

Review

Meta-analyzing left hemisphere language areas: Phonology, semantics, and sentence processing

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The advent of functional neuroimaging has allowed tremendous advances in our understanding of brain–language relationships, in addition to generating substantial empirical data on this subject in the form of thousands of activation peak coordinates reported in a decade of language studies. We performed a large-scale meta-analysis of this literature, aimed at defining the composition of the phonological, semantic, and sentence processing networks in the frontal, temporal, and inferior parietal regions of the left cerebral hemisphere. For each of these language components, activation peaks issued from relevant component-specific contrasts were submitted to a spatial clustering algorithm, which gathered activation peaks on the basis of their relative distance in the MNI space. From a sample of 730 activation peaks extracted from 129 scientific reports selected among 260, we isolated 30 activation clusters, defining the functional fields constituting three distributed networks of frontal and temporal areas and revealing the functional organization of the left hemisphere for language. The functional role of each activation cluster is discussed based on the nature of the tasks in which it was involved. This meta-analysis sheds light on several contemporary issues, notably on the fine-scale functional architecture of the inferior frontal gyrus for phonological and semantic processing, the evidence for an elementary audio–motor loop involved in both comprehension and production of syllables including the primary auditory areas and the motor mouth area, evidence of areas of overlap between phonological and semantic processing, in particular at the location of the selective human voice area that was the seat of partial overlap of the three language components, the evidence of a cortical area in the pars opercularis of the inferior frontal gyrus dedicated to syntactic processing and in the posterior part of the superior temporal gyrus a region selectively activated by sentence and text processing, and the hypothesis that different working memory perception–actions loops are identifiable for the different language components. These results argue for large-scale architecture networks rather than modular organization of language in the left hemisphere.

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Introduction

In the nineteenth and twentieth centuries, our understanding of how the human brain analyzes and produces language was shaped by aphasiology. This approach helped to define a model of language architecture, in which Broca's and Wernicke's areas—two fairly large and loosely defined cortical areas located in the left frontal and temporal lobes—were assigned the leading roles in language production and comprehension, respectively (Geschwind, 1970).

In the 1980s, the advent of non-invasive functional brain imaging techniques, such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), shifted the emphasis towards investigating the neural bases of language in the normal human brain. These techniques have enabled the investigation of specific components of brain language implementation through the tailoring of experimental neuro-linguistic paradigms. Fifteen years have passed since the initial pioneering studies (Petersen et al., 1988; Zatorre et al., 1992), and the amount of information coming from functional imaging studies offers the opportunity to propose an updated view on brain–language relationships.

Starting from 260 articles published between 1992 and 2004, the present meta-analysis is constituted with 129 scientific reports, including 262 component-specific cognitive contrasts reporting 730 activation peaks in the left hemisphere cortex. These contrasts were selected from studies investigating three language-processing component classes, namely, “phonological,” “semantic,” and “sentence processing” components. This classification emerges not from language models per se but more pragmatically from the design of the selected functional imaging protocols, which compared cognitive conditions with increasingly complex verbal material.

Selection of articles and contrasts to be included in the present meta-analysis was based upon five major criteria: 1—we limited the investigation to studies on normal volunteers; 2—we retained those that reported their results in stereotactic coordinates, thereby excluding articles using a region-of-interest (ROI) approach; 3—we selected component-specific contrasts, thereby excluding studies that used low-level reference tasks, such as cross-fixation

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or rest, for semantic and sentence processing investigations; 4—we selected activation peaks located in the left–middle and inferior frontal gyrus, including the insula, the superior, middle, and inferior temporal gyri and inferior parietal gyrus; 5—peaks that fell outside the brain or in the white matter were thus excluded. The selected peaks for each class were then submitted to a spatial clustering algorithm in the standard neuroanatomical reference space shared by the brain mapping community (i.e., Montreal Neurological Institute (MNI) space), after appropriate conversion when necessary.

The present approach is in line with Poldrack's meta-analysis of the inferior frontal gyrus that allowed an anatomo-functional segregation for phonological and semantic processing (Poldrack et al., 1999). It is based on the whole brain three-dimensional and quantitative methodology that our laboratory has developed for the identification of the different pathways for word reading (Jobard et al., 2003). This approach appears complementary to recent reviews on language that investigated one language component (word processing (Indefrey and Levelt, 2004; Price, 2000), semantic processing (Bookheimer, 2002), sentence processing (Friederici, 2002)) and confronted a reduced number of investigations to propose a synthesis of functional imaging results within a given theoretical frame. These latter reviews are based on a fine-grained analysis of the paradigms and provide important insights on the neural representation of language. However, they describe functional anatomy of language at the gyral level only, leaving open the question of a more accurate cortical localization of a given process and thus that of specificity and interactions of different processes at regional level. Complementary to these works, the present methodology provides a fine-grained analysis of the brain functional activations, searching for the existence of areas dedicated to each of the language components—for instance, the segregation of semantic and phonological areas within the inferior frontal gyrus—and/or the opportunity to question the role of nearby or overlapping cortical areas. Given its power in terms of number of subjects and range of language paradigms, our meta-analysis approach offers the possibility of identifying regions that could have been overlooked by single protocols and that would correspond to invariants of a given language component. We think that such an approach is the only way to provide empirical arguments to support the theoretical shift proposed by M. Mesulam and J. Fuster that cognition in the brain is supported by overlapping and interactive large-scale cognitive networks rather than modules (Fuster, 2003; Mesulam, 1990).

Methods

Contrast selection

To meta-analyze the language neuroimaging literature, a classification of language-processing components had to be adopted in order to sort the various cognitive states that were reported. We retained mainly component-specific contrasts, i.e., contrasts designed to target a precise component; low-level contrasts, such as comparisons between a language task with a resting state or a low level baseline, were discarded because such contrasts result in the activation of multiple peaks corresponding to multiple cognitive components.

Because of the inherent constraints of the difference paradigm, the organization of language levels documented with functional

imaging is not based on the historical order followed by the development of linguistic theories (namely syntactic, semantic, and then pragmatic), but rather on the hierarchical linguistic complexity of the verbal stimuli, namely, phonological, semantic, and syntactic (Tables 1, 2, and 3). Such a hierarchy is close to the developmental steps of language acquisition in children: from the processing of language sounds to the understanding and elaboration of sentences (Damon, 2000).

The 262 component-specific contrasts gleaned from the 129 reports were classified in three language components. Phonological processing had been investigated in 45 studies, including 86 contrasts leading to the detection of 125 activation peaks in the left frontal lobe and 122 peaks in the left temporal and inferior parietal areas. Phonological tasks (Table 1) required the subjects to repeat or articulate syllables; to read, listen, or attend to syllables or letters; to read a pseudo-word (constructed upon the orthographic rules of a given language but without meaning) or count the number of syllables it encompassed; to count the number of syllables in a word; or to discriminate whether a word ended with the same sound. Studies of the selective human voice area were also included. Working-memory tasks on letters were included at the phonological level since such tasks are known to be based on the silent rehearsal of the different letters to recall (phonological loop).

The meta-analysis included 67 studies on semantic processing. Within these studies, 111 contrasts led to 145 frontal peaks of activation and to the detection of 177 temporal and parietal peaks of activation. Semantic tasks (Table 2) called either for simple access to meaning (word reading, word listening); categorization (decide whether a presented stimulus shows a living or non-living creature, a natural or manufactured object, a word or not); association (e.g., word generation: generate a verb semantically related to visual or auditory words or pictures); semantic retrieval (such as the retrieval of an object property); selection among semantic knowledge (tasks where semantic association activation are compared whether the word to retrieve has high or low competitors); or semantic priming tasks.

There are relatively fewer reports on sentence processing than on phonology or semantics, and the present analysis was based on 36 functional imaging studies. Among these, 65 contrasts resulted in 59 peaks of activation in the frontal lobe and 102 activation peaks in the temporal lobe (Table 3). These tasks included paradigms on sentence/text comprehension processing such as passive listening or reading compared to the listening or reading of pseudo-sentences (unlinked words). It also included paradigms targeting a specific component of sentence comprehension such as selective attention to voice or speaker during sentence listening; emotional judgment; comparison of sentence comprehension with high or low mental imagery content; working memory for sentences compared to that for words; sentence completion; and plausibility judgment on the sentence semantic content. We also included a set of reports that used more constrained tasks to investigate syntactic processing that were classified as syntactic processing. These studies compared the processing of complex sentences to simple ones, also called syntactic movement (e.g., object–subject sentences compared to subject–object sentences: The red book John gave to his sister/John gave the red book to his sister; or embedded sentences).

Data collection and standardization

Although all peak coordinates we selected were reported as “stereotactic,” it is well known that some discrepancies exist

Table 1

List of the 45 studies including the 86 contrasts that investigated phonological processing filed into the meta-analysis, with a short description of the paradigms

Frontal type of contrast (number of contrasts)	Temporal and parietal type of contrast (number of contrasts)
Articulation, repetition (16) (Bookheimer et al., 2000; Braun et al., 1997; Heim et al., 2002; McGuire et al., 1996; Price et al., 1996c; Riecker et al., 2000; Warburton et al., 1996; Wildgruber et al., 2001)	Articulation, repetition (10) (Bookheimer et al., 2000; Braun et al., 1997; Calvert et al., 1999; Howard et al., 1992; Price et al., 1996c; Warburton et al., 1996; Wildgruber et al., 2001)
Reading, listening, attending to, discriminating syllables or letters (13) (Beauregard et al., 1997; Jancke and Shah, 2002; Jessen et al., 1999; Joanisse and Gati, 2003; Paulesu et al., 2000; Poeppel et al., 2004; Sekiyama et al., 2003; Zatorre et al., 1992)	Reading, listening, attending to, discriminating syllables or letters (20) (Beauregard et al., 1997; Belin and Zatorre, 2003; Hugdahl et al., 2003; Jancke et al., 2002; Jancke and Shah, 2002; Jessen et al., 1999; Joanisse and Gati, 2003; Poeppel et al., 2004; Sekiyama et al., 2003; Zatorre et al., 1992)
Reading, syllable counting with pseudo-words (10) (Herbster et al., 1997; Kotz et al., 2002; Mechelli et al., 2000; Meyer et al., 2002; Paulesu et al., 2000; Poldrack et al., 1999)	Listening, reading, discriminating pseudo-words (11) (Binder et al., 2000; Cappa et al., 1998; Fiez et al., 1996; Herbster et al., 1997; Hickok et al., 2003; Hugdahl et al., 2003; Meyer et al., 2002; Paulesu et al., 2000)
Discriminating, syllable counting, word rhyming (14) (Booth et al., 2002; Heim and Friederici, 2003; Poldrack et al., 1999; Price et al., 1997; Roskies et al., 2001; Zatorre et al., 1996)	Reading, discriminating, syllable counting, rhyming task with words (8) (Booth et al., 2002; Buchanan et al., 2000; Heim and Friederici, 2003; Scott et al., 2003; Zatorre et al., 1996)
Working memory on letters (8) (Bunge et al., 2001; Cohen et al., 1997; Hautzel et al., 2002; Paulesu et al., 1993; Rypma et al., 1999)	Working memory on letters (7) (Bunge et al., 2001; Cohen et al., 1997; Hautzel et al., 2002; Paulesu et al., 1993; Rypma et al., 1999)
	Human selective voice area (2) (Belin et al., 2000, 2002)

