Syntax and the brain: disentangling grammar by selective anomalies

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Abstract

Many paradigms employed so far with functional imaging in language studies do not allow a clear differentiation of the semantic, morphological and syntactic components, as traditionally defined within linguistic theory. In fact, many studies simply consider the brain's response to lists of unrelated words, rather than to syntactic structures, or do not neutralize the confounding effect of the semantic component. In the present PET experiment, we isolated the functional correlates of morphological and syntactic processing. The neutralization of the access to the lexical-semantic component was achieved by requiring the detection of anomalies in written sentences consisting of pseudo-words. In both syntactic and morphosyntactic processing, the involvement of a selective deep component of Broca's area and of a right inferior frontal region was detected. In addition, within this system, the left caudate nucleus and insula were activated only during syntactic processing, indicating their role in syntactic computation. These findings provide original *in vivo* evidence that these brain structures, whose individual contribution has been highlighted by clinical studies, constitute a neural network selectively engaged in morphological and syntactic computation.

Key words: syntax, morphosyntax, PET, normal subjects

Introduction

Modern linguistics has succeeded in decomposing the complexity of grammars in the interaction of independent modules. More specifically, for any given sentence in any language three abstract levels of representation converge to give the associated structure; the phonological level (where the possible sequences of sounds are checked), the syntactic level (where words are combined yielding the proper hierarchical structures), the semantic level (where the meaning of the whole sentence is computed on the basis of the meaning of each lexical item). Thus, for example, an English native speaker knows that such expressions as "remnantzry", "dog a barks" and "happiness broke his arm" are not acceptable at the phonological, syntactic and semantic level, respectively.

Such a modular architecture, which is claimed to reflect the implicit knowledge of grammar that every human being is endowed with genetically, raises many empirical questions. A crucial one is whether this threefold abstract partition is actually isomorphic to some neurophysiological process, and more specifically whether these three levels of representation are subserved by distinct neural correlates. Of course, although the rules governing each level are independent, there is no direct way to test each of them in isolation, since by definition they are activated simultaneously. Several experiments have shown that semantic information as expressed by the lexicon is independently represented in the brain (Martin et al., 1995; Martin et al., 1996; Perani et al., 1999b; Vandenberghe et al., 1996); nevertheless, the fundamental question remains as to whether syntactic operations can be associated with some dedicated neural networks. Indeed, it must be highlighted that many neuroimaging experiments on human language have used as stimuli lists of words, rather than full sentences, which are in fact the actual units of spontaneous speech (Price, 1998).

Along with such an abstract model of the knowledge of grammar, the actual process of interpretation of a sentence of course requires assigning each element of the sentence to the proper slots in the actual mental representation-grid; this in turn implies the memory load capacity to keep phrases in an activated state. Syntactic processing during sentence reading has been addressed by several functional neuroimaging investigations focusing specifically on syntactic complexity, which

showed consistent activations in Broca's pars opercularis, during an on-line acceptability-judgment task (Caplan et al., 1998; Stromswold et al., 1996) and during a post-sentence presentation judgment task (Just et al., 1996). In the latter paper, Just and colleagues, in addition to left Broca's and Wernicke's regions, found activations also in right hemispheric homologue areas. The reported activations were indeed interpreted as being due to increasing syntactic complexity and, concerning Broca's area specifically, to augmented memory and computational load. Similar findings were reported for sentences presented in the auditory modality (Caplan et al., 1999): however, in contrast to the above mentioned studies, the pars triangularis and not the pars opercularis of the inferior frontal gyrus was activated. Caplan and colleagues (1998), in addition to Broca's area, found activations in the anterior cingulate gyrus and in the right medial frontal gyrus (similar finding are reported in Stromswold et al. (1996). This pattern, in the authors' opinion, correlates with phonological encoding and subvocal rehearsal, an hypothesis that is supported by other imaging studies (Paulesu et al., 1993; Zatorre et al., 1992). Subvocal rehearsal might be used for assigning the head of the sentence its thematic role, as in relative clauses (Swinney and Zurif, 1995; Swinney et al., 1996; Zurif et al., 1993).

