

WHEN BROCA EXPERIENCES THE JANUS SYNDROME:
AN ER-fMRI STUDY COMPARING SENTENCE COMPREHENSION
AND COGNITIVE SEQUENCE PROCESSING

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ABSTRACT

The determining of brain regions that exhibit specific activity during sentence comprehension compared to other non-linguistic cognitive tasks constitutes one of the important challenges in the domain of functional neuroimaging of the faculty of language. In the current paper we report an event-related functional magnetic resonance imaging (ER-fMRI) experiment, in which we directly compared the cerebral basis of sentence comprehension on the one hand, and of abstract sequence processing on the other hand. Previous experimental work done in our group, as well as different observations from recent behavioural, neurophysiological and functional neuroimaging experiments led us to propose the hypothesis that both of these tasks would share certain computational properties. Thus, this experiment was designed to show which brain regions would be implicated in both tasks and compare them to brain regions that would be specifically engaged in sentence comprehension. Results from this experiment suggest that distinct sub-regions in the left prefrontal cortex, potentially including Broca's area show distinct activation patterns during both of these tasks. Results are discussed in the context of a construction-based model of sentence processing (see Dominey and Hoen, 2006, this issue) that is based on a dual-path processing mechanism separating function and content information processing. We propose and discuss the hypothesis that subparts of Broca's area BA 44 and BA 45 would respectively be implicated in two different aspects of sentence comprehension: i) a general structure mapping capability and ii) the online integration of semantic representations onto structural constraints.

Key words: Broca's area, sentence comprehension, abstract sequence processing, fMRI, syntax

INTRODUCTION

Real-time sentence comprehension constitutes a highly integrated human cognitive ability that requires conjoined extraction and combination of many different information types, implicating the cooperation of numerous brain systems. In particular, two main sources of information, directly available from the sentence stimulus, are generally assumed to play distinct crucial roles in successfully determining the meaning of linguistic utterances, namely function and content information. Function information can be defined as a mosaic of indices located in various language-dependent proportions in: prosody, word-order regularities, word-category information and the existence, in certain languages, of a separated category of function-words (e.g., 'grammatical words' as determiners, prepositions, conjunctions or auxiliary verbs) (Bates and MacWhinney, 1989; Bates et al., 1982). Content information can be found at first instance in so-called content-words including nouns and verbs that carry the word-level meaning of sentences, with the sentence-level meaning derived as the product of the unification between these content and function components.

In the domain of visual word processing, different behavioural experiments have provided

extensive results suggesting that function and content information carried in certain languages by corresponding lexical categories (function- vs. content-words) were represented in two subvocabularies and that function-words in particular could be accessed by specific mechanisms (e.g., Bradley and Garrett, 1983; Bradley et al., 1980). Using the electrophysiological measurement of scalp event-related potentials (ERPs), different authors could show that function- *versus* content-words elicited different cortical responses identifiable respectively as a left anterior negativity and a centro-parietal N400 (Kutas and Hillyard, 1983; Van Petten and Kutas, 1991; Neville et al., 1992; Brown et al., 1999). These observations suggested that formerly identified behavioural distinctions would rely on the existence of specific cortical networks preferentially dedicated to the processing of function or content information.

In this context, we developed a model of sentence comprehension primarily based on a dual-stream mechanism, separately processing function and content information in order to realize the correct mapping of content items onto their sentence specific meaning, as assessed by their thematic roles (Who does what to whom?). In the current paper we show how developing this model

successively led us to consider i) an equivalence hypothesis between function information processing in the context of sentences and in the context of sequences of abstract symbols and ii) how the testing of this equivalence hypothesis led us to propose hypotheses on the role of Broca's area and the left inferior frontal cortex in sentence comprehension. In this introduction, we will start by reviewing classical psycholinguistic models of sentence comprehension based on the representation of hierarchical syntactic structures. We will then show how recent experimental evidence on online sentence comprehension tended to rethink these models by including shallow parsers in parallel with hierarchical syntactic parsers. Finally, we will show how in our group we developed such a shallow, non-hierarchical model of sentence comprehension (see Dominey and Hoen, 2006, this issue) and how this model led us to propose hypotheses on the role of Broca's area in sentence comprehension.

Models of Sentence Comprehension

The fundamental theoretical and experimental dichotomy existing between structure and content information can be traced in a particularly salient way in the historical development of psycholinguistic models of sentence comprehension. In this context, two main types of models emerged both dedicated to the representation of hierarchical syntactic structures as described in the universal/transformational grammar theory (Chomsky, 1957, 1965, 1995). These models respectively consider function or content information processing as central and predominant in successfully parsing sentences.

The first types of models are referred to as serial or structural models (Frazier and Fodor, 1978; Fodor and Frazier, 1980). These models are based on modular information processing that take place in a fixed time order. Their operating mode is generally centered on syntactic category information processing (Frazier and Rayner, 1982; Ferreira and Clifton, 1986). Computer based models inspired from this approach existed from its onset (Frazier and Fodor, 1978) and could reproduce, amongst others, experimental observations reflecting parsing strategies as minimal-attachment (Frazier and Fodor, 1978; see Frazier and Clifton, 1996, for review), or their behavioural manifestations as garden-path effects or syntactic ambiguity resolution (Kempen and Vosse, 1989; McRoy and Hirst, 1990). Recently, one model of this category (Kempen and Vosse, 1989) was extended to reproduce parsing strategies observed in agrammatic aphasic patients when confronted with a thematic role assignment task (Vosse and Kempen, 2000; Caplan et al., 1985). However, serial/structural models of that kind are often opposed the fact that parsing seems not only to reflect the integration of