The number of contrast that elicited activation peaks was 61 in the frontal lobe and 58 in the temporal and parietal lobes.

between laboratories over the world in the way subjects are transferred in the common space (Brett et al., 2002; Chau and McIntosh, 2005), which may bias the comparison of coordinates. A first source of discrepancy is the use of different spatial normalization algorithms. However, it has been previously demonstrated that this source has a moderate impact on the resulting inter-subject functional maps and results in the reported activation peak

coordinates (Crivello et al., 2002). The second and major source of discrepancy arises from the nature of the brain template used for the spatial normalization procedure. Reference brains indeed may not be exactly of the same size, and it is therefore crucial to correct for these size differences if one wishes to compare activation peaks issued from studies using different templates. Fortunately, two templates only are most widely used in the neuroimaging

Table 2

List of the 67 studies including the 111 contrasts that investigated semantic processing filed into the meta-analysis, with a short description of the paradigms

Frontal type of contrast (number of contrasts)	Temporal and parietal type of contrast (number of contrasts)
Reading words (6) (Cohen et al., 2002; Hagoort et al., 1999; Herbster et al., 1997; Heun et al., 2000; Price et al., 1996b)	Reading, listening to words (27) (Binder et al., 1996; Binder et al., 2000; Bookheimer et al., 1995; Büchel et al., 1998; Cohen et al., 2002; Démonet et al., 1994; Fiez et al., 1999; Giraud et al., 2000; Hagoort et al., 1999; Herbster et al., 1997; Howard et al., 1992; Menard et al., 1996; Moore and Price, 1999; Price et al., 1996b; Price et al., 1996c; Small et al., 1996; Specht and Reul, 2003; Wise et al., 2001)
Categorization (17) (Binder et al., 1996; Binder et al., 2003; Braver and Bongiolatti, 2002; Bright et al., 2004; Buchanan et al., 2000; Heim et al., 2002; Jennings et al., 1998; Noesselt et al., 2003; Perani et al., 1999; Poldrack et al., 1999; Scott et al., 2003)	Categorization (18) (Binder et al., 1996; Binder et al., 2003; Binder et al., 1999; Bright et al., 2004; Cappa et al., 1998; Chee et al., 1998; Fiebach et al., 2002; Grossman et al., 2002; Heim et al., 2002; Hugdahl et al., 2003; Jennings et al., 1998; Perani et al., 1999; Price et al., 1997; Scott et al., 2003)
Semantic association, word generation (17) (Adams and Janata, 2002; Booth et al., 2002; Damasio et al., 2001; Gurd et al., 2002; Kotz et al., 2002; Martin et al., 1996; McDermott et al., 2003; Noppeney and Price, 2004; Roskies et al., 2001; Savage et al., 2001; Vandenberghe et al., 1996; Vingerhoets et al., 2003; Warburton et al., 1996)	Semantic association, word generation (31) (Adams and Janata, 2002; Booth et al., 2002; Buckner et al., 2000; Chee et al., 2000; Crosson et al., 1999; Damasio et al., 2001; Davis et al., 2004; Etard et al., 1999; Fiez et al., 1996; Kosslyn et al., 1994; Martin et al., 1995; McDermott et al., 2003; Noppeney and Price, 2004; Roskies et al., 2001; Vandenberghe et al., 1996; Vingerhoets et al., 2003; Warburton et al., 1996; Wise et al., 2001)
Semantic retrieval (11) (Heun et al., 2000; James and Gauthier, 2004; Kelley et al., 2002; Ronnberg et al., 2004; Thompson-Schill et al., 1999; Wiggs et al., 1999)	Semantic retrieval (10) (Heun et al., 2000; James and Gauthier, 2004; Sevostianov et al., 2002; Thompson-Schill et al., 1999; Wiggs et al., 1999)
Selection (9) (Thompson-Schill et al., 1997; Wagner et al., 2001)	Selection (2) (Thompson-Schill et al., 1997)
Semantic priming (1) (Wagner et al., 2000)	Semantic priming (3) (Kotz et al., 2002; Wagner et al., 2000)

The number of contrast that elicited activation peaks was 61 in the frontal lobe and 91 in the temporal and parietal lobes.

Table 3

List of the 36 studies including the 65 contrasts that investigated sentence processing filed into the meta-analysis, with a short description of the paradigms

Frontal type of contrast (number of contrasts)	Temporal and parietal type of contrast (number of contrasts)
Sentence or text comprehension: passive listening or reading (3) (Meyer et al., 2004; Vingerhoets et al., 2003); working memory (1) (Hashimoto and Sakai, 2002); attention (2) (Homae et al., 2002, 2003); sentence completion (3) (Kircher et al., 2001; Nathaniel-James and Frith, 2002); plausibility judgment (3) (Baumgaertner et al., 2002; Bottini et al., 1994; Kuperberg et al., 2000); emotional judgment (1) (Kotz et al., 2003)	Sentence or text comprehension: passive listening or reading (13) (Crinion et al., 2003; Fletcher et al., 1995; Goel et al., 1998, 2000; Kansaku et al., 2000; Meyer et al., 2004; Scott et al., 2000; Vingerhoets et al., 2003); attention (5) (Homae et al., 2002; Homae et al., 2003; von Kriegstein et al., 2003); sentence completion (3) (Kircher et al., 2001); plausibility judgment (7) (Baumgaertner et al., 2002; Bottini et al., 1994; Kuperberg et al., 2000; Zysset et al., 2002); mental imagery (2) (Just et al., 2004); comprehension (3) (Ferstl and von Cramon, 2002; Maguire and Frith, 2004; Vogele et al., 2001)
Syntactic processing (19) (Ben Shachar et al., 2004; Caplan, 2001; Caplan et al., 1999; Constable et al., 2004; Cooke et al., 2002; Dapretto and Bookheimer, 1999; Embick et al., 2000; Luke et al., 2002; Stowe et al., 1998; Stromswold et al., 1996; Waters et al., 2003)	Syntactic processing (14) (Ben Shachar et al., 2004; Constable et al., 2004; Cooke et al., 2002; Embick et al., 2000; Gandour et al., 2003; Luke et al., 2002; Stowe et al., 1998; Waters et al., 2003)

The number of contrast that elicited activation peaks was 32 in the frontal lobe and 47 in the temporal and parietal lobes.

community: the Talairach stereotactic atlas (Talairach and Tournoux, 1988) and the MNI (Montreal Neurological Institute) atlas. To benefit from the MNI single-subject parcellation we developed (Tzourio-Mazoyer et al., 2002), we choose this last template as our working space. Therefore, we applied a correction to transform all the activation peak coordinates in Talairach reference space into MNI reference space (see <http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispac.html> for a detailed description of the transformation used). Activation peak coordinates found in studies performed with the SPM software prior to SPM96, with AFNI or with LIPSIA and specifying that the coordinates were reported in the Talairach space were transformed to the MNI space. Studies done with SPM96 or later versions were considered as using MNI template and therefore did not require any transformation.

After taking into account their procedure for normalization, we checked using a macroscopic parcellation of the MNI single-subject reference brain that the peaks were located in the middle or inferior frontal gyri, the superior, middle, or inferior temporal gyri, or the inferior parietal gyrus of the left hemisphere (Tzourio-Mazoyer et al., 2002) (Fig. 1, top). Those that did not intersect these anatomical regions of interest were excluded from the meta-analysis.

Peak clustering

For each language-component class, we then selected the corresponding set of peaks in the left temporal, inferior parietal, middle and inferior frontal gyri, or insula of the frontal lobe. Each set of peaks was segregated into a number of spatially distinct clusters, using a hierarchical classification algorithm that minimized the spatial extent of each cluster while maximizing the Euclidian peak-to-peak distance between clusters [no less than 7 mm in the x , y , and z directions; for details of the method, see Jobard et al. (2003)]. The result of the procedure provides mean coordinates for each cluster in the MNI space and the standard deviation calculated as the square root of the mean of squared Euclidian distances to the center of mass.

Because the clustering process was performed for each component independently, we further checked whether pairs of clusters belonging to different language-component networks were spatially distinct or not by testing two by two the significance of their mean Euclidian distance with paired t tests.

Results

The clustering process for each language component led to the segregation of three to five clusters in the left frontal lobe and five to seven in the left temporal and parietal areas (Fig. 1, bottom). Cluster standard deviations ranged from 8 to 19.5 mm (Table 4). While similar numbers of frontal and temporal peaks were found for phonological contrasts (frontal: 125, temporal: 122, see Table 4), a larger number of temporal peaks were noted for semantic (frontal: 145, temporal: 177) and sentence processing contrasts (frontal: 59, temporal: 102). For each of the 30 clusters tables giving the reference of the articles, a description of the contrasts investigated as well as the peaks coordinates (after transformation in the MNI space if necessary) is available as supplementary material.

Five frontal and six temporal clusters were identified for phonology (Table 4, Fig. 2). Frontal clusters were located in a caudal position, aligned vertically and somewhat following gyral anatomy with their center of mass located at the level of the upper Rolandic sulcus (RolS), lower precentral gyrus (Prec), dorsal part of the pars triangularis of the inferior frontal gyrus (F3td), Rolandic operculum (RolOp), and at the junction between the orbital part of F3 and the middle frontal gyrus (F3orb/F2). Four of the six temporal clusters were segregated along the superior temporal sulcus, from the most anterior part of T1 (T1a), through the planum temporale (PT), the middle part of T1 (T1), and up to the supramarginalis gyrus (SMG). The two other phonological temporal clusters were located in the vicinity of the middle temporal sulcus (T2m, T3p).