A recent fMRI experiment (Dapretto and Bookheimer, 1999) used a sentence comprehension task, in which different relative weights for syntactic and lexico-semantic processing had been introduced. Subjects were asked to decide whether a certain pair of sentences had the same meaning. Such pairs were constructed by either changing one single word in the same sequence, called "semantic condition", or changing the full sequence, called "syntactic condition". The subjects were requested to give "same" or "different" judgments. For example, in the syntactic condition, sentences such as "The policeman arrested the thief" or "The thief was arrested by the policeman" were judged as "same" whereas "West of the bridge is the airport" or "The bridge is west of the airport" as "different". Again, a selective activation in Broca's pars opercularis on the lateral brain surface was found to be associated with syntactic processing. Clearly, such a task was crucially centered on a major, although implicit, assumption, namely that changing the syntactic structure of a sentence does not affect the semantic component. So, the transformation of an active sentence like "the policeman

arrested the thief" into a passive sentence like "the thief was arrested by the policemen" is considered not to affect the semantic interpretation. Although the transformation from active to passive construction is surely a syntactic phenomenon, one cannot be sure that this is not affecting also the semantic component. Indeed, since at least Jackendoff (1968), it is well-known that passive constructions do not preserve the semantics content of their active counterparts. Famous examples, often quoted in the linguistic literature are the pairs like: "many arrows didn't hit the target" and "the target wasn't hit by many arrows". Clearly, the state of affairs which are compatible with the two sentences differ, since the target could still be hit by many arrows, if the first sentence is true, whereas this cannot be the case if the second one is. Indeed, these kind of observations lead Chomsky to formulate the so called "Extended Standard Theory" -see for example, Chomsky (1975) contra Chomsky (1965) based on Katz and Postal (1964)-, and have never been dismissed ever since that time.

The Dapretto and Bookheimer (1999) experiment represents an advancement with respect to previous works in the field. In the present study, we have adopted an alternative strategy, which allows to disentangle grammar and isolate syntax from semantics. The innovative strategy we pursued, was suggested on the basis of some crucial problematic aspects of the previous work in the field. Indeed, all previous neuroimaging experiments, either using words or sentences, left the access to semantics unaltered. To avoid these problematic issue, we have designed a paradigm which neutralizes the access to any semantic component. Such a problem was overcome by using non-words, that is invented words which are not related to any meaning in the lexicon, like "staze". Functional words and morphemes, instead, like articles, auxiliaries, prepositions, plural morphemes etc. have been fully preserved. In such a case, any anomaly in the syntactic structure could not influence any semantic interpretation which was missing in the input in the first place. All in all, even if a non-word is in fact assigned a syntactic category on the basis of its morphological structure and the context where it occurs, it is clearly impossible for it to have a proper semantic status for at least two reasons: first, it is by definition not assigned an extension in any possible world; second, which is

crucial, it can by no means contribute to the computation of the semantics of the whole sentence which we take to be its truth functional value (Dowty et al., 1981).

In our experiment we tested the subjects' linguistic knowledge at each level by selectively disrupting one level while maintaining the others intact. More specifically, we have asked the subjects to detect either phonological, morphosyntactic and syntactic anomalies in pseudo-word sentences which contained only one type of anomaly for each level (see methods). This in principle allows one to focus selectively on syntactic processing rather than on the different amount of syntactic complexity, as done in cited works. A major problem was also overcome which is implicit in this type of experiment. In fact, when the syntactic level is disrupted, a potential semantic anomaly is also produced; thus, for example, if one says "all the eaten have chickens snakes" the anomalous syntactic structure also disturbs the semantic interpretation which would be impossible to reconstruct.

Materials and methods

Subjects

The study was approved by the Ethics Committee of the Scientific Institute H San Raffaele, and each volunteer gave his written informed consent prior to the admission to the study.

Eleven male volunteer right-handed subjects (mean age 26 years, range 22 to 28 years) entered the study. All subjects had no history of neurological or psychiatric disorders. Right-handedness was verified using the Edinburgh Inventory (Oldfield, 1971).