syntactic category constraints but is also influenced by the frequency with which one particular type of construction occurs in a determined linguistic context (MacDonald et al., 1994; Trueswell, 1996) or by other contextual or discursive information (MacDonald et al., 1994; Tanenhaus and Trueswell, 1995; Altmann and Kamide, 1999; Spivey et al., 2001). The second family of models is commonly referred to as parallel or lexical models. Models of this type generally assume that parsing is conducted under the influence of multiple information sources that progressively guide the selection of one parsing solution amongst many equally possible choices and are therefore usually based on parallel, mostly connectionist architectures (Christiansen and Chater, 1994; Tabor and Tanenhaus, 1999; Tabor et al., 1997). These models usually put a stress on other lexical information than words' syntactic category and try to include influences from word and/or construction frequencies, lexical, contextual and discursive information as well as pragmatic knowledge (Ford et al., 1982; MacDonald et al., 1994; Tanenhaus and Trueswell, 1995). Recent extensions of these models are able to reproduce various behavioural observations on contextual frequency effects or data related to structural/semantic ambiguities, as in "The policeman that the burglar arrested" in which syntactic information and semantic habits are opposed (Tabor and Tanenhaus, 1999; Tabor et al., 1997). These two types of models have proven to be very successful in reproducing many behavioral observations related to online parsing strategies. Nevertheless, two important limits of these classical psycholinguistic models of sentence comprehension merit to be addressed. First, these models are models of sentence parsing, not sentence comprehension *per se*. For a sentence parsing model to become a sentence comprehension model, one would need to face it up to an external world that the model would have to describe (Tabor and Tanenhaus, 1999). Moreover, these two types of models share the same final goal of representing the hierarchical syntactic structure of sentences. However, recent experiments tend to demonstrate that online sentence comprehension in a vast number of cases may rely on imperfect, incomplete determining of syntactic structures of sentences. According to these recent views, the cognitive system appears to rely on economic strategies based on satisfaction criteria that would often make it choose incomplete, shallow parsing strategies rather than complete and perfect syntactic structure parsing or semantic analysis (Christianson et al., 2001; Sanford, 2002). In a recent series of experiments, Ferreira (2003), submitted subjects to a thematic role assignment task including active or passive sentences. Results show that sentences with passive syntactic structures are usually less well understood than the corresponding active sentences, especially when they contain unusual thematic

relations, as in the former example “The policeman that the burglar arrested”. In such sentences, the role of agent is attributed to the correct argument only in 74% of cases, suggesting that in more than one quarter of cases, either the system fails to correctly or completely parse the sentence, or ignores the result of its parsing to rely on other cues (as for example linguistic habits or real-world knowledge about who’s generally arresting whom). Other results from this work suggest that the first argument in a sentence is often assigned the role of agent, whatever the syntactic structure of the considered sentence may be, an observation supporting the existence of a preferred (canonical) thematic role assignment order in certain languages: Agent-Verb-Patient (see also MacWhinney et al., 1984 for comparable results). From these observations and others (see, e.g., Christianson et al., 2001; Sanford, 2002), it appears that the determining of hierarchical syntactic structures during sentence comprehension may well not occur in a complete fashion, but that other, shallow cognitive mechanisms, potentially quicker than syntactic parsing, may take place during sentence comprehension. To address this second issue, Townsend and Bever (2001), have proposed a model of sentence comprehension called “late assignment of syntax theory” (LAST), that is based on the co-existence of two sentence processing phases. The first one produces a “pseudo-parse” that does a generally quicker sentence analysis mainly based on linguistic habits and evident semantic associations. The second one is based on a classical algorithmic processing mechanism and performs syntactic structure determination. In our group, we developed a language acquisition model that learns to perform sentence comprehension, as evaluated by thematic role assignment and that addresses both limits identified for classical psycholinguistic models of sentence comprehension: i) it includes an external visual world that the model learns to describe and ii) parsing relies on a unique non-hierarchical representation system, based on the extraction of construction regularities (Goldberg, 1995) via a dual-path mechanism for processing function *versus* content information (see Dominey and Hoen, 2006, this issue).

A Construction-Based Model of Sentence Processing

Interestingly, the model was initially developed to simulate sensorimotor sequence learning, in which serial and abstract structures of sequences were processed by dissociated neurophysiological systems (Dominey et al., 1998). Serial structure was defined in terms of the serial order of sequence elements, while abstract structure was defined in terms of transformational structure within sequences. Thus, the sequences of letters ABCCAB and BKTTBK correspond to two distinct

serial structures that share a single common abstract structure (123-312) that can be used to generate an open set of isomorphic sequences (e.g., VFCCVF, etc.). This generative property suggests a potential link with generative aspects of grammatical structure (Dominey, 1997). We demonstrated that while the recurrent network of the dual process system is able to learn serial structure, abstract structure requires an additional memory system and its control, allowing representation of variables. This supported the subsequent observations of Marcus et al. (1999) concerning the processing architectures capable of handling variables and their assignment. We subsequently demonstrated that this dual process model could account for human infant sensitivity to serial (Saffran et al., 1996), temporal (Nazzi et al., 1998) and abstract (Marcus et al., 1999) structure (Dominey and Ramus, 2000). We reasoned that if this dual process system represents a highly simplified model of the initial state of sensitivity to these structural regularities in the infant, then these capabilities should provide the basis for more adult-like language processing. To characterize such a behavioral capability, we turned to Caplan et al. (1985) who developed a syntactic comprehension task in which subjects read a variety of sentences and are required to respond to each by indicating the agent, object and recipient for the sentence, in that order. The task has been well explored, and used to quantify the performance of human subjects after brain lesions, and for these reasons has also been used as target behavior for a number of simulation studies (e.g., Haarmann et al., 1997; Vosse and Kempen, 2000). In the context of the model, a sentence would be presented as a sequence of words, and then the model should respond by identifying the appropriate agent, object, and recipient. Figure 1 illustrates how this works for the dative-passive grammatical construction. The operation of the model is based on two central ideas. First, for each distinct grammatical construction (e.g., active, dative passive, etc.) there is a fixed transformation between the input order of open class elements and the output semantic structure including the predicate and thematic roles agent, object, recipient. This reflects ideas about sentence-to-meaning mapping that are developed in the construction grammar literature (Goldberg, 1995, 2003). Second, each grammatical construction is uniquely identified by its configuration of closed-class elements. This second point represents a specific implementation of the more general cross-linguistic “competition model” hypothesis of Bates and MacWhinney (1982), in which open-class words are assigned to their thematic roles based on competing cues including word order and/or grammatical function-words or morphemes across languages (Bates et al., 1982). As illustrated in Figure 1, the input-output transformation behavior