Peaks corresponding to semantic contrasts were segregated into four frontal and seven temporal clusters (Table 4, Fig. 3). The four semantic frontal clusters, again aligned vertically, covered the inferior frontal gyrus from its upper part at the junction with the precentral gyrus (PrF3op), through the dorsal part of the pars opercularis (F3opd) and ventral part of its pars triangularis (F3tv), down to its pars orbitaris (F3orb). Their center of mass was located in a significantly different position than their phonological counterparts (Table 5). The seven semantic temporal clusters overlapped the middle and inferior temporal gyri, two of them significantly overlapping the T1a and T3p phonological clusters. The five other semantic temporal and parietal clusters were at distance from phonological clusters: the most rostral was located at the level of the temporal pole (Pole), the most caudal in the angular gyrus (AG),

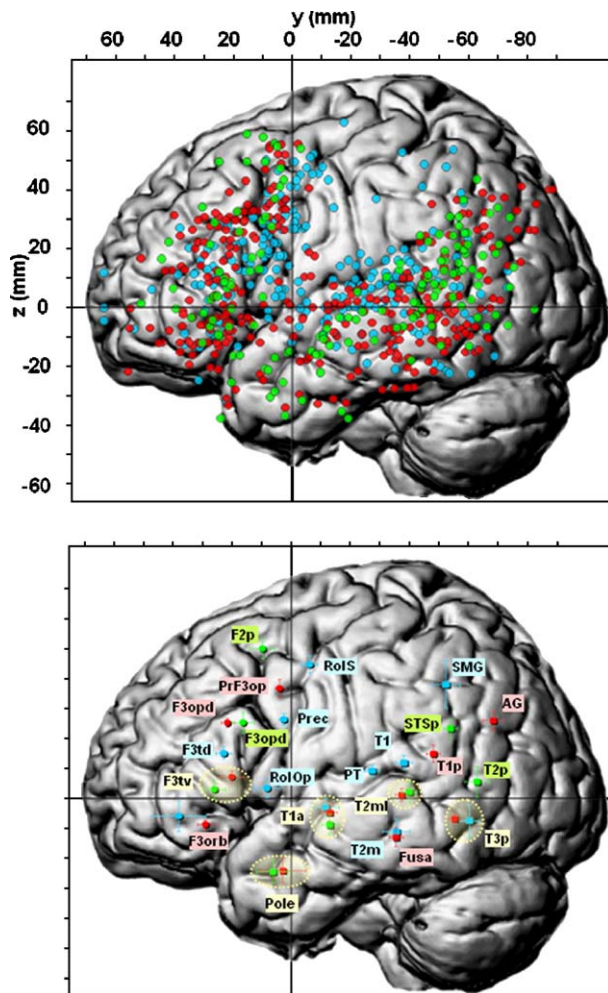


Fig. 1. Overview of the meta-analysis. Top: sagittal projection map of the 730 activation peaks. Each activation peak is color-coded according to its contrast category: phonology (blue), semantic (red), and syntax (green). Bottom: clusters identified for phonological (blue), semantic (red), and syntactic (green) processing and obtained from the spatial clustering of the peaks. Clusters of different components that were not spatially distinct are circled (yellow). Error bars correspond to twice the standard error on the y and z stereotactic coordinates. The left hemisphere lateral surface rendering of the MNI single-subject brain template, together with the corresponding stereotactic grid, is displayed for anatomical reference. RoIS, Rolandic sulcus; RoOp, Rolandic operculum; F3t, pars triangularis of the left inferior frontal gyrus; F3op, pars opercularis of the left inferior frontal gyrus; F3orb, pars orbitalis of the left inferior frontal gyrus; SMG, supramarginalis gyrus; PT, planum temporale; T1, superior temporal gyrus; T2, middle temporal gyrus; T3, inferior temporal gyrus; Prec, precentral gyrus; F2, middle frontal gyrus; PrF3op, precentral gyrus/F3op junction; STS, superior temporal sulcus; AG, angular gyrus; Fusa: anterior fusiform gyrus; a, anterior; p, posterior; l, lateral; m, middle; d, dorsal; v, ventral.

and the last three were found at the level of the anterior fusiform gyrus (Fusa), the posterior part of the superior temporal gyrus (T1p), and the lateral and middle part of T2 (T2ml).

Finally, we identified three frontal and five temporal clusters devoted to sentence processing (Table 4, Fig. 4). In the frontal lobe, F3opd and F3tv were close to or overlapped with semantic clusters (Table 5), whereas the third cluster was at distance from both phonological and semantic clusters, its center of mass being located in the dorsal part of the middle frontal gyrus (F2p).

Looking at the spatial distribution of the peaks issued from reports dealing with syntactic processing, they appear to be located in the dorsal part of the clusters. In the temporal lobe, three clusters overlapped with semantic ones (Pole, T1a, and T2ml), while two others were distant from both phonological and semantic clusters, one at the level of the posterior part of the superior temporal sulcus (STSp), the other in the posterior part of the middle temporal gyrus (T2p). No particular spatial distribution of the peaks issued from studies of syntax was noted in the temporal lobe.

In summary, clustering of left frontal and temporal activation foci reported in 129 literature reports dealing with the neuroimaging of language reveals distinct, albeit partially overlapping, networks for phonology, semantics, and sentence processing. Language component networks appear to grossly follow the lobe gyral architectures, with phonological clusters located in a more caudal and dorsal position in the frontal and temporal lobes, respectively. The T1a area appears to be common to all three language components, while the Pole and T2ml are common to semantic and sentence's clusters and T3p to semantic and phonology clusters. In the frontal lobe, only semantic and syntactic clusters overlapped in the F3opd and F3tv clusters.

Discussion

Methodological issues

The first point that has to be discussed concerns the consequences of the methodological constraints applied on the studies selection. It must be underlined that the restriction we applied prevented us to include some studies that provide key elements in the comprehension of language networks. This pitfall is inherent to any meta-analysis, and we tried to overcome this limitation by integrating such articles within the discussion.

The second point is related to the large-grained resolution in terms of language components and levels of processing. The approach that was here chosen, namely to work at a good cortical resolution without any a priori, required operating on a large number of studies per category and thus decreased the final resolution in terms of paradigms. In a second step, however, the discussion on the functional role of each identified cluster relied on a finer-grained analysis of the tasks that contributed to it.

The third point concerns inherent limitations related to the low spatial resolution of the present methodology. First, there is the fact that, although we attempted to correct for the different templates used in the set of studies, the correction applied is not perfect and leads to larger variability than occurs in the intra-group studies (Brett et al., 2002; Chau and McIntosh, 2005). Second is the fact that the 7-mm limit we set for the spatial clustering procedure prevents detection of clusters of lower resolution in the intra-component analysis as well as in the inter-component analysis.

The following discussion concerning the language organization thus takes into account these methodological limitations, particularly when clusters from different language components cannot be distinguished in terms of spatial localization. Although the cortical areas containing overlapping components from different clusters may include different functional fields that could be segregated using a more refined intra-group analysis, they can be considered as the seat of close interactions between these language components.

Given these reservations, one should consider that, although the resolution of the present meta-analysis is low in terms of

Table 4

Center of mass of the clusters identified for each of the linguistic components of language processing in both left frontal and left temporal lobes

	Phonological				SD (<i>x, y, z</i>)	Semantic				SD (<i>x, y, z</i>)	Sentence				SD (<i>x, y, z</i>)
	<i>x</i>	<i>y</i>	<i>z</i>			<i>x</i>	<i>y</i>	<i>z</i>			<i>x</i>	<i>y</i>	<i>z</i>		
Frontal	RoIS (21)	-47	-6	44	10.7	PrF3op (27)	-42	4	36	11.4	F2p (14)	-37	10	48	12.3
	Prec (36)	-48	2	26	9.6	F3opd (41)	-44	21	24	11.1	F3opd (15)	-49	16	24	11.2
	F3td (38)	-44	23	15	11.6	F3tv (38)	-43	20	4	16.0	F3tv (30)	-44	26	2	14.9
	RoLOp (18)	-48	8	3	14.2	F3orb (39)	-37	31	-9	14.0					
	F3orb/F2 (12)	-33	37	-6	19.0										
Total peaks (125)					(145)					(59)					
Temporal and parietal	SMG (10)	-42	-52	37	16.4	AG (27)	-45	-68	26	14.1					
	T1 (35)	-50	-38	12	12.4	T1p (15)	-55	-48	15	12.1	STSp (27)	-50	-54	22	11.6
	PT (23)	-60	-27	9	8.4										
	T1a (27)	-56	-12	-3	14.7	T1a (30)	-56	-13	-5	11.6	T1a (16)	-57	-13	-8	10.9
	T3p (17)	-50	-60	-7	14.5	T3p (38)	-46	-55	-7	11.1	T2p (16)	-40	-63	5	15.1
	T2m (10)	-51	-35	-11	12.5	T2ml (21)	-59	-37	1	8.0	T2ml (25)	-57	-40	2	12.0
						Fusa (30)	-38	-35	-13	13.6					
Total peaks (122)					Pole (16)	-41	3	-24	19.5	Pole (18)	-47	6	-24	15.7	
					(177)					(102)					

Clusters are characterized by their abbreviated anatomical label and their center of mass stereotactic coordinates (*x, y, z*, in mm) and standard deviation (SD calculated as the square root of the mean of squared Euclidian distances to the center of mass). Each cluster gathers a number of activation peaks of component specific contrasts (shown in parentheses). RoIS, RoLOp: Rolandic sulcus, Rolandic operculum, respectively; F3t, F3op, and F3orb: pars triangularis, opercularis, and orbitaris of the left inferior frontal gyrus, respectively; SMG: supramarginalis gyrus; PT: planum temporale; T1, T2, and T3: superior, middle, and inferior temporal gyrus, respectively; Prec: precentral gyrus; F2: middle frontal gyrus; PrF3op: precentral gyrus/F3op junction; STS: superior temporal sulcus; AG: angular gyrus; Fusa: anterior fusiform gyrus; a, p, l, m, d, v: anterior, posterior, lateral, middle, dorsal, ventral, respectively.

identification of functional fields, it is the first that provides whole-brain results that are under the gyral level.

Phonological networks

The present meta-analysis reveals that all frontal phonological areas except one (F3td) were located in the posterior part of the frontal lobe distributed along the precentral gyrus. In the temporal lobe, the 122 peaks were aggregated in clusters located along the superior temporal gyrus and the supramarginal gyrus. We propose that these areas are organized into two neural components dedicated to speech sound perception and production: a fronto-temporal auditory-motor network and a fronto-parietal loop for phonological working memory. In addition, a set of modality-dependent temporal clusters overlapping with semantic clusters was identified, suggesting the existence of crossroad areas linking semantic and phonological processes.

Auditory-motor speech coordination network

Three frontal areas involved in phonological processing seem to be concerned with sensory-motor control, including an upper motor area for mouth motion control, a lower premotor area in the precentral gyrus that is dedicated to pharynx and tongue fine-movement coordination, and a sensory-motor integration region in the Rolandic operculum (Table 4, Fig. 2, bottom).

The cluster straddling the upper part of the RoIS closely matches the mouth primary motor area, as identified by a previous meta-analysis (Fox et al., 2001). The contrasts that correspond to this cluster included covert and overt articulation of phonemes (Bookheimer et al., 2000), syllables (Wildgruber et al., 2001), letters (Jessen et al., 1999), and pseudo-words (Riecker et al., 2000), as well as word repetition (Price et al., 1996c), and silent rehearsal of letters during working-memory tasks (Cohen et al., 1997; Rypma et al., 1999). This area shows an asymmetry favoring left hemisphere activity, attesting to its specialization for language, and is correlated with syllable rate production (Fox et

al., 2000). The fact that the leftward asymmetry decreases as the frequency of syllable production increases (Wildgruber et al., 2001) indicates a contribution to low-level aspects of speech motor control. Not only the production but also auditory discrimination of syllables (Hickok and Poeppel, 2004) activates this motor area, showing that the perception of syllables is achieved through the simulation of the motor activity necessary to produce the corresponding syllable. This hypothesis is confirmed both by a recent report showing that listening to syllables activates motor areas at the same location as RoIS, which was shown to be involved during speech production in the same subjects (Wilson et al., 2004). It is also strengthened by the evidence of activation of articulation muscles during speech listening (Fadiga et al., 2002), resulting from a transcranial magnetic stimulation study.