Tasks Design

The study consisted of three experimental and one baseline conditions. Subjects were asked to covertly read sentences presented visually and, for the three experimental conditions only, to make acceptability judgments at the corresponding sentence-structure levels. The sentences all consisted of pseudowords only ('pseudosentences'), so as to neutralize the access to semantic components: this

'Quasi-Italian', devoid of any open-class word, but maintaining inflections and function-words, was employed in order to isolate the correlates of morphosyntactic and syntactic processing. According to the experimental tasks, anomalies either at the phonotactic, the morphosyntactic or the syntactic level were introduced. Syntactic anomalies presented sentences with wrong linear order but proper agreements. Morphosyntactic anomalies presented sentences with proper word order but agreement errors. Phonotactic anomalies presented sentences containing Italian unlegal consonant strings.

Examples:

Baseline: "Il gulco gianigeva le brale."

$(D_{m/sing} \ N\text{-}_{m/sing} \ V\text{-} \ AGR/T_{3rd \ sing} \ D_{f/plur} \ N\text{-}_{f/plur})$

Syntactic anomalies: * "Gulco il gianigeva le brale."

$(N\text{-}_{m/sing} \ D_{m/sing} \ (Synt.\text{-}anomaly) \ V\text{-} \ AGR/T_{3rd \ sing} \ D_{f/plur} \ N\text{-}_{f/plur})$

Syntactic anomaly = wrong word order: N- D- instead of D- N-

Morphosyntactic anomalies: * "Il gulco ha gianigiata questo bralo."

$(D_{m/sing} \ N\text{-}_{m/sing} \ Aux \ PP\text{-} \ AGR/T_{f/3rd \ sing} \ (Morph.\text{-}anomaly) \ D_{m/plur} \ N\text{-}_{m/plur})]$

Morphosyntactic anomaly = -a, fem./sing. instead of m/sing. (-o)

Phonotactic anomalies: * "Il gulco gianigzleva le brale."

$(D_{m/sing} \ N\text{-}_{m/sing} \ V\text{-} \ (Phonot.\text{-}anomaly) \ AGR/T_{3rd \ sing} \ D_{f/plur} \ N\text{-}_{f/plur})$

Phonotactic anomaly = gzl, string of consonants not present in Italian

For each condition, 3 sets each of 13 pseudosentences were formed, corresponding each to an experimental block. For the three experimental conditions only, 9 of the 13 pseudosentences within a block contained corresponding anomalies, whereas the other 4 were correct. Order of sentence presentation within blocks was fully randomized. All blocks within a condition were balanced for sentence length. Pseudosentences were presented individually on a NEC computer screen (distance from the eyes: 60 cm, angle: 30˚), typed in black uppercase characters on a white background. Sentence presentation time was 4000 ms, with an Inter Stimulus Interval of 1000 ms. Subjects read the sentences covertly and, either pressed a response-box button when they had completed sentence

reading (for the baseline condition), or pressed the response-box when they detected an anomaly (for the experimental conditions). Reaction times and response accuracy were recorded.

A preliminary dyslexia test battery was administered to all subjects, in order to exclude possible pseudoword processing deficits. All experimental and behavioral subjects included in the analysis performed as normal.

PET data acquisition

Regional cerebral blood flow (rCBF) was assessed with positron emission tomography (PET) on each of the eleven experimental subjects, while they were instructed to execute one of the four tasks. Three repetitions of each condition were run for each subject, for a total of 12 PET scans per subject. Condition-presentation order was balanced across subjects (Latin square design).

rCBF was measured by recording the distribution of radioactivity following an intravenous injection of ^{15}O-labeled water (H2^{15}O) with a GE-Advance scanner (General Electric Medical System, Milwaukee,WI) which has a field of view of 15.2 cm. Data were acquired by scanning in 3D mode. A 5 mCi slow bolus of H2^{15}O, 4 cc in 20 sec, plus 4 cc of saline solution in 20 s, were injected (Silbersweig et al., 1993). After attenuation correction (measured by a transmission scan using a pair of rotating pin sources filled with 68Ge), the data were reconstructed as 35 transaxial planes by three-dimensional filtered back projection with a Hanning filter (cut-off 4 mm filter width) in the transaxial plane, and a Ramp filter (cut-off 8.5 mm) in the axial direction. The integrated counts collected for 90 s, starting 30 s after injection time, were used as an index of rCBF.