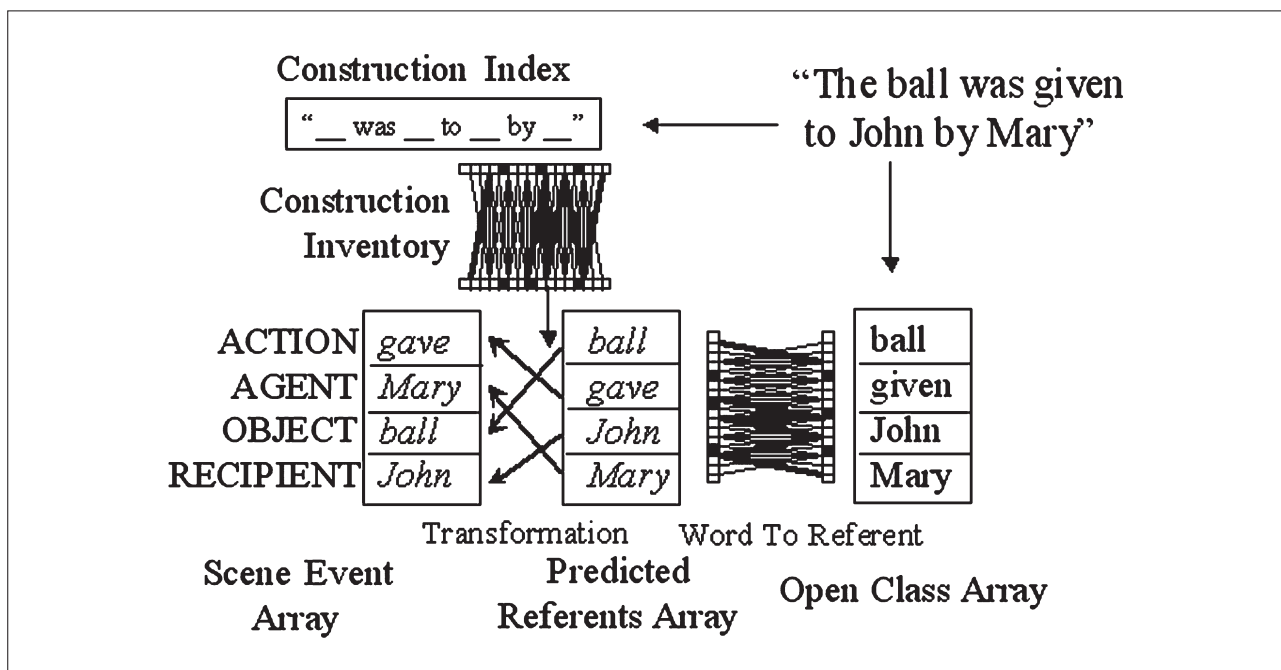


Fig. 1 – Structure-mapping architecture for sentence processing. Open and closed class words are processed in separate streams. Open class words in Open Class Array are translated to their referent meanings via the World To Referent mapping. This referent semantic content is inserted into the Predicted Referents Array (PRA). PRA elements are mapped onto their roles in the Scene Event Array by the Sentence To Scene mapping, specific to each sentence type. This mapping is retrieved from Construction Inventory, via the Construction Index that encodes the closed class words that characterize each grammatical construction type.

of the model corresponds to the selection of grammatical constructions, or sentence to meaning mappings based on the configuration of closed-class elements specific to each grammatical constructions.

In more abstract, non-linguistic terms, this corresponds to a set of specific abstract structures implemented in the Construction Inventory, appropriately selected by closed-class coding in the Construction Index. The crucial point is that via the model we establish a functional/behavioral “equivalence hypothesis” based on the relation between the mapping of sentences to meaning via grammatical constructions on one hand, and the manipulation of transformational structure in abstract sequences on the other. Indeed, the same system can learn to correctly associate sentence specific thematic roles to content arguments but can also learn to manipulate serial-order transformation rules in sequences of abstract symbols, as long as these symbols can be separated in two categories namely function- and content-symbols. If we consider for example two abstract structures: “123123” and “123312” and associate the first one with what is now going to be a function-symbol “Y” and the second one with the function-symbol “X”. We obtain 123Y123 and 123X312, two abstract structures of sequences respectively associated to the presence of a particular function symbol. Then we obtain a generative system, comparable to a very simplified artificial grammar, which has restricted generative properties due to the constraints of the association between abstract structures and function-symbols.

ABCXCAB or VHRYVHR would be acceptable sequences in this system and ABCXABC or VHRYRVH would be examples of non-acceptable sequences in this “microscopic” artificial grammar. Interestingly, the same computational architecture as the sentence processing model previously described can also learn to handle sequences of that kind as described in Figure 2.

This time, the sequence of items enters the model and the correct abstract structure can be selected after the recognition of one or another function symbol because again there is a fixed transformation between the input order of the first triplet of letters in the sequence and the output, represented by the last triplet of letters in the sequence.

From Modeling Sentence Comprehension to the Cerebral Bases of Sentence Comprehension

The striking prediction that resulted from this hypothesized equivalence between structure mapping in sentences and sequences was that, if the same mechanism is performing thematic role assignment and abstract sequence processing (as in the model), then we should expect to observe behavioral and neurophysiological relations between these two types of behavior in human subjects. Indeed, we first observed that in agrammatic aphasic patients the performance on these two tasks is highly correlated (Dominey et al., 2003; Lelekov et al., 2000). Extending these results, we recently demonstrated that training agrammatic aphasics on these abstract sequences

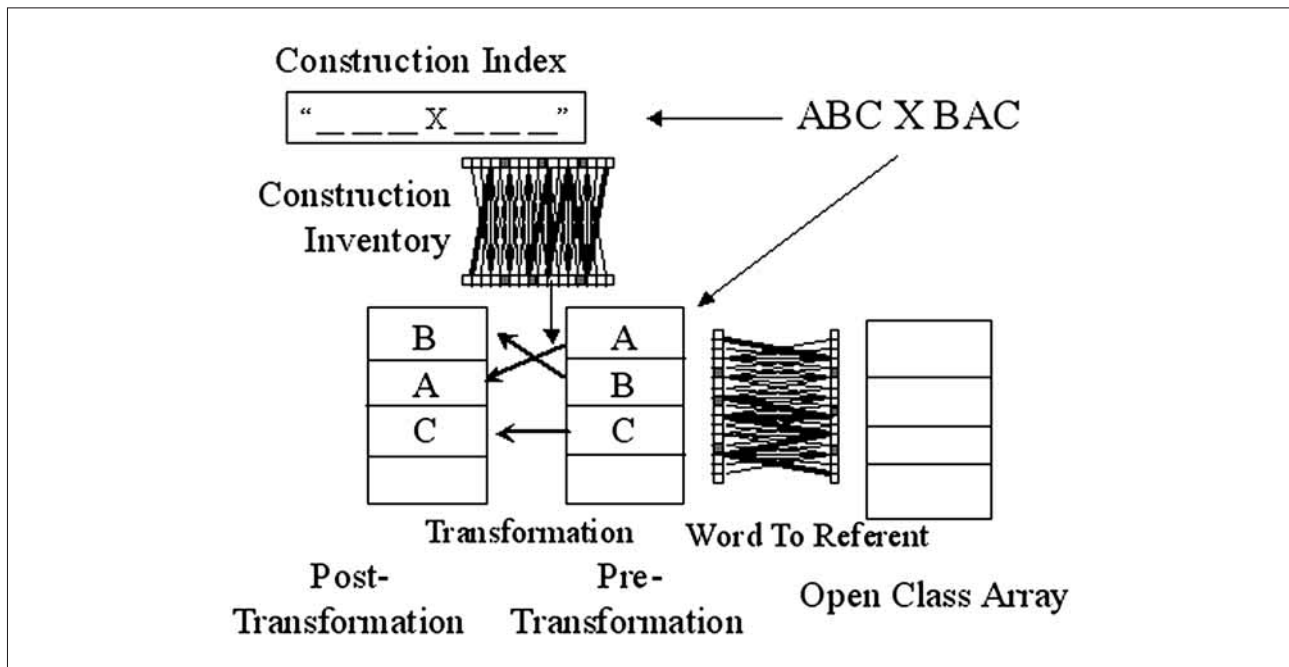


Fig. 2 – Abstract sequence processing. Here, the generalized transformation mechanism is invoked for non-linguistic sequence processing.

