must be able to interact with, other areas which are clearly not restricted to language processing. These areas appear to support cognitive functions which are useful in a number of processes, including language. In this sense language processing shares

components with several non-linguistic tasks, suggesting a revision of the idea of modularity, at the very least. Language as a complete anatomical network is not modular, relative to other cognitive functions. Component functions within the language network may be specific to language. However, to demonstrate that this is so, researchers must show that these component functions are not shared with a multitude of other cognitive domains, rather than arguing from one cognitive domain, such as general intelligence, as in the argument for modularity which was sketched above.

Of course, as we noted above, the fact that the same areas of the brain are active in two very different tasks when measured by PET or fMRI does not necessarily mean that the same neural networks are active within that area. Research on the visual system, for example, has shown that individual neurons within a given area may be specialized for processing specific aspects of the input. Thus, there is a possibility that different networks of neurons within the same general area are activated in different cognitive functions. This possibility can be tested, however. If there is an interaction between the different tasks, it indicates that the same resources are used by both tasks.⁶ We discussed this form of argumentation above for the case of non-syntactic verbal memory load and sentential complexity. The same sort of approach should be taken in investigating other areas with overlapping functions.

Without such rigorous testing, it seems preferable to assume a single function in a completely overlapping piece of cortex which is activated by two different cognitive tasks unless there is reason not to do so. First, we should ask whether it is reasonable to assume that there is one basic function, which is involved in both language and other cognitive functions. For example, let us take music, complex motor operations and language. At the very least, all these tasks rely on fine-grained sequencing. The inferior frontal gyrus homologue in apes is known to contribute to motor planning and delayed motor responses in this sense.

For an example which is external to the traditional language system, let us consider the cerebellum and language. Earlier we discussed the possible contributions of the cerebellum to the comprehension of syntactically ambiguous sentences. The cerebellum is involved in both motor processing and in error detection in the motor and other cognitive domains (see review in Stowe et al., *in press*). Either of these functions might be invoked during sentence comprehension. A covert motor representation could be used to maintain information about the sentence, as in articulatory rehearsal. Under this view, the function of the cerebellum is a pure motor function, as opposed to a linguistic function, but it may nevertheless be important for carrying out syntactic reanalysis. Additionally, there is a clear component of error detection in the processing of ambiguous sentences, given an incorrect initial analysis (garden path). Error detection is thus also a possible function of this area in sentence processing.

⁶ Actually, we should point out that an interaction only shows up under some circumstances. An underadditive interaction, in which the more difficult level of one factor shows no effect of the other can indicate a ceiling effect; at some point an area in the brain is full, and no more blood can additionally be rerouted to that area, for example. This does not mean that the two functions do not interact then. An overadditive interaction, where the effect of difficulty in one manipulation increases with the difficulty of the second manipulation, does. An interaction of the type we discussed, associated with a shift in strategy for dealing with one task, on the other hand, suggests that the difficulty of the other manipulation has limited the available resources.

The conception of the function of the cerebellum as an error detector raises an additional question about modularity within the language network. If there are core components of the network which are indeed domain-specific for language, for example, Broca's area or Wernicke's area, are these areas modular in a second sense, that is, are they informationally encapsulated? To what extent can they both provide information to and receive information from other cognitive domains? In order for the cerebellum to be sensitive to errors, it must receive partial representations from the syntactic processor and compare the expectations of that representation with incoming data. For the detection of the error to be useful for language comprehension, the information must be communicated to any language specific modules.

Another similar instance is the function of the left superior frontal gyrus in processing of syntactically ambiguous sentences. We suggested that this area may be activated when a plausibility evaluation of the meaning of a sentence is necessary in order to make a choice between two possible interpretations. Again, the ability to make a decision depends on accessibility of a partial representation of the linguistic representation of the alternatives, and its usefulness in choosing between syntactic structures depends on feedback about the results of this choice is necessary, otherwise the decision is pretty useless; behavioral data suggest that subjects do indeed typically make a choice between the possibilities in advance of receiving syntactic disambiguation and that this choice makes the less preferred structure harder to understand (e.g. MacDonald, 1993).

To the extent that detailed internal information (in this case, partially constructed semantic representations must be output in order to make a decision) is exchanged between the non-domain-specific areas and the core language areas, the components are not informationally encapsulated and are not, in Fodor's (1983) terms, modular. Similar observations have been brought forward by Tsimpli and Smith (1999) and Smith (2003) in their discussion of the language module and the Theory of Mind module; they distinguish modules from quasi-modules, where the former, but not the latter are informationally encapsulated. Moreover, the fact that these quasi-modules exploit a non-perceptual vocabulary also suggests that they should be distinguished from modules in the classical Fodorian sense; the examples that Fodor (1983) discusses, coming from auditory perception and vision, involve input systems. Even in input systems, though, there is some evidence against strict informational encapsulation; the McGurk effect, for instance, illustrates that auditory perception can be mandatorily influenced by visual input.

Although the interactions within the network of specialized functions underlying language comprehension are not clear at this moment, the existence of more or less continuous interactions is not implausible. There is plenty of evidence from other cognitive domains which suggests that functional specialization within the brain does not necessarily implicate non-interactive modularity. Recent research in vision suggests that at both the neuronal level (Gilbert et al., 1990) and at the anatomical network level (Wray and Edelman, 1996), there can be functional specialization while the 'modules' interact more or less continuously. Network level interactions appear to be necessary for constant color perception given contextual variability (e.g. Wray and Edelman, 1996). Another example of interaction is found in visual attention. Functional MRI experiments have shown that primary visual cortex is affected by visual attention; however, ERP and MEG results show that the effects of attention are too late to occur during the initial processing of the visual

input (Martinez et al., 1999). This suggests that attention acts to provide re-entrant feedback to the primary visual cortex, i.e. top-down interaction. The example is particularly interesting because the visual system, and its resistance to external information, was one of the primary examples offered for the existence of independent informationally encapsulated modules in human cognition.

To sum up, on the basis of identification of the parts of the complex network involved in sentence comprehension and conjectures about the functions of the non-domain-specific components, the concept of modularity of language needs to be revised. Future research should focus on (1) specifying the precise functions of the non-domain-specific components of the language network, (2) investigating whether the same function is involved during language processing as during other cognitive tasks, and (3) determining the extent of interaction between different components of the language network.

5. Conclusions

Functional neuroimaging, within 10 years, has produced evidence which leads us to question many of the standard assumptions about the areas of the brain which are necessary and sufficient for the development and use of language. It has confirmed many of the observations based on neuropsychological data, but it has added evidence which suggests significant reinterpretations of these data. We have discussed four standard claims about the relationship between language and its neurological bases. Each of these is thrown into question by these new forms of evidence, and some can be totally discarded. In the future, neuroimaging methods may lead to even more massive revisions of our view of the neurological structure underlying language.

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