The lower precentral cluster (Prec) gathers peaks that show greater activity during phonological than semantic tasks, such as reading pseudo-words versus reading words (Herbster et al., 1997), detecting pseudo-words versus detecting words (Kotz et al., 2002), detecting rhymes versus detecting synonyms (Roskies et al., 2001), phonetic monitoring versus word and pseudo-word listening (Zatorre et al., 1992), and syllable counting versus word categorization (Poldrack et al., 1999). Because tongue (Riecker et al., 2000) and complex oro-laryngeal movements (Braun et al., 1997) also recruit this area, its involvement in phonology probably reflects the silent rehearsal component that is common to all of these tasks, as well as working-memory tasks (Bunge et al., 2001; Cohen et al., 1997; Hautzel et al., 2002; Paulesu et al., 1993; Rypma et al., 1999).

The area that encompasses the Rolandic operculum and the postcentral gyrus of the insula (RoLOp) is activated by overt or covert syllable articulation (Heim et al., 2002), pseudo-word articulation (Herbster et al., 1997; Warburton et al., 1996), or word repetition (Price et al., 1996a). A role in sensory-motor adjustments during speech articulation must be evoked for this area as it includes regions that are related to sensory integration. However, in contrast to the

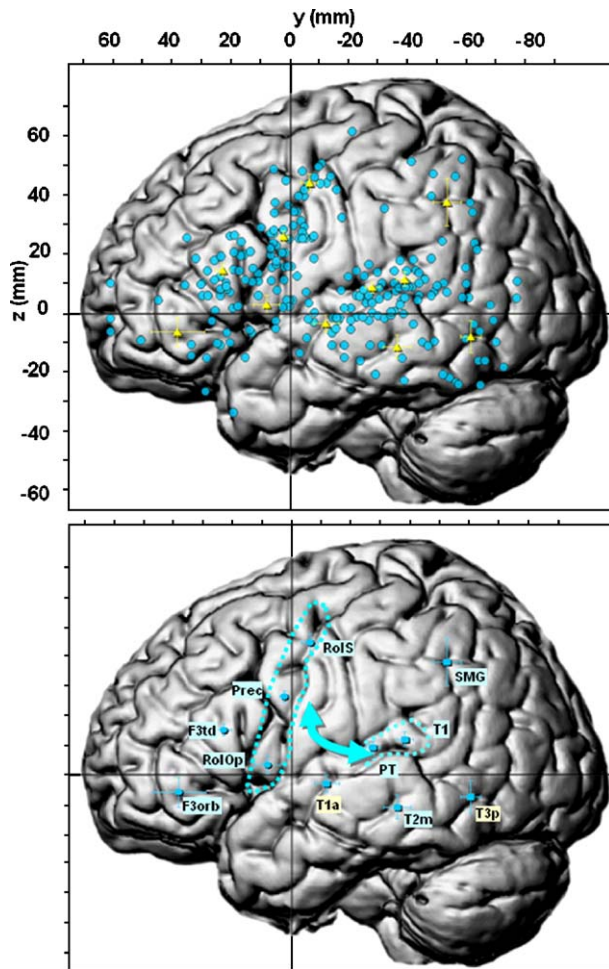


Fig. 2. Phonological clusters. Top: sagittal projection map of the 247 activation peaks issued from studies on phonological processing (blue); clusters are segregated by the algorithm for spatial classification and their standard error on the y and z axes (yellow). Bottom: illustration of the audio-motor loop that includes motor and premotor clusters along the precentral sulcus in the frontal lobe and auditory unimodal PT and T1 clusters in the temporal lobe (see Fig. 1 for legend).

mouth area, activity asymmetry in this region depends on the nature of the material: leftward asymmetry is observed during silent recitation of the month of the year, and rightward asymmetry during silent singing (Wildgruber et al., 1996).

Standard anatomical descriptions of white-matter bundles (Dejerine, 1980; Nieuwenhuys et al., 1988), as well as recent tensor diffusion imaging (Parker et al., 2005), show that the arcuate fasciculus (also called the superior longitudinal fasciculus) connects the precentral and pars opercularis areas of the inferior frontal gyrus to the posterior part of the superior temporal gyrus, including the planum temporale (PT) and the lateral part of the superior temporal gyrus. PT involvement in syllable perception and voice onset time (VOT) processing, as assessed with intra-cerebral recordings (Liégeois-Chauvel et al., 1999), was demonstrated with fMRI by Jancke et al. (2002). This was confirmed by Joanisse and Gati who reported PT enrollment in consonant and tone sweep, both of which require the processing of rapid temporal characteristics of auditory signals (Joanisse and Gati, 2003). PT phonological specialization relative to semantic processing is also supported by reports of higher activity in this area during pseudo-word than in word detection in an

auditory selective attention task (Hugdahl et al., 2003). Its anatomofunctional leftward hemispheric specialization is expressed by the fact that the PT exhibits a larger surface area in the left hemisphere (Geschwind and Levitsky, 1968) and shows a larger functional involvement during right-ear presentation than during dichotic presentation of syllables (Jancke and Shah, 2002).

In most cases, left PT activation is observed during auditory stimulus presentation, but tasks based on visually presented letter assembly can also elicit PT activation (Jessen et al., 1999; Paulesu et al., 2000; Rypma et al., 1999). Participation of a unimodal associative auditory area in the absence of an auditory stimulus was confirmed by Hickok et al., who reported coactivation of the PT and the posterior superior temporal gyrus in the temporal lobe during both speech listening and covert speech production (Buchsbaum et al., 2001; Hickok et al., 2003; Okada et al., 2003), together with the motor regions, i.e., the inferior

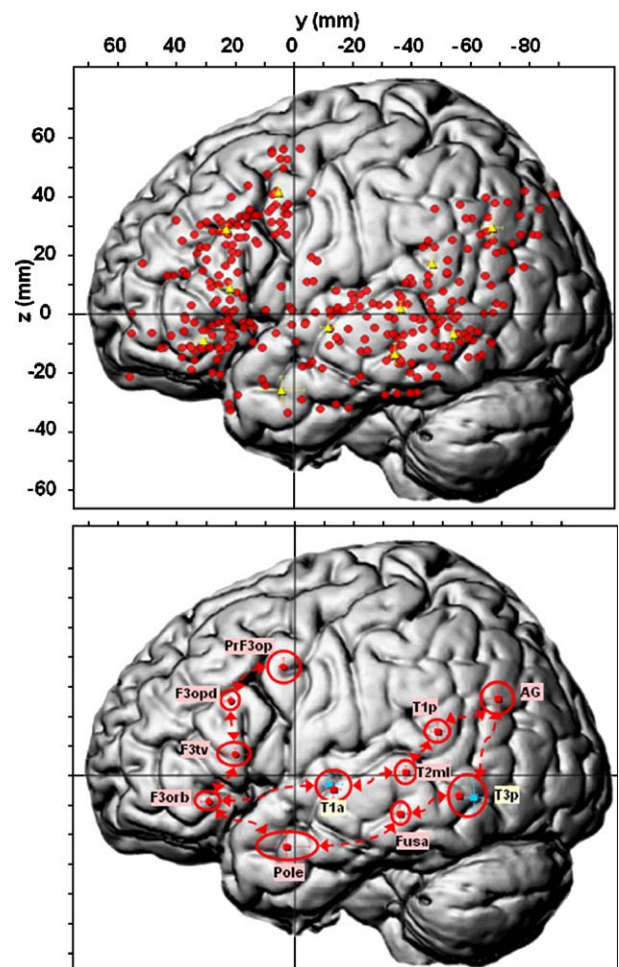


Fig. 3. Semantic clusters. Top: sagittal projection map of the 322 activation peaks derived from studies on semantic processing (red); clusters are segregated by the algorithm for spatial classification and their standard error on the y and z axes (yellow). Bottom: semantic networks include a dorsal and a ventral component in the temporal lobe. The ventral component is dedicated to visual material and includes T3p at the interface between phonological and semantic processes for audio-visual processing (yellow). The dorsal component is dedicated to auditory material and includes the voice area (yellow) at the interface between phonological and semantic processing. In the frontal lobe, the semantic areas are located in the anterior part of the inferior frontal gyrus (see Fig. 1 legend for abbreviations).

Table 5
Statistical comparison of the Euclidian distance between clusters of different language components

	Cluster 1	Cluster 2	Euclidian D (mm)	SD (mm)	P (<i>t</i> test)
Frontal	F3td phono	F3opd sem	10	2.56	<0.001
	F3td phono	F3opd sen	12	3.50	<0.001
	F3td phono	F3tv sem	11.4	3.20	<0.001
	F3td phono	F3tv sen	13	3.22	<0.001
	F3tv sem	F3tv sen	6	3.80	0.10
	F3opd sem	F3opd sen	7	3.35	0.05
	PrF3op sem	F2p sen	14	3.87	<0.001
	PrF3op sem	RoIS phono	14	3.24	<0.001
	F2p sen	RoIS phono	20	3.92	<0.001
	Temporal and parietal	Pole sem	Pole sen	7	6.04
T1p phono		T1p sem	12	4.09	<0.01
T1p phono		T1p sen	19	3.48	<0.001
T1p sem		STSp sen	11	3.86	<0.01
STSp sen		AG sem	15	3.61	<0.001
T2m pho		Fusa sem	13	4.89	<0.05
T2ml sen		T2ml sem	4	3.02	0.20
T2p sen		T3p phono	16	3.09	<0.01
T2p sen		T3p sem	15	4.20	<0.001
T3p phono		T3p sem	6	3.53	0.10
T1a phono		T1a sem	2	3.48	0.60
T1a sem	T1a sen	4	3.49	0.30	
T1a sen	T1a phono	6	4.13	0.20	

Paired *t* tests were used to assess the significance of the Euclidian distance between the pairs of clusters.

sem: semantics, sen: sentence processing; phono: phonology RoIS, RoOp: Rolandic sulcus, Rolandic operculum, respectively; F3t, F3op, and F3orb: pars triangularis, opercularis, and orbitaris of the left inferior frontal gyrus, respectively; SMG: supramarginalis gyrus; PT: planum temporale; T1, T2, and T3: superior, middle, and inferior temporal gyrus, respectively; Pr: precentral gyrus; F2: middle frontal gyrus; PrF3op: precentral gyrus/F3op junction; STS: superior temporal sulcus; AG: angular gyrus; Fusa: anterior fusiform gyrus; a, p, l, m, d, v: anterior, posterior, lateral, middle, dorsal, ventral, respectively.

precentral gyrus and the frontal operculum in the frontal lobe. The perception–action cycle that is supported by these fronto-temporal areas connected through the arcuate fasciculus fibers (Fig. 2, bottom) permits the implementation of a motor-sound-based, rather than pure-sound-based, phoneme representation (Hickok and Poeppel, 2004). In such a model, articulatory gestures are the primary and common objects on which both speech production and speech perception develop and act, in agreement with Liberman's motor theory of speech (Liberman and Whalen, 2000).