led to a significant and selective transfer to their improved performance in the corresponding grammatical forms (Hoen et al., 2003). Interestingly, agrammatic patients generally suffer from Broca's aphasia consecutively to perisylvian cortical lesions. These patients usually show preserved comprehension abilities for short and highly semanticised sentences, but exhibit important difficulties understanding syntactically complex or semantically reversible sentences (Caramazza and Zurif, 1976; Caplan et al., 1985; Bates et al., 1991). Agrammatism can be considered as a pathology of function-information processing in general, agrammatic production being characterized by short, syntactically simple utterances lacking much function-words and function-marks (Miceli et al., 1989). The processing of word-order information, another crucial function cue, also seems to be impaired, patients showing a strong preference for simple Agent-Object-Patient sentences in production (Saffran et al., 1980), as well as in comprehension (Schwartz et al., 1980). This suggested a first correlation between the processing of structural rules in sentences and abstract sequences as well as a potential link to left inferior prefrontal functions.

Then, we developed a sequence judgment task to compare it to classical sentence judgment tasks commonly used in ERP experiments (e.g., Friederici et al., 1996, 1999) or fMRI experiments (e.g., Baumgaertner et al., 2002). In these sentence judgment tasks, subjects generally read word-by-word presented sentences and are required to indicate if they are acceptable or not. Depending on the studies, sentences contain different types of structural, syntactic or semantic violations. In the

sequencing task we developed, subjects are asked to read and judge as acceptable sequences of letters presented item-by-item. Before the experiment, subjects learn the two simple abstract structural rules mentioned before (123Y123 and 123X312), that define the acceptable or correct sequences they will be presented to during the experiment (ADFYADF or ADFXFAD for example). In these 7-letters sequences, the fourth element is considered as a function-symbol as it is related to the underlying abstract sequence structure and its nature is predictive of the forthcoming elements in the sequence. The first triplet of letters constitutes the content context of the sequence and the last triplet of letters is constrained by the nature of the function item "Y" or "X" and the corresponding rule. A simple repetition of the first triplet is indicated by the function item "Y", whereas an order-transformed triplet is indicated by "X". Non-acceptable sequences can be constructed by introducing one violating letter in the sequence. Abstract rule violations can be created by introducing a bad application of the abstract construction rule constraining sequences, for example: ADFXADF. In this example, subjects learned that in a sequence containing a letter "X", the second triplet of letters is constructed by taking the first triplet in the order 123 and transforming it to the order 312, hence "FAD", the correct sequence being ADFXFAD. The appearance of the letter "A" in ADFXADF clearly violates the structure of the sequence, but not its content as letter "A" is actually part of the correct sequence, only its position is in this case wrong. Content violations can be created by inserting one completely new letter in the sequence, as in

ADFXFAU, where the letter “U” constitutes another type of violation as it is not expected in the sequence. However, “pure” content violations, analogous to semantic violations in sentences are impossible to create in the content-poor material of our abstract sequences. Using this type of sequencing task and comparing it to a classical sentence judgment task, we could demonstrate that ERP profiles observed in both tasks were quite comparable. First we demonstrated that the reading of function-symbols indicating the processing of a serial order transformation in sequences was associated to a left anterior negative ERP component (Hoen and Dominey, 2000). Then we showed that in both cases, the different types of violations could be dissociated by ERP markers. Content violations were associated to the appearance of a single centro-parietal negative component (the N400 in sentences; Kutas and Hillyard, 1983). Structure violations were associated to a P600 effect in sentences (Osterhout and Holcomb, 1992) and to a complex response composed of a centro-parietal negativity followed by a P600-like response in sequences (Hoen and Dominey, 2004). Again, the processing of function-symbols requiring a serial order manipulation of letters in sequences evoked a left anterior negativity very similar to that evoked by the reading of function-words indicating non-canonical thematic role assignment in passive sentences.

These observations in agrammatic aphasic patients, generally suffering from lesions in the left perisylvian area including Broca’s area and the comparability of evoked potential responses to function-symbols and function-words indicating non canonical thematic role assignment led us to propose the hypothesis that regions of the left prefrontal cortex, possibly including Broca’s area may well be involved in structure mapping both in sentences and sequences.

The Present Study

In order to address this issue, we performed a direct comparison of the cortical neural networks respectively implicated in correct sentence comprehension on one hand and abstract sequence processing on the other hand in an event-related functional magnetic resonance imaging (ER-fMRI) experiment. In the sentence judgement task subjects were asked to read active or passive sentences presented word-by-word and were required to judge them as acceptable or not. In the present version of the task, in order to prevent subjects from focusing on any particular linguistic dimension of the sentences, stimuli could contain either structural or semantic violations. Structural violations were created by moving one word to a wrong, unattended sentence position, leading to a strong word-order and word-category mismatch, classically associated in ERP experiments to the

P600 marker (e.g., Osterhout and Holcomb, 1992; Friederici et al., 2002). In the current study, we were only interested in normal, correct sentence comprehension, and these violations were introduced amongst our stimuli only to ensure that subjects correctly read and understood the sentences and did not focus on any particular component (syntax or semantics) during their reading, but paid attention equally well to both dimensions. Therefore, only fMRI results concerning normal sentence processing will be taken into account. In the sequence processing task, subjects were asked to read and judge sequences of letters as described before, again in this experiment, only the processing of correct sequences constituted our main interest and violations of both types were included only to ensure that subjects correctly performed the sequence judgment task and did not rely on other strategies than real sequence processing to successfully complete the task. Therefore, our analyses of the present experimental data will concentrate on correct sentence and sequence processing.

MATERIALS AND METHODS

Subjects

Seventeen right-handed subjects (9 female, 8 male), aged 19 to 28 (mean = 22.82, SD = 2.27), were scanned and paid for their participation. All participants were submitted to a pre-experimental medical visit conducted by a medical doctor, to ensure they were free of any counter-indication to fMRI scanning. Subjects were all native French speakers and free of any neurological or language related (developmental or acquired) impairments. The study was approved by the local ethical committee (Lyon-A) and conducted according to the French law for biomedical research. After pre-processing of acquired functional and anatomical scans, 3 subjects were excluded from further analyses because of normalization errors due to too large head movements. Final analyses were therefore conducted on 14 subjects (7 female, 7 male).