Image transformations and statistical analysis were performed in MATLAB 4.2 (Math Works, Natick, MA, USA) using statistical parametric mapping (SPM-96, Wellcome Department of Cognitive Neurology, London, UK). The original brain images were first realigned and then transformed into a standard stereotactic space (defined by the International Consortium for Brain Mapping project (ICBM) (NIH P-20 grant), and closely approximates the space described in the atlas of Talairach and Tournoux (1988). In order to increase signal to noise ratio and accommodate normal variability in functional gyral anatomy each image was smoothed in three dimensions with a Gaussian filter (16 x 16 x 16 mm). A repeated-measures ANCOVA was used for the comparison of

different tasks, in which every subject was studied under all conditions. Global differences in cerebral blood flow were covaried out for all voxels and comparisons across conditions were made using t statistics with appropriate linear contrasts (Friston et al., 1995a; Friston et al., 1995b). The set of t values for each voxel of the image comprise the statistical parametric map (SPM{t}).

The following contrasts were evaluated:

Commonalities: overall main effects masked with each of the individual contrasts:

1. (Ph + M + S) - B; masked with (Ph - B); (M -B); (S - B).

2. (M + S) - Ph; masked with (M - Ph); (S - Ph).

Simple Main effects:

3. M -Ph

4. S - Ph

B = baseline task; Ph = phonotactic task; M = morphosyntactic task; S = syntactic task

Results

Behavioral data:

All subjects performed the tasks with high accuracy (range B: 92-100 %; Ph: 92-100 %; M: 77-100 %; S: 69-100 %). A multivariate repeated measure Anova was performed on the accuracy rates (expressed in % of correct answers; correct answer defined as: answer given within time < 4000 ms, and correct anomaly detection). Experimental conditions (Means: B = 99,0 %; Ph = 98.8 %; M = 92.5 %; S = 95.5 %) were significantly different: F = 5.175, p = 0.005. Post-hoc Student t-test paired comparisons that reached the p<0.05 significance level were between M and B conditions (p = 0.0019) and between M and F (p = 0.027). Within-conditions block presentation order was not significant as a main effect (Means; 1. Block = 96.5 %; 2. Block = 95.6 %; 3. Block = 97.4 %): F = 2.289, p = 0.127. The interaction between block presentation order and conditions was not significant: F = 0.317; p = 0.925.

The same analysis was also performed on the Reaction Times (RT) of the 11 experimental subjects gave the following results: Experimental conditions (Means: B = 1946 ms; Ph = 1693 ms; M = 1891 ms; S = 1867 ms) were not significantly different: F = 1.977, p = 0.139). Within-conditions block presentation order was significant as a main effect (Means; 1. Block = 1959 ms; 2. Block = 1806 ms; 3. Block = 1784 ms): F = 4.210, p = 0.030. The interaction between block presentation order and conditions was not significant: F = 1.230; p = 0.299.

Functional data :

The 3 experimental conditions share a common neural network as revealed by the main effect, masked with the individual simple main effects, using the baseline as a reference condition. The common pattern of significant activations included Broca's area pars opercularis (Ba 44) and the left inferior parietal lobule (Ba 40); on the right hemisphere, the lateral premotor area (Ba 6), the cuneus (Ba 18) and the middle occipital gyrus (Ba 19 and 18). Bilateral activations included the superior parietal lobule (Ba 7), the precuneus (Ba 7), the fusiform gyrus (Ba 18/37), the cerebellum and the cerebellar vermis (see table 1, a for stereotaxic coordinates and fig. 1, A).

The common activations for Syntactic and Morphosyntactic conditions, as revealed by the main effect masked with each of the individual contrasts compared to the Phonological condition, were located in the rostral depth of the circular sulcus in the left inferior frontal gyrus (Ba 45) and in the right homologue of Broca's area (Ba 44) (see table 1, b for stereotaxic coordinates).

The direct comparison of Syntactic vs Phonotactic condition yielded significant activations again in the depth of the circular sulcus in the left inferior frontal gyrus (Ba 45), and in the right homologue of Broca's area (Ba 44,45); further activations were in the left caudate nucleus and insula (see table 1, c for stereotaxic coordinates and fig.1, B). Comparable activation foci in the depth of the circular sulcus (Ba 45) and in the right homologue of Broca's area (Ba 44,45) were found in the direct comparison of Morphosyntactic vs Phonotactic condition. In addition the vermis was also activated (see table 1, d for stereotaxic coordinates and fig. 1, C).