Phonological working-memory loop

One of the issues investigated by neuroimaging concerns the relationships between phonological and semantic processing in the left frontal lobe. As a matter of fact, lesion studies have not clearly resolved whether the analysis of language sounds and the processing of language meaning are segregated or not in the left F3. Recent investigations on this topic have produced contradictory results. In this line, an intriguing finding of this meta-analysis is the specific involvement of the dorsal part of the pars triangularis of the inferior frontal gyrus (F3td) in phonology, whereas this area was considered, until recently, to be a semantic area (Poldrack et al., 1999). As a matter of fact, in a landmark study, Poldrack et al. (1999) carried out a meta-analysis of activation peaks, comparing tasks that called for either

semantic or phonological processes. The results led these authors to propose a segregation of F3 into two functional areas: the posterior and dorsal part (pars opercularis, F3op), involved in phonological processing, and the anterior and ventral part (pars triangularis F3t and orbitaris F3orb), involved in semantic processing.

There is no doubt, however, that the dorsal cluster of the F3t (F3td) mainly contains peaks that have higher activity during phonological processing than during semantic processing; for example, counting the number of syllables in a word versus abstract/concrete categorization (Poldrack et al., 1999), pseudo-word repetition versus verb generation (Warburton et al., 1996), word articulation versus word reading (McGuire et al., 1996), non-word

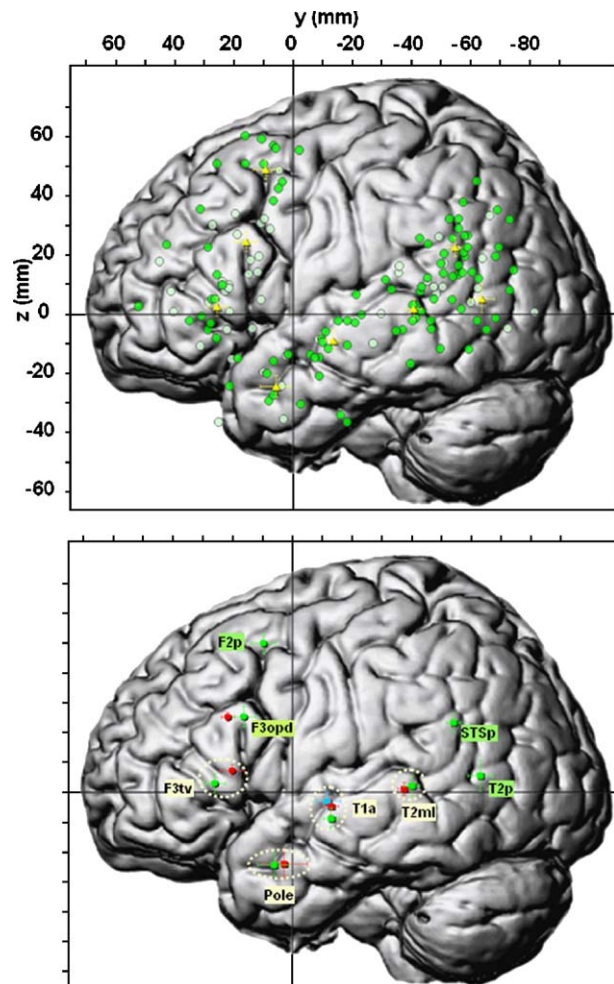


Fig. 4. Sentence (and text) clusters. Top: sagittal projection map of the 161 activation peaks derived from studies on sentence (green) and syntactic (light green) processing; clusters are segregated by the algorithm for spatial classification and their standard error on the *y* and *z* axes (yellow). Note that in the frontal lobe the peaks issued from studies investigating syntax are located more dorsally. In the temporal lobe, the spatial distribution of sentence and syntax peak is not different. Bottom: four of the sentence clusters are in close relationship with semantic ones, and clusters involved in both language components are circled (yellow). Four sentence clusters were in a significantly different position from semantic ones: one in the posterior part of the middle frontal gyrus (F2p), one in the dorsal part of upper part of the pars opercularis (F3opd), one in the posterior ending of the superior temporal gyrus (STSp), and the last in the posterior part of the middle temporal gyrus that is very likely activated by the mental-imagery component of sentence processing (T2p).

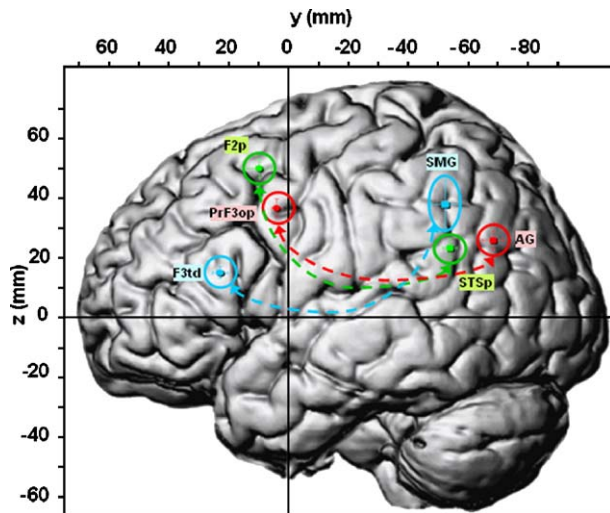


Fig. 5. Working-memory loops. The working-memory loop for phonological material connects higher-order areas that correspond to the F3td in the frontal lobe and SMG in the parietal lobe (blue). The working-memory loop for semantics includes a frontal area at the junction of the precentral gyrus and opercular part of the inferior frontal gyrus (PrF3op) and, in the parietal lobe, the angular gyrus (AG, red). The working-memory network for sentence and text comprehension includes the posterior part of the middle frontal gyrus (F2p) and the posterior part of the superior temporal sulcus (STSp, green).

versus word reading (Paulesu et al., 2000), reading consonant strings versus reading words (Jessen et al., 1999), and phonetic discrimination versus word listening (Zatorre et al., 1996). Unlike the Rolandic and precentral clusters, this area does not include activation peaks that are related to tongue or mouth movement. Instead, it exhibits a high proportion of peaks that are related to explicit working-memory tasks (Bunge et al., 2001; Cohen et al., 1997; Hautzel et al., 2002; Jonides et al., 1998; Rypma et al., 1999) during which subjects are required to keep in mind lists of letters or numbers through a short delay. Such tasks require the subject to mentally rehearse the list during the delay in what was defined by Baddeley as the phonological loop (Baddeley, 1992). Furthermore, the more anterior location of the frontal component of working-memory phonological processing, compared to auditory–motor language sound representation, is coherent with the postero-anterior frontal lobe hierarchical organization from motor to executive functions (Fuster, 1998).

Assigning a role in phonological working memory to F3td would be consistent with reports of its recruitment during tasks that rely heavily on this process, such as counting the syllables of a pseudo-word (Poldrack et al., 1999), repetition of a word (Price et al., 1996c) or pseudo-word (Warburton et al., 1996), or syllable identification in the presence of a low signal-to-noise ratio (Sekiyama et al., 2003). Moreover, five contrasts involving phonological working-memory tasks resulted in co-activation of peaks located in both F3td and supramarginalis gyrus (SMG) (Hautzel et al., 2002; Jonides et al., 1998; Rypma et al., 1999). Our meta-analysis confirms that the SMG is activated by working-memory tasks but not by rhyming tasks. It might therefore be considered as the phonological store area—part of the phonological loop postulated by Baddeley (1992) and initially demonstrated with functional imaging by Paulesu et al. (1993). Additional support for this model has been provided by Cohen, who showed a load effect (an increase in activity correlated with the amount of material to keep in mind) on F3td and SMG co-activation during

working-memory tasks based on letters (Cohen et al., 1997). Both regions, connected by both the arcuate fasciculus (Catani et al., 2005) and short connections (Duffau et al., 2003), constitute the neural basis of a perception–action cycle (Fuster, 1998, 2003) for phonological working memory (Fig. 5).

Semantic neural architecture

Semantic frontal areas

The meta-analysis shows that distinct phonological and semantic networks do exist in the frontal lobe and that the phonological areas are located caudally to semantic ones, along the precentral gyrus. The opercular part of F3 (F3op) appears to host semantic areas, while sub-parts of the F3t area are differentially recruited: the dorsal part by the working-memory component of phonology and the ventral part by semantic processing (Fig. 1, bottom, and Fig. 6). These observations led to the proposal of a functional parcellation of F3 slightly different from the F3op/F3t segregation proposed by Poldrack et al. (1999) for phonological and semantic processing.

As a matter of fact, the allocation of a phonological role to F3op had been questioned by Wagner et al. (2001), who showed that it was responsible for recovery of meaning and selection in semantic

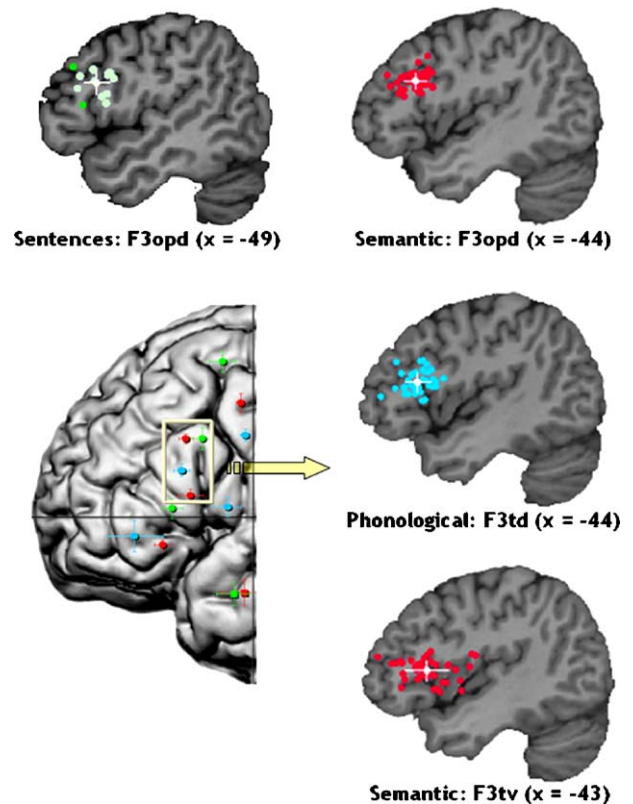


Fig. 6. Phonological, semantic, and sentence clusters in the left inferior frontal gyrus. Illustration of the spatial segregation of the semantic and sentence clusters located in the dorsal area of upper part of the pars opercularis (F3opd). Note that syntax peaks (light green) are in high proportion in the sentence cluster that is more dorsal (top horizontal row). Illustration of the phonological and semantic segregation in the inferior frontal gyrus: semantic clusters are located within the ventral part of the pars triangularis (F3tv) and opercularis (F3opd) and are significantly different from the phonological cluster F3td in terms of Euclidian distance (right vertical column).

knowledge (defined in a first study by Thompson-Schill (Thompson-Schill et al., 1997; Wagner et al., 2001)). Bookheimer in her review also underlined these apparently contradictory results (Bookheimer, 2002). The present results reconcile these discordant views: if semantic areas are indeed anterior to phonological ones, phonological areas are spread along the precentral gyrus rather than in the opercular part of F3.