Procedure

Subjects were installed lying inside the scanner where they could see a computer screen back-projected through a mirror system on which visual stimuli were presented. Before each scanning session, subjects were informed of distortion effects of head and body movements on functional and anatomical scans. Before scanning, subjects had to learn the two rules that directed sequence construction and were trained on an off-line version of the different tasks. Only when subjects

TABLE I
Examples of the different stimuli used in the sentence/sequence judgement task.
In violation conditions, violating items are printed bold and italic

Type	Complexity	Condition	Corresponding stimulus example
Sentences	Active	Correct	Le pianiste a donné un concert au parc (The pianist gave a concert at the park)
		Content violation	Le pianiste a donné un concert au <i>banc</i> (The pianist gave a concert at the <i>banc</i>)
		Structural violation	Le pianiste a donné un <i>au</i> concert parc (The pianist gave a <i>at</i> concert the parc)
	Passive	Correct	Un concert a été donné au parc par le pianiste (A concert was given at the park by the pianist)
		Content violation	Un concert a été donné au <i>banc</i> par le pianiste (A concert was given at the <i>bench</i> by the pianist)
		Structural violation	Un concert a été donné au <i>par</i> parc le pianiste (A concert was given at the <i>by</i> park the pianist)
Sentences	Repetition	Correct	N O P Y N O P Y
		Content violation	N O P Y N O A Y
		Structural violation	N O P Y <i>P</i> N O Y
	Transformation	Correct	N O P X P N O X
		Content violation	N O P X P N A X
		Structural violation	N O P X N O P X

correctly mastered the sequence and sentence judgment tasks, as indicated by the fact that subjects performed the training sessions of 10 trials in each condition without any errors, scanning could start.

Task

Subjects were asked to carefully read sentences or sequences displayed item-by-item on the video screen and to indicate, via a mouse held in their right hand, if stimuli were acceptable or not. Subjects were not required to indicate the type of violation they had encountered whenever it was the case, they were only asked to detect incongruencies without specifying their type.

Stimuli

(see Table I for examples)

Abstract Sequences

As in previous studies based on this paradigm (Hoen and Dominey, 2000, 2004), sequences were composed of 8 elements, successively presented one at a time, with the same global structure. Elements 1 to 3 consisted of an initial letter-triplet, randomly selected between A and V. Element 4 was the function-symbol, “X” or “Y”, linked to an arbitrary rule specifying the nature of elements 5 to 7. Finally, element 8 was a repetition of the function-symbol and indicated the end of the sequence.

Types: eighty correct sequences were constructed, separated in two types:

1. Type 1, or “Repetition”: the second triplet consisted in a simple repetition of the first letter-triplet, according to the abstract rule: 123 Y 123 Y.

2. Type 2, or “Transformation”: the second triplet, in positions 5 to 7, consisted of a repetition of the first letter triplet in positions 1 to 3, but with different serial order, according to the abstract rule: 123 X 312 X.

Violations: eighty violation sequences were constructed, 40 for each type, divided in two conditions:

1. Content violation: the element 7 was replaced by a new letter, that didn’t match the former sequential context. 123 Y 124 Y or 123 X 314 X.

2. Rule violation: the elements 5 to 7 corresponded to a wrong application of the rule (i.e., application of the rule not indicated by the function symbol), this violation appeared first on element 5. 123 Y 312 Y or 123 X 123 X.

Sentences

One hundred and sixty French sentences were constructed, composed of 8 (active sentences) to 10 words (passive sentences). They were presented word by word at a central fixation point, words being written in low case, except the first letter of the first word in a new sentence that was printed in upper case.

Types: eighty correct sentences were constructed, separated in two types:

1. Type 1, or “Active”: sentences were 8 words, 3 argument active sentences.

2. Type 2, or “Passive”: the same sentences were proposed in the passive voice, forming normal 10 words French Dative Passive sentences.

Violations: eighty violation sentences were constructed, 40 for each type, divided in two conditions:

1. Semantic violation: the indirect object noun was always replaced by a semantically anomalous word, in position 8 in active sentences, in position 7 in passive sentences.

2. Structural violation: the preposition preceding the indirect object was moved to an anomalous position.

fMRI Acquisition Paradigm

In order to allow mixing of correct and violation-containing stimuli, we used an ER paradigm. Events were defined as one sentence or sequence respectively presented word-by-word or letter-by-letter. As sentences and sequences varied in length from 8 (active sentences and sequences), up to 10 items (passive sentences), individual durations for each item in each particular condition were calculated to ensure a constant total event duration of one repetition time (TR), fixed here at 3 sec (TR = 3 sec). Thus, individual item durations ranged from 375 msec for words in active sentences, down to 300 msec for words in passive sentences.

Null Events

In order to increase temporal variability between successive occurrences of different events, as well as to model different non task-specific activities such as response selection, programming and execution of the motor response, we introduced a null-event in our stimuli set (Friston et al., 1998, 1999). Null events consisted of a fixation cross, displayed during one TR. Subjects were asked to respond to this null event by randomly pressing one or the other response button.

Scanning Sessions

Acquisition of functional scans was divided in four different sessions. Each session comprised 120 trials (30 corrects, 30 content violations, 30 structure violations and 30 null-events). Sessions were of four different types: 1) Active sentences, 2) Passive sentences, 3) Repetition sequences and 4) Transformation sequences. Thus, sequences and sentences were not mixed in same sessions as well as sentences or sequences of different complexities, to avoid extreme task complexity that would be due to permanent task switching between stimuli. Session orders were counterbalanced across subjects. Each scanning session was separated from the next by a short break, lasting from 5 to 10 minutes depending on subjects demand.