Discussion

The detection of errors in pseudosentences is associated with the activation of an extended network of brain regions, involving the classical language areas as well as several other associative occipito-temporal and parietal areas (Table 1a). Common to all three experimental conditions was the activation of high-order visual areas, which may reflects aspects of visual processing specific for the error detection task in comparison with the reading condition. In particular, error detection engages more extensive attentional resources than simple reading, and might thus result in stronger parietal activation (Wojciulik and Kanwisher, 1999). The main issue underlying the present investigation was to address sentence processing at the syntactic level, while keeping this component as far as possible disentangled from lexical semantics: we will discuss the activations specifically related to morphological and syntactic processing, which included Broca's area, the caudate nucleus and the cerebellum.

Broca's area has been traditionally associated with morphosyntactic processing. The main basis for this association is the fact that the clinical picture of agrammatism, characterized by morphological errors in production and (inconstantly) by disordered syntactic comprehension (Caplan et al., 1981), is usually part of the symptom complex of Broca's aphasia (see Grodzinsky (2000), for a recent review). The classical syndrome of Broca's aphasia, however, combines the morphosyntactic disorder with impairments in other domains, such as articulation and phonological and lexical-semantic processing. It is common clinical knowledge that the full syndrome of Broca's aphasia actually follows from extensive anterior perisylvian damage extending beyond Broca's area proper. Most patients with this complex syndrome have been affected by extensive lesions, typically centered on Broca's area (Ba 44 and 45), but extending towards other brain regions: precentral gyrus, insula, anterior temporal cortex (Déjerine, 1914). There has been a considerable effort in the clinico-pathological literature to "fractionate" the speech and language components of Broca's aphasia, and to associate them with specific neural substrates. The most successful aspect of this endeavor is probably related to the articulatory disorder, variously labeled as apraxia of speech,

cortical dysarthria, aphemia or anarthria. Clinico-pathological studies have indicated a specific role of the precentral gyrus (Lecours, 1976; Tonkonogy and Goodglass, 1981), and in particular of its insular part (Dronkers, 1996). When the lesion spares this area, and is limited to Broca's area proper, the clinical picture is different from typical Broca's aphasia. According to some early CT studies (Mohr et al., 1978), small lesions in Broca's area are associate with mild, transient aphasia. Tonkonogy and Goodglass (1981) reported a case with a clinical picture of anomia. When clinico-radiological correlation studies have attempted to define the relationship between syntactic disorders and lesion location within what we may call the Broca's region, the results have been largely disappointing. Lesions in several areas within the whole left perisylvian cortex, and in rare cases also in the right homologous region, have been shown to be associated with defective syntactic processing (Tramo et al., 1988). An exception is a recent study, which suggested that the effects of Broca's area involvement dissociate from those of a more anterior involvement of the left prefrontal cortex: patients with the latter location of lesions have unimpaired syntactic processing skills, but show pronounced deficits in narrative serial ordering, i.e. in producing temporally coherent sequences of actions (Sirigu et al., 1998).

The results of clinico-anatomical correlation studies must now be reconsidered in the light of the results of functional neuroimaging. The left dorsolateral prefrontal cortex, including Broca's area proper, has been shown to be activated by a variety of tasks involving different kinds of linguistic and cognitive processing. In particular, auditory-verbal short term memory tasks have been shown to be associated with activation of the posterior part of Ba 44, which appears to be involved in phonological recoding and rehearsal processes (Paulesu et al., 1993). The same region was shown to be activated also in phonological discrimination tasks (Zatorre et al., 1992). Different areas (Ba 45 and 47) appear to be related to memory encoding, as well as by lexical-semantic processing (review in Gabrieli et al. (1998). A direct contrast between these different regions was shown by a fMRI study of word fluency, in which phonological cueing was associated with activation in the opercular, semantic cueing with anterior triangular component of Broca's area (Paulesu et al., 1997). The

"semantic" area appears to be modulated by specific demands of the task, such as the amount of search required (Thompson-Schill et al., 1997), or the semantic category (Perani et al., 1999a).