The PrF3op cluster indeed aggregates peaks of sets of contrasts dealing with controlled semantic retrieval (Thompson-Schill et al., 1997; Wagner et al., 2001; Wiggs et al., 1999); it is the seat of semantic priming (Wagner et al., 2000) and part of the supramodal network identified by Vandenberghe et al. (1996) for word and picture semantic processing. Note that this area is more activated by semantic than phonological processing in the Poldrack et al. (1999) study conducted on semantic and phonological areas in the left F3.

The second frontal area dedicated to semantic processing was located in the orbital part of F3 (F3orb), a region that Demb et al. have proposed to be involved in the online retrieval of semantic information (Demb et al., 1995). This hypothesis is confirmed here since the F3orb is recruited during semantic retrieval in both oral and sign language (Ronnerberg et al., 2004) and is more activated during semantic than episodic retrieval (Wiggs et al., 1999). Such a role would also explain its involvement during categorization (Adams and Janata, 2002; Binder et al., 2003; Braver and Bongiolatti, 2002; Bright et al., 2004; Buchanan et al., 2000; Jennings et al., 1998; Noesselt et al., 2003; Noppeney and Price, 2004; Perani et al., 1999; Poldrack et al., 1999), association (Booth et al., 2002; Damasio et al., 2001), and word generation (Gurd et al., 2002; Martin et al., 1995) tasks. Notably, a study demonstrated that the co-activation of F3orb and PrF3op areas was modulated by the degree of control that is required during semantic retrieval (Wagner et al., 2001).

The two clusters that overlapped syntactic clusters (F3opd and F3tv) will be discussed in the section on sentence processing.

Semantic temporal areas

No fewer than seven semantic clusters were identified in the left temporal lobe (Fig. 3), organized along two routes: one dorsal and one ventral. Interestingly, only three of these clusters (T1p, Fusa, and AG) aggregated peaks from semantic tasks only; the others were co-located with clusters aggregating peaks issued from phonological (T1a, T3p) or syntactical (T2ml, Pole) tasks (Fig. 4). Analysis of the semantic contrasts that elicit activation peaks in the temporal lobe reveals a clear functional organization, including a modality-specific verbal area (T1p), a modality-independent verbal area (T2ml), and amodal conceptual areas (AG, Fusa).

The T1p cluster was activated by semantic contrasts based on written words, such as reading words versus pseudo-words or pseudo-fonts (Fiebach et al., 2002; Fiez et al., 1999; Howard et al., 1992; Moore and Price, 1999; Small et al., 1996), and categorization of written words (Chee et al., 2000; Grossman et al., 2002; Heim et al., 2002; Jennings et al., 1998; Perani et al., 1999). On the basis of its location, we propose that the T1p area processes the letters and graphemes converted into syllable sounds and maintained in working memory by means of the phonological networks that operate during reading; this processing makes them accessible in a verbal amodal format for further syntactic (in T1p) or conceptual (in AG) processing (Fig. 7). This hypothesis could be further investigated by analyzing, with modern neuro-anatomical techniques, the location of lesions in patients with alexia.

The AG cluster aggregated high-order contrasts bearing on both visual and auditory words and pictures (9 visual words, 7 auditory words, 11 pictures of objects or scenes) and can be considered as involved in conceptual knowledge. This multimodal region, composed of a high-order heteromodal association cortex, can be

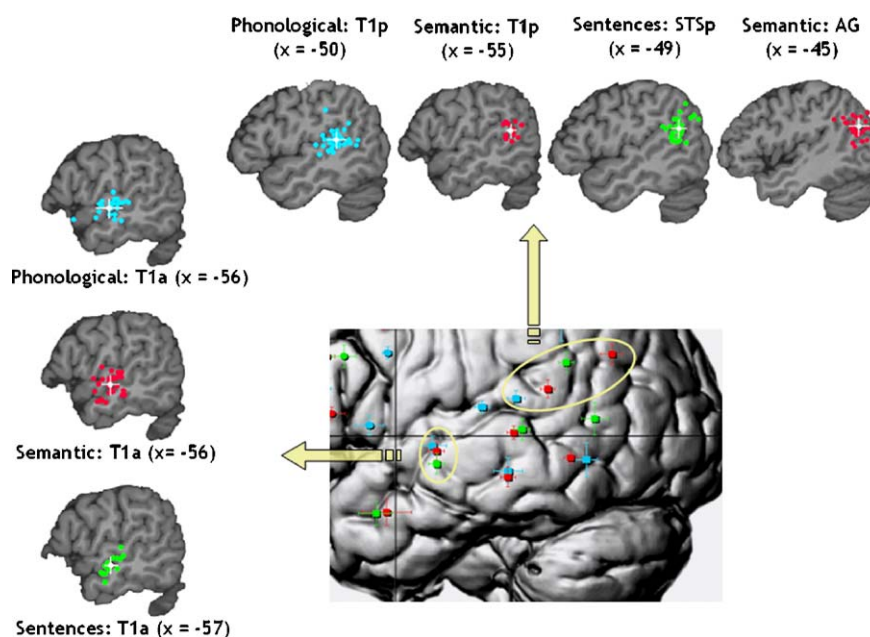


Fig. 7. Integration of verbal material along the superior temporal gyrus. An antero-posterior flux of processing starts by a phonological analysis in the planum temporal (PT) and the superior temporal gyrus (T1); then the stimulus is processed in the semantic area dedicated to auditory processing (T1p) to be converted in an amodal format; it enters into syntactic analysis in the posterior part of the superior temporal sulcus (STSp), and then conceptual analysis is performed within the angular gyrus (AG). A second route goes from phonological areas towards the voice area (T1a) and the temporal pole (Pole), allowing access to the limbic regions for emotional and memory processing. The voice area is the only region in which phonological, semantic, and sentence processing clusters can be found in close spatial proximity (left).

seen as the transmodal gateway that coordinates reciprocal interactions between the sensory representation of words or objects and the symbolic association that gives them meaning, a definition proposed by Mesulam for Wernicke's area (Mesulam, 2000). Pre-surgical cortical mapping confirmed the integrative semantic role of this region: electrical interference at the level of the posterior part of the left superior and middle temporal gyri resulted in the transient emergence of a transcortical sensory aphasia. Notably, these symptoms resembled those of Wernicke's aphasia, in that there was no impairment in the phonological decoding of syllables (Boatman et al., 2000). Recent lesion studies converge on the same conclusion: impairment of this multimodal integration area results in the appearance of marked semantic problems without alteration of phonological performance (Hart and Gordon, 1990). Furthermore, aphasic individuals with posterior superior temporal sulcus (STS) lesions present the same deficits in the verbal and non-verbal realms: they have difficulties associating both an image and a sound with a sentence. For example, they find it equally difficult to associate the image of a cow with the sentence "the cow moos" as with a mooing sound (Saygin et al., 2003).

The Fusa area is involved in word reading as compared to pseudo-word, non-word, or false-font perception (Fiebach et al., 2002; Herbster et al., 1997; Moore and Price, 1999; Price et al., 1996b), as well as during auditory word listening as compared to non-word listening (Démonet et al., 1994). As for what was observed for AG, it is implicated in the semantic processing of both words and pictures (Vandenberghe et al., 1996), as well as during reading in different modalities—tactile and visual—in blind and sighted subjects (Büchel et al., 1998). Its implication in semantic association tasks (Binder et al., 1996, 1999; Bright et al., 2004; Davis et al., 2004) attests to its specialization in the processing of word meanings, even though it is also activated by simple word perception tasks. This last result confirms the hypothesis of Nobre et al. (1994), who stated "the intriguing possibility (is) that semantic or conceptual representations of words may also be accessed directly within the ventral pathway," suggesting that this area could be a word–concept node. Their electrical recording study revealed that this most anterior part of the ventral pathway responded specifically to words and to the semantic context in which they were presented. The Fusa area can be assimilated into the basal temporal language area (BTLA), the electrical stimulation of which provokes deficits of both confrontation naming and auditory response naming (Burnstine et al., 1990; Malow et al., 1996), as well as deficits in language comprehension and production (Lüders et al., 1991).

Semantic antero-posterior connections

In the classical Broca–Wernicke model (Geschwind, 1970), which was based on conduction aphasia symptoms, the arcuate fasciculus links the language temporal and frontal poles, namely, the Broca's and Wernicke's areas, which were defined as the F3 and posterior part of the superior temporal gyrus, respectively. We believe with others (Dronkers, 2000) that this model should be re-evaluated.

We propose that AG and Fusa—the two amodal conceptual temporal areas devoted to meaning—and the temporal pole together with the F3orb frontal cluster constitute a temporo-frontal semantic network (Fig. 3, bottom). This semantic network can be considered to construct an overall meaning on the basis of the association of integrated knowledge issued from the main domain of external (audition, vision) and internal (long-term memory, emotion)

messages; this construction of sense forms the foundation of language communication. Connections within this semantic network would be established by the inferior longitudinal fasciculus (also called occipito-temporal fasciculus) that links the posterior STS and angular sulcus to the BTLA and the temporal pole, as documented in vivo with diffusion tensor imaging (Catani et al., 2002), relayed by the uncinate fasciculus that connects the temporal pole to the orbital part of the inferior frontal gyrus (Catani et al., 2002; Dejerine, 1980; Nieuwenhuys et al., 1988). This is supported by a study using a functional connectivity approach that revealed a strong link between the ventral part of the left inferior frontal gyrus, the posterior part of the left STS, and the ventral route—including the BTLA—during the reading of words, a link that disappears during the processing of false fonts (Horwitz et al., 1998). Arguments for the existence of such a network might also be found in a recent report of induction of semantic errors during electrical stimulations of cortex and deep white-matter fibers in the posterior ending of the STS and the orbital part of F3 (Duffau et al., 2005).

Following the same functional neuroanatomy principles, we postulate the existence of a second fronto-parietal network for working memory, consisting of the PrF3op and the AG areas and connected through the arcuate fasciculus (Fig. 5). As a matter of fact, recent diffusion tensor imaging has shown that this bundle connects the posterior part of F3 (as well as the middle frontal gyrus) and the inferior parietal cortex (Catani et al., 2005). In this perception–action cycle for semantic working memory, AG would be the site where semantic associations are elaborated, whereas PrF3op would be the area where selection among semantic knowledge guided by task requirements would be computed (Wagner et al., 2001).

The hypothesis that different networks could underlie the working-memory processes for phonological and semantic language components is supported by neuropsychological studies: in patients suffering from left-hemisphere lesions, Martin et al. have evidenced a dissociation of phonological and semantic retention alterations (Martin et al., 1994).