Stimuli Randomization

In each session, the sequence of stimuli presentation was optimized by generating 10,000 random permutations of integers between 1 and 120 and by chunking the obtained sequences in four lists of 30 numbers, each one representing the rank of occurrence of one stimulus type in one session. Obtained stimuli sequences were then tested for optimality (implemented in Statistical Parametric Mapping – SPM99; Dale, 1999; Friston et al., 1999) and the best sequences, taking an optimality criterion for contrast correct stimuli *versus* null events were kept. This was done in order to reach an optimized temporal delay between successive occurrences of the same condition (Dale, 1999; Friston et al., 1999; Dale and Buckner, 1997; Buckner et al., 1998; Josephs and Henson, 1999; Miezin et al., 2000).

fMRI Acquisition

Imaging data were collected using a clinical Phillips NT scanner, operating at 1.5 Tesla. For each subjects, two types of scans were acquired: one structural T1 (anatomic) picture and functional gradient echo planar T2 scans contrasting the blood oxygenation level-dependent (BOLD) effect (TR = 3 sec, TE = 45 msec, matrix 64 × 64 mm, FOV = 256 × 256 mm). For each subject, the functional scans were acquired in 4 sessions and a total of 240 volumes by session were obtained, as well as 7 dummy scans at the beginning of each session, in order to obtain stable T1 equilibrium, these dummy scans were excluded from further analysis. Each functional scan was composed of 27 axial slices of 5 mm (resolution: 4 × 4 × 5 mm), centred in order to cover whole subjects brain and cerebellum. Functional volumes were acquired using an interleaved sequence, starting by odd slices, bottom slice first and finishing by even slices. Acquisition of anatomical T1 image occurred after end of session 2. Total scanning duration was of approximately an hour.

fMRI Data Pre-Processing

All data analyses were conducted using statistical parametric mapping (Friston et al., 1995a) in the SPM99 software (Wellcome Department of Cognitive Neurology, London, UK), used as a toolbox in the Matlab environment, in its 5.3 version (©MathWorks Inc., 1999). First, slicetiming was applied, in order to correct for time acquisition delays between different slices in the interleaved mode. The correction used a sinc interpolation method, all slices being re-aligned in time to the 15th slice. To remove spatial shifts artefacts between slices due to subjects movements inside the scanner, each volume was realigned to the first volume in a session and then realigned

across sessions for each subject. Estimated movement parameters were kept for further modelling of residual movement artefacts. Spatial realignment of slices was then performed together with spatial normalization to the standard stereotactic space provided by the Montreal National Institute (MNI), T1 template provided in SPM99 (Cocosco et al., 1997), by applying a sinc interpolation in space (Friston et al., 1995b). Finally, a spatial smoothing step was applied to functional scans, using a Gaussian kernel (FWHM = 10 mm).

Modelling the BOLD Response

For each independent session, statistical model included one main event condition (sentences or sequences) and the null-event. In our case, null events should be modelled as they consisted in the visual presentation of a flashing fixation cross and required subjects to produce a behavioural response by pushing alternatively the left or right response button, which could explain some of the variance present in the data. The influence of the presence of a violation in sentences or sequences was modelled using a binary linear parametric regressor (Büchel et al., 1998), associated to the main condition (sentence or sequence) and having a value of 0 for violation trials and a value of 1 for correct trials, in order to specifically isolate the response related to correct events. For each individual subjects, the variance due to residual movement effects was modelled by adding 6 regressors corresponding to the 6 movement parameters determined at the realign pre-processing stage.

Contrasts and Statistical Inferences

To study activations related to processing main correct conditions, statistical SPM $\{t\}$ maps corresponding to the contrast between the parametric regressor separately modelling the variance for correct events and the null-event were obtained at first-level for each of the 4 sessions in each subject. Then, for the two sessions corresponding to correct sentence processing or correct sequence processing, 28 contrast images were reintroduced at a second level in a second one-sample t-test, concatenating data obtained in two separate sessions, in order to gain statistical power and obtain activation maps corresponding to the main correct conditions. Results of these one-sample t-tests are reported with p-values corrected at ($p = .05$) at the voxel level. To study the conjunction of the two tasks and in order to limit false positives due to the use of a conjunction analysis (Price and Friston, 1997), conjunction was performed after applying an inclusive mask ($p = .05$) to isolate the regions activated in the sentence comprehension task that were also significantly

activated in the sequencing task. Finally, to study regions participating only in the sentence comprehension task, we performed a two sample t-test contrasting sentence processing – sequence processing. For this comparison only, we report activations that are significant at ($p = .05$) corrected at the cluster level, and for which values at the voxel level were significant at ($p = .05$) corrected after small volume correction, on voxel clusters exceeding $k = 50$ voxels, in regions where activations were indeed predictable (BA 45/47 cluster of activation in sentences alone).

RESULTS

In the present results section, we will report, for each observed activation, size of the concerned cluster (n of activated voxels), p-values (corrected at .05) obtained at cluster and at activation peak (voxel level). We will then report activation peaks coordinates transformed in Talairach space (Talairach and Tournoux, 1988). We will first report activation patterns observed for the two main events: correct sentence processing and correct sequence processing. Then, we will show results from conjunction analysis performed on both sentence and sequence tasks. Finally we will give results observed for the sentence minus sequence contrast, showing the neural network specifically implicated in sentence processing compared to sequence processing. The different finer contrasts: complex sequences *versus* simple sequences and passive *versus* active sentences, as well as the contrasts involving the comparison of correct *versus* violated sequences or sentences were analyzed but didn't reveal any statistically robust results. This lack of significant effect may be attributed to the (too) small number of trials in each condition in our experiment, as well as to the fact that the stimuli order was not optimized to favour these specific contrasts. We will thus only report results from the main task comparison.

Contrast 1: Correct Sentence Judgement versus Null-Event The Neural Network Implicated in On-Line Sentence Comprehension

Brain regions showing greater activity for the on-line monitoring of visually presented sentences are listed in Table IIa. They constitute a vast neural network covering occipital (BA 19, BA 37), temporal (BA 22, BA 21) and parietal (BA 40/7) areas as well as large prefrontal region implicating superior (BA 6, supplementary motor area – SMA), medial (BA 6, BA 9/46/44) and inferior (BA 47/45/44) regions of the left prefrontal cortex. Activations are strongly lateralized in favour of the left hemisphere but homologous right hemisphere areas often show significant activation levels as well.