The complex contribution of Broca's region to semantic processing, which is underlined by these studies, represents a problem for the interpretation of the few investigations of syntactic processing, which failed to unravel the syntactic from the semantic component (see introduction). Our results, based on a paradigm which aims to disentangle grammar from the semantic component, suggest that it is a specific portion of Broca's area, i.e. Ba 45 within the depth of the lateral sulcus in the inferior frontal gyrus, to be activated by both the morphosyntactic and the syntactic task. On the other hand, the common activation for the three experimental conditions in Broca's area was centered within the pars opercularis (Ba 44); this activation, observed also by others (Caplan et al., 1998; Dapretto and Bookheimer, 1999; Just et al., 1996; Stromswold et al., 1996), may not thus be specifically related to syntactic processing. A similar area was found to be activated by both syntactic and semantic anomalies in a recent event-related fMR study, in which subject read minimal verb phrases (of the type "forgot made" or "wrote beers") (Kang et al., 1999).

The activation of the right-sided homologue of Broca's area is also interesting. Data from patients who had undergone full or partial callosal section as a treatment for epilepsy suggest two parallel and complementary functions for Broca's area and its right hemispheric homologue. The right hemisphere of split-brain patients, though severely limited in its capacity to use syntactic information in comprehension (Gazzaniga, 1980; Gazzaniga et al., 1984; Zaidel, 1983) is quite capable of judging whether a spoken sentence is grammatical or not (Baynes and Gazzaniga, 1988). It thus seems that, while a deep component of Broca's area is likely to be the preferred locus for syntactic analysis and computation, a right hemispheric region, homologous to Broca's area is capable of conscious abstractions pertaining to the level of metalinguistic knowledge, which are clearly required for acceptability-judgment tasks of the type we have used.

The selective activation we found of the left caudate region for the syntactic anomaly condition is consistent with the hypothesis that the basal ganglia might be involved in syntactic processing. Agrammatism can be observed in patients with left subcortical lesions. Broca's-like

production deficits have been observed, as the result of extensive subcortical damage affecting connections to and from Broca's area, leaving the latter region and more generally the prefrontal cortex intact (Alexander et al., 1987; Mega and Alexander, 1994; Naeser et al., 1982). Further, neuropsychological studies of patients with Parkinson Disease (PD) have shown selective deficits in syntactic judgment tasks as well as in the comprehension of syntactically conveyed discourse meaning (Grossman et al., 1991; Lieberman et al., 1990). It must be underlined, however, that PD patients have also other cognitive disorders, pertaining to abstraction, problem solving and working memory (Cummings and Benson, 1984; Flowers and Robertson, 1985). The problem of the relationship of working memory with sentence comprehension is complex; it has been claimed that a "specialization" exists for assigning the syntactic structure of a sentence and using that structure in determining sentence meaning, separate from the system underlying the use of sentence meaning (Caplan and Waters, 1999). The visual presentation used in the present experiment can be expected to reduce the burden on working memory, as the whole pseudo-sentences were always physically present during the task. It must be however underlined that activations in Broca's area have been observed in association with the processing of both written (Caplan et al., 1998) and auditory (Caplan and Waters, 1999) sentences. A recent case study of a patient with mild parkinsonism due to anoxic damage to the putamen and the head of the caudate nucleus is indicative of the complex relationship between syntactic complexity and working memory load (Pickett et al., 1998). The patient presented "frontal" deficits: she scored below average in sequencing ability and showed perseverations in rule applications, which required switching from one criterion to the next one; she also showed an impaired comprehension in sentence meaning conveyed by syntax: however, her verbal and visual short-term memory were intact. Interestingly, her sentence comprehension capability increased proportionally with increasing syntactic complexity. The authors interpret this somewhat striking finding, as an interplay of two cognitive strategies employed by the patient, namely her tendency to perseverate being overcome by her intact verbal short-term memory in more complex sentences. These findings might suggest, that syntactic complexity might in fact relate to an increased verbal memory load. The most probable location to play this role seems to be Broca's area

(see introduction), particularly in relation with subvocal rehearsal processes. The left basal ganglia may play an essential role in establishing an interplay with frontal regions of the cortex, Broca's area in particular, that allows sentence word order to be checked, stored and retrieved at the right time, and the appreciation of hierarchical syntactic structure.