Posterior areas shared by phonological and semantic processing

Although there was no match between the lists of frontal clusters that were segregated for either phonology or semantics, we identified two temporal areas where a cluster for phonology and a cluster for semantic processing overlapped (T1a and T3p). We propose that these areas are transitional zones between the perception and semantic integration of language stimuli. Interestingly, recruitment of each of these two areas is modality-dependent: the anterior part of the superior temporal gyrus (T1a) is dedicated to auditory material, whereas the posterior part of the inferior temporal gyrus (T3p) is dedicated to visual material. These auditory and visual phonological–semantic interface areas could thus be crucial during the development of language and especially the learning of reading in children (Fig. 7).

The T1a phonological cluster includes the so-called "voice-specific area," a region that is specifically activated by human voice and speech sounds (Belin et al., 2002). In contrast to posterior temporal phonological clusters (PT, T1), T1a gathers activation peaks of phonological contrasts based on tasks devoid of speech, motor, or working-memory components, such as simple listening to syllables (Poeppel et al., 2004; Sekiyama et al., 2003; Zatorre et al., 1992), pseudo-words (Belin et al., 2002; Binder et al., 2000), and detection of rhymes (Booth et al., 2002).

The present analysis did not allow for dissociation of the phonological from the semantic T1a cluster, but intra-group studies have enabled a functional segregation of the T1a region into a dorsal part (including the voice area) that is dedicated to phonology and a ventral part that is involved in the processing of intelligible words (Binder et al., 1997; Scott et al., 2000; Vouloumanos et al., 2001). In the present analysis, the semantic T1a cluster consisted, as in intra-group studies, of peaks identified in simple word-listening or reading tasks (Binder et al., 1996; Bookheimer et al., 1995; Giraud et al., 2000; Hagoort et al., 1999; Herbster et al., 1997; Sevostianov et al., 2002; Specht and Reul, 2003; Wagner et al., 2000; Wise et al., 2001) and dichotic word-listening tasks (Hugdahl et al., 2003). The evidence of a dorso-ventral gradient from voice to intelligible speech was beyond the ability of this meta-analysis.

The T1a counterpart for visual material is situated in the ventral route in the posterior part of the inferior temporal gyrus (T3p). T3p is a site of increased activity during letter (Beauregard et al., 1997; Paulesu et al., 2000) and pseudo-word (Paulesu et al., 2000) reading, as well as during audiovisual integration of syllables (Calvert et al., 1999; Sekiyama et al., 2003) (presentation of faces pronouncing the syllables), indicating a role in audiovisual integration that is not restricted to grapho-phonemic conversion. Although not significantly different spatially, the T3p semantic cluster is located in a slightly more ventral position (6 mm) than the T3p phonological clusters, and it is likely that they correspond to functionally distinct sub-areas that are beyond the resolution of the present analysis.

The T3p semantic cluster collects peaks of contrasts that involve reading words versus consonant letter-strings (Cohen et al., 2002) or versus pseudo-words (Fiez et al., 1999; Hagoort et al., 1999). However, the functional role of T3p is not limited to word processing as it is recruited by semantic association tasks involving pictures of objects (Adams and Janata, 2002; Kosslyn et al., 1994; Martin et al., 1995; Thompson-Schill et al., 1999; Wiggs et al., 1999) or visual scenes (Damasio et al., 2001). Its specificity for verbal processing is reflected by its sensitivity to verbal semantic priming (Buckner et al., 2000), and it can be considered as an area that is essential for verbal semantic knowledge retrieval as it is recruited by tasks such as semantic association (Booth et al., 2002), categorization (Binder et al., 2003; Chee et al., 1998), and word generation (Crosson et al., 1999; Etard et al., 1999; Thompson-Schill et al., 1997; Vingerhoets et al., 2003; Warburton et al., 1996). This region is a site that allows fast access to deep semantic processing for visual (verbal or otherwise) entries. This evidence leads us to conclude that assessing the specificity of this region for word reading in terms of BOLD increase in activity remains to be demonstrated (Price and Devlin, 2004; Vigneau et al., 2005).

Sentence processing areas

Different from what was observed for phonology and semantics, semantic and syntactic areas appear, at least in part, intermingled: five among the eight clusters identified from the sentence analysis contrasts were close to semantic clusters: two in the frontal lobe (F3opd and F3tv) and three in the temporal lobe (Pole, T2ml, and T1a; Fig. 4). This is related to the fact that, even in studies that focused on the neural bases of syntax, researchers have usually contrasted meaningful complex sentences to syntactically simpler sentences or to sentences devoid of meaning. Interpreting activations resulting from such contrasts appears

difficult since they can as well be related to the increase in semantic and/or syntactic processing required during complex sentence comprehension. An investigation on the neural basis of the syntactic and semantic components of sentence comprehension has indeed underlined the existence of a substantial spatial functional overlap of semantic and syntactic language functions (Roder et al., 2002). The difficulty in dissociating these components during sentence comprehension is increased in the present meta-analysis that includes reports on sentence processing that did not use paradigms designed to segregate semantic and syntactic components of sentence comprehension (for example, listening to sentences contrasted to listening of unintelligible speech (Scott et al., 2000)).

In the following discussion on the functional role of the different sentence processing clusters, we attempted to disentangle semantic and syntactic processes by a finer-grained analysis of the paradigms. Considering that the number of studies specifically investigating syntax was too limited to enter into a separate clusterization, we choose to identify them on the illustrations. This was done within the frame of the issue of the existence of a distinct neural module that would be responsible for the construction and analysis of the sentence structure, i.e., morpho-syntactic processing, since the evidence of neural areas dedicated to syntactic processing would provide support for Chomsky's hypothesis that syntax, the core of the universal grammar, is independent from semantics.

Frontal regions for sentence processing

Two frontal regions, F3opd and F3tv, were the seat of semantic and sentence clusters in close proximity. In addition to the close relationship existing between semantic and syntactic processes mentioned above, the fact that sentence and semantic clusters could not be clearly dissociated in these areas can be related to different causes.

One is a lack of resolution power of the present meta-analysis that cannot provide clear-cut information on the existence of different functional entities within a discrete cortical area when the aggregated clusters are too scattered and have large standard deviations, as in the present case.

The second is related to the frontal lobe functional organization that may be process-dependent rather than linguistically organized. As a matter of fact, the left F3, also called the ventral prefrontal cortex, has been consistently involved, together with its right homolog, during working-memory and manipulation tasks on both verbal and non-verbal material; yet, the expected result of a preferential involvement of the left F3 for verbal tasks was not found in Wager and Smith's meta-analysis of working-memory studies (Wager and Smith, 2003), leading the authors to emphasize that the frontal lobe appears process-dependent rather than material-dependent, which differs from posterior brain areas. Concerning the type of process involved, Owen and colleagues, in their recent meta-analysis on working memory (Owen et al., 2005), showed that the left F3 in charge of the explicit retrieval of one or a few pieces of information is also recruited during selection, comparison, and judgment of stimuli, when spatial and non-spatial information is held on-line, or task switching, leading the authors to suggest that it responds in a modality-independent manner to an explicit and intended act or plan. Although we will discuss in the following the putative role of these clusters within the frame of language functions, we should keep this in mind and put them into perspective.

The F3opd semantic cluster aggregated peaks issued from tasks calling for semantic retrieval and selection. This includes categorization tasks (Noesselt et al., 2003); lexical decision tasks (Binder et al., 2003; Perani et al., 1999; Poldrack et al., 1999); generation tasks such as the generation of an adjective (Kelley et al., 2002), a color (Martin et al., 1995), an action (Adams and Janata, 2002; Damasio et al., 2001; Martin et al., 1995), or the gender of the stimulus (Heim et al., 2002) that were compared to phonological or visual decision tasks. Notably, this cluster also aggregated high-selection generation tasks conducted by Thompson-Schill et al. (1997) and Wagner et al. (2001) to uncover areas for controlled semantic retrieval. Note that these results are in line with those obtained by Friederici who found a semantic role for an area close to the present F3opd cluster (−46 21 25) where a specific increase of activation during a semantic judgment task was observed (Friederici et al., 2000).

The overlapping sentence processing cluster was at a Euclidian distance of 7 mm, the limit of the resolution of the present study ($P = 0.05$). Among the 14 peaks, it aggregated 10 peaks issued from contrasts that targeted specifically syntactic processes: comprehension of complex sentences compared to simple ones, such as studies on syntactic movement (Ben Shachar et al., 2004) including object–subject sentences (Caplan, 2001; Caplan et al., 1999; Constable et al., 2004; Stromswold et al., 1996), as well as the detection of grammatical errors (Embick et al., 2000). The fact that it was more activated during a syntactic decision than during a working-memory task indicates that the working-memory component of complex-sentence comprehension is not at the origin of its activity (Hashimoto and Sakai, 2002; Luke et al., 2002). In addition, peaks within the F3opd cluster issued from studies more specifically investigating syntactic processing appear to be located more dorsally (Fig. 6). We believe that these considerations can be taken as indication that the upper and posterior part of the pars opercularis of the inferior frontal gyrus includes two adjacent areas with different functional roles: one devoted to semantics, and the other, located caudally, to syntactic processing.

The second frontal cluster where sentence processing and semantic clusters partially overlapped (F3tv) included 30 peaks among which 14 belonged to studies on syntax, with high-level reference conditions (such as presentation of sentences with a semantic content), decreasing the weight of the semantic component in the interpretation of the activations (Ben Shachar et al., 2004; Caplan, 2001; Constable et al., 2004; Cooke et al., 2002; Stowe et al., 1998; Stromswold et al., 1996; Waters et al., 2003). In addition, several of the semantic contrasts that were gathered in the semantic F3tv cluster were related to grammatical processing such as lexical categorization (Adams and Janata, 2002; Binder et al., 1996; Bright et al., 2004; Hagoort et al., 1999; Perani et al., 1999), including verb (Buchanan et al., 2000) and gender categorization (Heim et al., 2002) or the organization of a list using semantic associations (Savage et al., 2001). Nevertheless, the F3tv semantic cluster localized at 7 mm from the syntactic peak did not differ in terms of location and also included peaks from semantic tasks such as categorization (Adams and Janata, 2002; Bright et al., 2004), generation of words (Vingerhoets et al., 2003) or action (Martin et al., 1995), semantic association (Booth et al., 2001), and decision (Binder et al., 1996; Bright et al., 2004), preventing at the present resolution the attribution of a pure syntactic role to this area.

The sole frontal region aggregating activation during tasks on sentence processing while not being at a close proximity with semantic ones is F2p. The number of peaks it aggregated was

limited to 7 studies that did not specifically target syntactic processes, including sentence (Baumgaertner et al., 2002; Bottini et al., 1994) and text reading (Vingerhoets et al., 2003), except for one study on comprehension of object–subject sentences compared to simple ones (Constable et al., 2004). The fact that it was activated during both syntactic decision and working-memory tasks on words and sentences (Hashimoto and Sakai, 2002; Luke et al., 2002) suggests that it is recruited by working-memory processes involved during the comprehension of complex linguistic material.