TABLE II
Contrasting correct- versus null-events

Cluster size (N voxels)	Cluster level p-values (corrected)	Voxel level p-values (corrected)	Talairach coordinates for peak activation			Corresponding Brodmann area (peak/extension)	Corresponding cortical region (peak)
a) Correct sentence processing vs. null-event							
Left hemisphere							
2318	.000	.000	- 46	6	40	BA 6/9/46	Precentral sulcus/middle frontal gyrus
-	-	.000	- 40	13	23	BA 9/46/44	Middle frontal gyrus -
-	-	.001	- 51	23	3	BA 47/45/44	Inferior frontal gyrus
1822	.000	.000	- 38	- 78	- 1	BA 19/37	Inferior occipital gyrus
-	-	.000	- 40	- 55	- 11	BA 37/18/19	Fusiform gyrus
116	.000	.004	- 57	- 39	0	BA 21/22	Middle temporal gyrus
70	.001	.003	- 57	- 12	- 4	BA 21	Middle temporal gyrus
9	.019	.023	- 48	- 38	15	BA 22	Superior temporal lobe
6	.024	.037	- 57	- 23	- 2	BA 21	Superior temporal gyrus
Right hemisphere							
2150	.000	.000	42	- 74	- 3	BA 19/18/37	Inferior occipital gyrus
142	.000	.000	2	9	55	BA 6	Supplementary motor area
82	.001	.003	34	- 50	45	BA 40/7	Inferior parietal lobule
31	.008	.008	57	30	21	BA 46/45	Middle frontal gyrus
18	.010	.018	51	9	29	BA 9/44	Inferior frontal gyrus
32	.005	.004	28	- 64	- 42	-	Right cerebellum
b) Correct sequence processing vs. null-event							
Left hemisphere							
1072	.000	.000	- 50	- 6	38	BA 6/9/46	Precentral sulcus/middle frontal gyrus
-	-	.000	- 53	- 5	31	BA 6/44	Precentral sulcus/inferior frontal gyrus
-	-	.000	- 48	0	44	BA 6	Precentral gyrus
865	.000	.000	- 42	- 74	- 3	BA 19/37	Inferior occipital gyrus
-	-	.000	- 40	- 57	- 9	BA 37	Fusiform gyrus
457	.000	.000	- 30	- 54	45	BA 7/40	Superior parietal lobule
-	-	.024	- 38	- 46	56	BA 5	Postcentral parietal gyrus
437	.000	.000	0	7	53	BA 6	Supplementary motor area
Right hemisphere							
1109	.000	.000	44	- 55	- 11	BA 19/37	Fusiform gyrus
-	-	.000	46	- 70	- 3	BA 19	Inferior occipital gyrus
354	.000	.001	34	- 54	45	BA 40/7	Inferior parietal lobule
135	.001	.002	57	9	35	BA 6/9/46	Precentral sulcus/middle frontal gyrus
77	.002	.014	46	- 3	54	BA 6	Precentral gyrus
-	-	.017	44	- 11	58	BA 6/4	Precentral gyrus/central sulcus
31	.010	.016	2	- 71	- 28	-	Right cerebellum

*Contrast 2: Correct Sequence Judgement
 versus Null-Event The Neural Network
 Implicated in On-Line
 Sequence Monitoring*

Brain regions showing greater activity for the real-time processing of sequences of visual items are listed in Table IIb. They constitute a vast neural network covering occipital (BA 19, BA 37), parietal (BA 40/7, BA 5) areas as well as large prefrontal region implicating superior (BA 6, SMA) and medial (BA 6, BA 9/6/44) regions of the left prefrontal cortex, with activation extending to the dorsal posterior part of the inferior frontal gyrus (BA 44). Activations show a weaker tendency to be lateralized in favour of the left hemisphere, the same neural network being globally implicated in both hemispheres.

*Contrast 3: Conjunction Analysis
 Extracting Areas Activated during the Sentence
 Judgement Task that are also Implicated
 in the Sequencing Task*

Table III and Figure 3 show the results of the masked conjunction analysis. In order to restrain the eventuality of obtaining too much false positive activations, we restrained the conjunction analysis to regions that showed significant activation in the sentence comprehension task using an inclusive masking strategy. Results of the conjunction analysis suggest that a large number of cortical areas, forming a large network along the dorsal pathway, are commonly activated both in sentence processing and in abstract sequence processing. This network includes activation loci in the left and right parietal and frontal cortices.

TABLE III
Masked conjunction analysis: brain regions jointly activated by sentence and sequence judgement

Cluster size (N voxels)	Cluster level p-values (corrected)	Voxel level p-values (corrected)	Talairach coordinates for peak activation			Corresponding Brodmann area (peak/extension)	Corresponding cortical region (peak)
Left hemisphere							
2807	–	.000	– 48	4	37	BA 6/9/46	Precentral sulcus/middle frontal gyrus
–	–	.000	– 44	0	46	BA 6	Precentral gyrus
–	–	.000	– 38	– 3	52	BA 6	Precentral sulcus
1756	–	.000	– 40	– 76	– 1	BA 19/37	Inferior occipital gyrus
–	–	.000	– 40	– 57	– 9	BA 37	Fusiform gyrus
507	–	.000	– 30	– 54	45	BA 7/40	Superior parietal lobule
–	–	.000	– 24	– 66	33	BA 7	Precuneus
70	–	.000	– 48	– 38	– 18	BA 13/22	Insula
Right hemisphere							
2774	–	.000	44	– 57	– 12	BA 37	Fusiform gyrus
–	–	.000	46	– 72	– 3	BA 19	Middle occipital gyrus
–	–	.000	34	– 59	– 19	BA 37	Fusiform gyrus
737	–	.000	34	– 52	45	BA 40/7	Superior parietal lobule
734	–	.000	2	8	53	BA 6	Supplementary motor area
456	–	.000	51	7	29	BA 44	Inferior frontal gyrus
–	–	.007	61	– 6	41	BA 6/4	Precentral gyrus/central sulcus
–	–	.032	57	– 11	47	BA 3	Postcentral parietal gyrus
236	–	.000	42	– 13	58	BA 4	Central sulcus
–	–	.025	46	– 24	58	BA 3	Postcentral parietal gyrus
116	–	.000	57	28	24	BA 46	Middle frontal gyrus
29	–	.007	26	– 66	– 40	–	Right cerebellum