The foci of selective cerebellar activation associated with morphosyntactic anomalies detection is also consistent with clinical data. There are now a handful of case reports of production agrammatism after cerebellar damage (Silveri et al., 1994; Zettin et al., 1997), suggesting an involvement of the cerebellum in the production of morphologically correct sentences: whether this represents a genuine disorder of language production, or can be interpreted as a consequence of a highly specific impairment in motor planning and execution requires further investigation.

In conclusion, strong converging evidence appears to be now available, leading to a better understanding of the anatomo-functional structure of the neural network involved in sentence processing at the morphosyntactic and syntactic level. The overall pattern resulting from this experiment suggests that syntactic capacities are not implemented in a single area. Rather, they constitute an integrated system which involves both left and right neocortical areas, as well as other portions of the brain, such as the basal ganglia and the cerebellum, providing independent evidence for the interpretation of clinical data. Furthermore, the lack of a complete overlap between the neurological correlates of the syntactic and the morphosyntactic components of the language faculty fits well with the distinction made in linguistics on theoretical grounds: further experimental work is necessary to clarify this important issue.

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Table 1

a. (Ph + M + S) - Baseline masked with simple main effects

	x	y	z	Z scores
L inferior frontal gyrus (44)	-46	18	24	4.80
L inferior parietal lobule (40)	-36	-42	44	3.82
L superior parietal lobule (7)	-30	-68	48	5.28
	-34	-50	52	4.57
	-32	-58	52	4.49
L precuneus (7)	-26	-70	40	5.03
L occipital/fusiform gyrus (18/37)	-30	-82	-16	3.97
	-20	-80	-16	3.30
	-22	-84	-8	3.19
L cerebellum	-50	-64	-24	3.99
	-44	-72	-24	3.77
	-20	-42	-48	3.36
R lateral premotor (6)	34	-2	60	4.14
R superior parietal lobule (7)	30	-64	56	4.52
R precuneus (7)	10	-72	56	5.99
	20	-76	48	5.37
	26	-80	40	5.25
R cuneus (18)	22	-82	4	4.20
	14	-78	8	3.87
R occipital/fusiform gyrus (18/37)	22	-84	-8	4.22
	16	-80	-20	3.98
	14	-82	-8	3.80
R middle occipital gyrus (19)	28	-82	20	4.71
	30	-94	16	4.36

	28	-84	12	4.77
R cerebellum	42	-68	-32	4.02
cerebellar vermis	-4	-70	-36	5.39
	-8	-52	-32	3.21

28	-84	12	4.77
42	-68	-32	4.02

b. (M + S) - Ph masked with simple main effects

	x	y	z	Z scores
L inferior frontal gyrus (circular sulcus) (45)	-28	34	8	4.19
R inferior frontal gyrus lateral (44)	56	18	12	3.12

c. S - Ph

	x	y	z	Z scores
L inferior frontal gyrus (circular sulcus) (45)	-28	32	4	3.53
L insula	-36	-14	16	2.88
	-36	-22	24	2.52
L nucleus caudatus	-24	-2	20	2.79
R inferior frontal gyrus (44,45)	58	22	8	3.03
	60	14	12	2.71

d. M - Ph

	x	y	z	Z scores
L inferior frontal gyrus (circular sulcus) (45)	-28	34	8	3.89
R inferior frontal gyrus (44,45)	50	14	12	3.10
	58	22	16	2.59
cerebellar vermis	6	-80	-44	3.21
	6	-70	-36	2.88
	12	-64	-8	3.13

Ph = phonotactic task; M = morphosyntactic task; S = syntactic task

Legend for Figure 1

Foci of significant activation for the corresponding contrast are superimposed on a set of axial slices, derived from a T1 Magnetic Resonance Imaging single-subject image (SPM-96), which has been normalized to the standard stereotactic space (ICBM), closely approximating the space described in the atlas of Talairach and Tournoux (1988). Below each axial slice, the corresponding coordinate level along the z axic is indicated (in mm).

A. (S + M + Ph) - Baseline masked with the individual simple main effects, $Z > 3.09$ (see table 1, a).

B. S - Ph, $Z > 2.33$ (see table 1, c).

C. M - Ph, $Z > 2.33$ (see table 1, d).

Ph = phonotactic task; M = morphosyntactic task; S = syntactic task

Figure 1