Temporal regions

As underlined by Dronkers et al. (2004), the focus of investigators on Broca's area in studies of the neural bases of syntax has caused the role of the temporal lobe to be overlooked. The present meta-analysis confirms the key role of temporal regions in sentence processing, as illustrated by the larger number of peaks found in the temporal than in the frontal lobe (Table 4).

Involvement of the temporal pole in sentence and text comprehension is now well-recognized. This finding first emerged from a study that reported a strong Pole activation during speech listening (Mazoyer et al., 1993). Interestingly, peaks aggregated in this area seem to be related to the comprehension of sentences or texts rather than to syntactic processing itself: the Pole is activated when subjects have to proceed to either syntactic or semantic judgments on sentences (Bottini et al., 1994; Luke et al., 2002), and it is more activated by normal sentences conveying meaning than by sentences made of pseudo-words (Vingerhoets et al., 2003) or ending with a pseudo-word (Baumgaertner et al., 2002). Its activation includes contrasts in which sentences or text (presented either visually or orally) are compared with words (Stowe et al., 1998) or unintelligible speech presentation (Crinion et al., 2003; Scott et al., 2000), thus including semantic processing. Within the Pole region, there are also peaks of semantic contrasts dealing with word/object access to semantic knowledge, in particular, categorization (Bright et al., 2004; Damasio et al., 2001; Scott et al., 2003; Vandenberghe et al., 1996). As patients with temporal pole lesions show an alteration in comprehension of complex sentences only, Dronkers et al. have proposed that “this region has a very basic role in syntactic processing rather than a more specific role in processing complex structures.” We postulate this role to be the encoding and retrieval of complex linguistic material from long-term memory. As a matter of fact, activity in this region increases with the linguistic complexity of the stimulus (Fletcher et al., 1995; Mazoyer et al., 1993). In addition, the Pole recruitment during episodic retrieval of object attributes (Wiggs et al., 1999) and story recall (Andreasen et al., 1995), as well as the observation of a deficit in grasping text coherence in patients who had undergone anterior temporal lobectomy (Milner, 1958), fits with the idea that it is part of a long-term memory network in action for linguistic material. Its proximity to the hippocampal formation supports this hypothesis.

Although T2ml is the seat of overlap between a semantic and a sentence processing cluster, it appears very likely that T2ml is a semantic area devoted to verbal knowledge. It is activated almost exclusively by semantic tasks that are based on word presentation in the auditory (Binder et al., 2000; Specht and Reul, 2003; Warburton et al., 1996; Wise et al., 2001) or visual modality (Davis et al., 2004; Moore and Price, 1999; Vandenberghe et al., 1996), as opposed to tasks based on pictures or scenes. Its specificity for words is further confirmed by several observations. First, its

activity is larger for word than for image categorization. Second, its activity is correlated with the number of words that are heard and retrieved from memory (Wise et al., 2001); such a correlation between activity and the frequency of word presentation, but not with that of noise, was lost in two patients with Wernicke's aphasia (Mummery et al., 1999). Third, it is involved in semantic categorization (Binder et al., 1996; Chee et al., 1998; Vandenberghe et al., 1996) and verb generation (Fiez et al., 1996).

The cluster located at 4 mm from the T2ml semantic cluster aggregated peaks issued from various sentence processing tasks, including simple-sentence comprehension (Kansaku et al., 2000; Vingerhoets et al., 2003); complex-sentence comprehension (Ben Shachar et al., 2004; Bottini et al., 1994); comparison to pragmatically (Kuperberg et al., 2000), syntactically, or semantically incoherent sentences (Luke et al., 2002); and attention to their verbal content (von Kriegstein et al., 2003). Its role in sentence processing appears crucial when words become essential to sentence understanding, as shown by its recruitment during syllogistic reasoning on sentences as compared to abstract symbols (Goel et al., 2000) and also by its sensitivity to the context effect: T2ml is more activated when the word that ends the sentence is coherent but unexpected than when it is the expected word, and it is not activated when a non-word ends a sentence (Baumgaertner et al., 2002). The functional imaging evidence that T2ml is an area devoted to word meaning during sentence comprehension nicely corroborates what Dronkers et al. have observed. Using Voxel-based Lesion Symptoms Mapping (VLSM), they found that aphasic patients presenting a lesion in an area that matches the T2ml cluster constitute a particular sub-group characterized by a profound deficit in word comprehension (Dronkers et al., 2004).

Although one should note that the T1a cluster aggregating peaks from sentence processing tasks was in a more ventral position than the phonological (minus 6 mm in the *z* axis), it was not dissociable from the semantic cluster. During sentence processing, the contrasts that targeted the inferior bank of the STS were sentence or text listening, including comparison of meaningful with unintelligible discourse (Crinion et al., 2003; Kansaku et al., 2000; Meyer et al., 2004; Scott et al., 2000; Vingerhoets et al., 2003). The fact that it was also part of the network of areas that were activated by syntactic evaluation tasks based on silent reading (Bottini et al., 1994; Luke et al., 2002; Vingerhoets et al., 2003) evokes a possible role in the processing of grammatical prosody. This hypothesis is supported by its recruitment during both attention to speaker voice and verbal content (von Kriegstein et al., 2003).

It must be underlined here that the site of the human voice area (T1a) was the only one in which activation peaks of phonological, semantic, and sentence processing contrasts were in close proximity, highlighting the crucial role of voice processing in language development through both phylogenesis and ontogenesis. A recent report has indeed shown that the anterior part of the superior temporal gyrus of monkeys hosts a species-specific call area, which shows unique leftward asymmetry and might be a precursor for the evolution of language (Poremba et al., 2004).

Two among five clusters involved in sentence processing were spatially distinct from other language components in the temporal lobe: one in the posterior part of the superior temporal gyrus (STSp) and one in the posterior part of the middle temporal gyrus (T2p, Fig. 4).

The sentence processing T2p cluster was recruited by paradigms using a visual presentation of the sentences (Fletcher et al.,

1995), including complex sentences compared with simple ones (Constable et al., 2004; Cooke et al., 2002; Stowe et al., 1998) and semantic judgment on sentences (Luke et al., 2002). Interestingly, it was also recruited by auditory presentation of sentences: it was activated when a person had to generate a mental image from high-imagery sentences presented either visually or orally, compared to the presentation of low-imagery sentences (Just et al., 2004). As previously proposed (Mazoyer et al., 1993), this area is likely related to the mental imagery component of sentence comprehension, showing that cooperation between visual and language systems participates in the elaboration of sentence meaning.

Although STSp has been implicated in a study on syntactic complexity (Constable et al., 2004) and seemed to be activated more when individuals made a judgment on grammatical errors compared to pronunciation errors (Embick et al., 2000), its role seems to process the semantic integration of complex linguistic material. This statement comes from the observation that it is recruited when subjects listen to coherent rather than syntactically or pragmatically incoherent sentences (Kuperberg et al., 2000; Luke et al., 2002), and it is involved in context processing and syntactic generation—more activated when subjects have to choose between two words to end a sentence or have to generate the final word of a sentence (Kircher et al., 2001). STSp activity is very likely related to the linkage of linguistic structure to meaning: it is more activated when sentences are linked as dialogue (Homae et al., 2002) or syllogisms (Goel et al., 1998) than when they are unlinked and more activated during text comprehension, either presented auditory (compared to reverse speech (Crinion et al., 2003; Kansaku et al., 2000) or words (Jobard et al., 2004)) or visually (compared to words (Jobard et al., 2004) or pseudo-word reading (Vingerhoets et al., 2003)). This role of STSp in high-order integration of linguistic material is also attested by its larger implication during the comprehension of theory of mind (TOM) stories than when unlinked sentences (Fletcher et al., 1995; Gallagher et al., 2000) or mechanical inference stories (Saxe and Kanwisher, 2003) have to be processed.

Finally, we propose that the F2p and STSp could constitute a third working-memory network, connected like their phonological and semantic counterparts by the arcuate fasciculus (Catani et al., 2002, 2005), dedicated to the integration of complex verbal material involved during the comprehension of complex sentences, dialogues, and texts (Fig. 5).

Summary and conclusions

This exploratory approach of left hemisphere language areas provided a set of results that reinforces and refines hypotheses emerging from isolated functional imaging studies.

Above all is the involvement of an elementary audio–motor loop for phonological processing, allowing a motor-sound-based representation for language sounds and involved in whether language is heard or enunciated, as had been proposed by Buchsbaum for auditory areas (Buchsbaum et al., 2001) and by Wilson for motor areas (Wilson et al., 2004). This loop is composed of Heschl's gyrus and the planum temporal in the temporal lobe as its perceptive component and of the mouth motor area and inferior precentral cortex corresponding to its motor component in the frontal lobe.

Then, our results provide a refinement of the inferior frontal gyrus functional organization for phonology and semantics: the

present meta-analysis confirms and specifies the antero-posterior dissociation of phonological and semantic areas proposed by Poldrack et al. (1999) and, thanks to the evidence of a working-memory phonological area located anteriorly in the pars triangularis, allows conciliation of results for this area that were apparently contradictory.

Original results also emerged that could not have been elicited from functional imaging studies examined individually. These results are the existence of crossroad regions where an overlap of functional areas for phonological and semantic processing was observed in the posterior brain. Although such overlap does not mean a co-localization of these functional areas (given the limited resolution of the present method), they target cerebral sites where a close interaction of language components possibly occurs thanks to cortical vicinity. These crossroad areas were modality-dependent, related to the auditory modality in the anterior temporal cortex (T1a) and to the visual modality in the posterior part of the inferior temporal gyrus (T3p). Interestingly, T1a, which includes the human selective voice area, was also a seat of overlap with syntactic processing. This evidence provided the basis for considering it as a key area for language development and communication. Such a hypothesis finds some support in the observation of a dysfunction of this area in autistic adults (Gervais et al., 2004).

Another important result is the evidence in the dorsal part of the F3 pars opercularis of an area that is dedicated to syntactic processes. The present results also underlined the crucial role of temporal areas for sentence comprehension, where the processing of sentence meaning and construction are co-localized, as in the F3 pars triangularis. Integration of complex linguistic material, such as texts, appears to recruit the most posterior part of the superior temporal gyrus together with the dorsal part of the middle frontal gyrus, possibly in relation with an increase in working-memory demand.

Finally, the question of the functional relationships and connectivity within these left hemisphere language areas cannot be resolved by the present approach, and, although we proposed a network organization for the different areas, it remains to be firmly established. As a matter of fact, right hemisphere language areas and sub-cortical areas are not included, and no data on the connectivity was available in the common space. Given these limitations, we propose on the basis of the perception–action cycle model proposed by Fuster (1997, 2003) the existence of distinct working-memory networks for each component, made of fronto-parietal reverberating loops. An accurate knowledge of the connectivity and chronometry of these loops will need further investigation with fiber tracking and electrophysiological approaches.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neuroimage.2005.11.002.

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