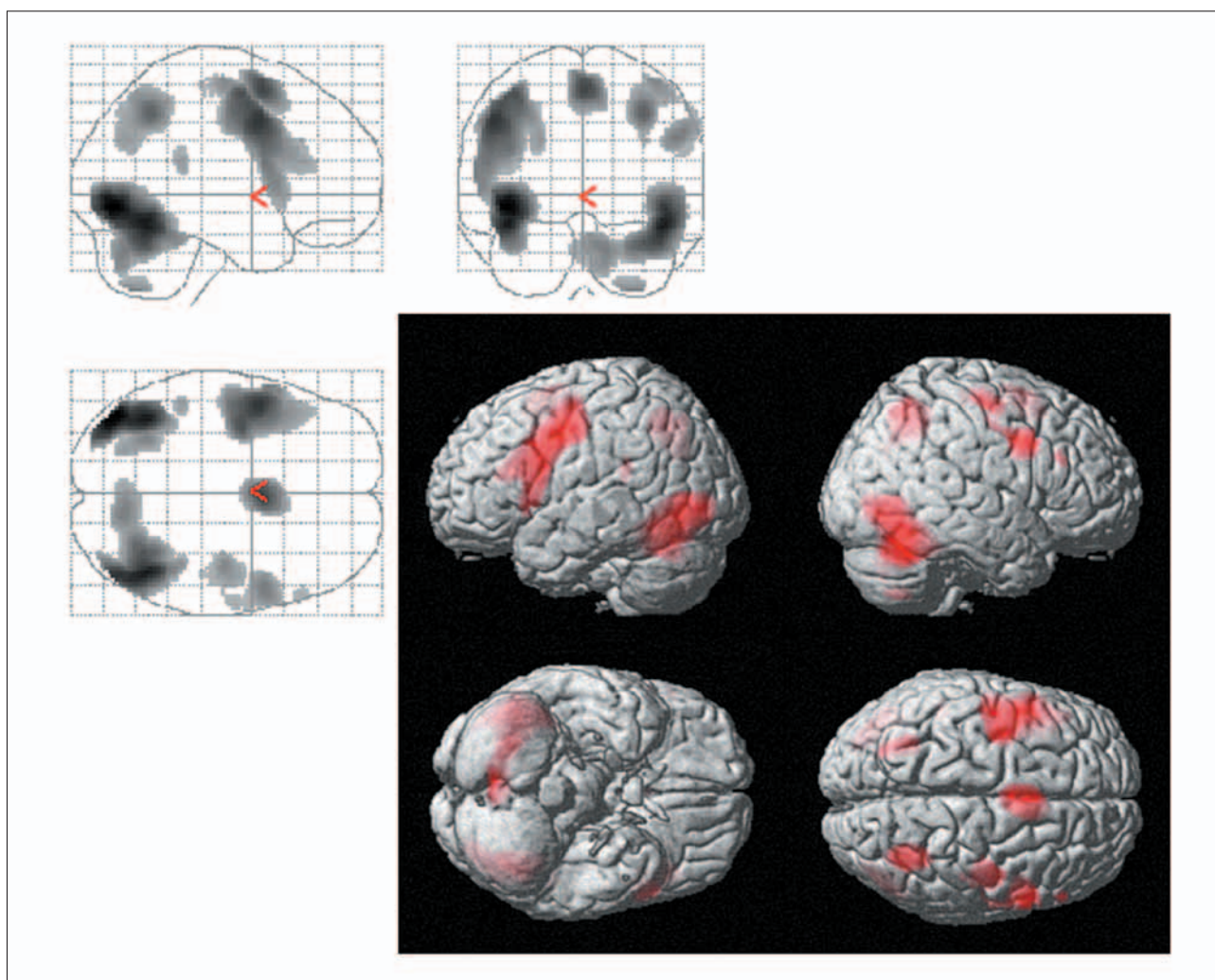


Fig. 3 – SPM maps obtained for the masked conjunction (up-left) and the same activations mapped on a template brain (down-right). *p* corrected < .001. Network of areas activated both during sentence and sequence judgement tasks.

TABLE IV
Difference analysis: brain regions specifically activated by judging sentences

Cluster size (N voxels)	Cluster level p-values (corrected)	Voxel level p-values (corrected)	Talairach coordinates for peak activation			Corresponding Brodmann area (peak/extension)	Corresponding cortical region (peak/extension)
Left hemisphere							
1078	.002	.000	- 14	- 84	- 3	BA 18	Lingual gyrus
537	.030	.001	- 55	- 4	- 12	BA 21	Middle temporal gyrus/inferior temporal gyrus
533	.030	.064	- 57	- 43	2	BA 21/22	Middle temporal gyrus
-	-	S.V.C = .000					
350	.089	.014	- 40	34	- 10	BA 45/47/11	Inferior frontal gyrus/middle frontal gyrus
-	S.V.C = .001	-	-	-	-		
Right hemisphere							
1280	.001	.000	24	- 78	- 1	BA 18	Lingual gyrus
127	.389	.014	63	1	- 15	BA 21	Middle temporal gyrus
-	S.V.C = .002	-	-	-	-		

Contrast 4: Difference Sentence versus Sequence Judgement

Table IV displays the results observed for the subtraction between correct sentence processing *versus* correct sequence processing, revealing brain activations that are specific to the sentence judgement task compared to the sequence judgement task. Results observed for this difference include regions forming a large network along the ventral pathway. This network includes activations loci in the left lingual, temporal and inferior prefrontal gyri and homologous right hemisphere activations in the lingual and medial temporal regions.

DISCUSSION

In the present experiment, we directly compared cortical networks implicated in two different tasks that we hypothesised share certain computational components: the judgement of normal French sentences on one hand and the judgement of abstract sequences of letters generated by simplistic artificial grammar like structural rules on the other hand. Former studies from our group, both in the domain of neuropsychology (Lelekov et al., 2000; Dominey et al., 2003; Hoen et al., 2003) and human electrophysiology (Hoen and Dominey, 2000, 2004) gave us first insights into this possible cognitive-domain sharing. The goal of the current study was to identify, in an ER-fMRI paradigm, those cerebral regions specifically implicated in sentence comprehension, compared to brain regions that demonstrate conjoined recruitment by both types of tasks. Main observations from this experiment show that on the one hand, a substantial number of areas (regions in green on Figure 4), including portions of the anterior left inferior frontal gyrus (BA 45/47), can be identified as specifically engaged in sentence comprehension when compared to processing abstract sequences.

On the other hand, another consequential network of cortical areas (regions in red on Figure 4) seems to participate in both of these tasks, including left frontal regions as the precentral sulcus and middle frontal gyrus of the left hemisphere (BA 6/9/46).

Brain Regions Shared between Sentence and Sequence Processing

Our results suggest that different cortical loci are commonly implicated in the processing of sentences and abstract sequences of letters. These various regions include visual processing areas as the left inferior occipital gyrus and bilateral fusiform gyrus, parietal regions as the superior parietal lobule and more classically language related inferior parietal regions. In particular, a large activation was found in the left prefrontal cortex including the precentral sulcus and gyrus as well as the middle frontal gyrus (BA 6/9/46). This result is consistent with different previous fMRI studies that showed activation of these areas in sentence comprehension tasks (e.g., Baumgaertner et al., 2002; Kuperberg et al., 2003), particularly for sequential or structural processing aspects in sentences (Dapretto and Bookheimer, 1999; Kang et al., 1999; Newman et al., 2003). This region was also often found activated in multimodal non-linguistic tasks that specifically implicate temporal sequencing aspects (Dove et al., 2000; Dreher et al., 2002; Koechlin et al., 1999; Bor et al., 2003; Marshuetz et al., 2000; Drummond et al., 2003). The activation in our study extends to the superior part of BA 44, but not to its most inferior part, within Broca's area proper. Also the precise location of this region was shown to exhibit important individual variability (Amunts et al., 1999), various hypotheses could explain this result. In the domain of sentence processing, activations in BA 44op proper were often observed when sentences of differing syntactic complexity were contrasted, either by PET (Stromswold et al., 1996) or by fMRI (e.g., Newman et al., 2003; Fiebach et

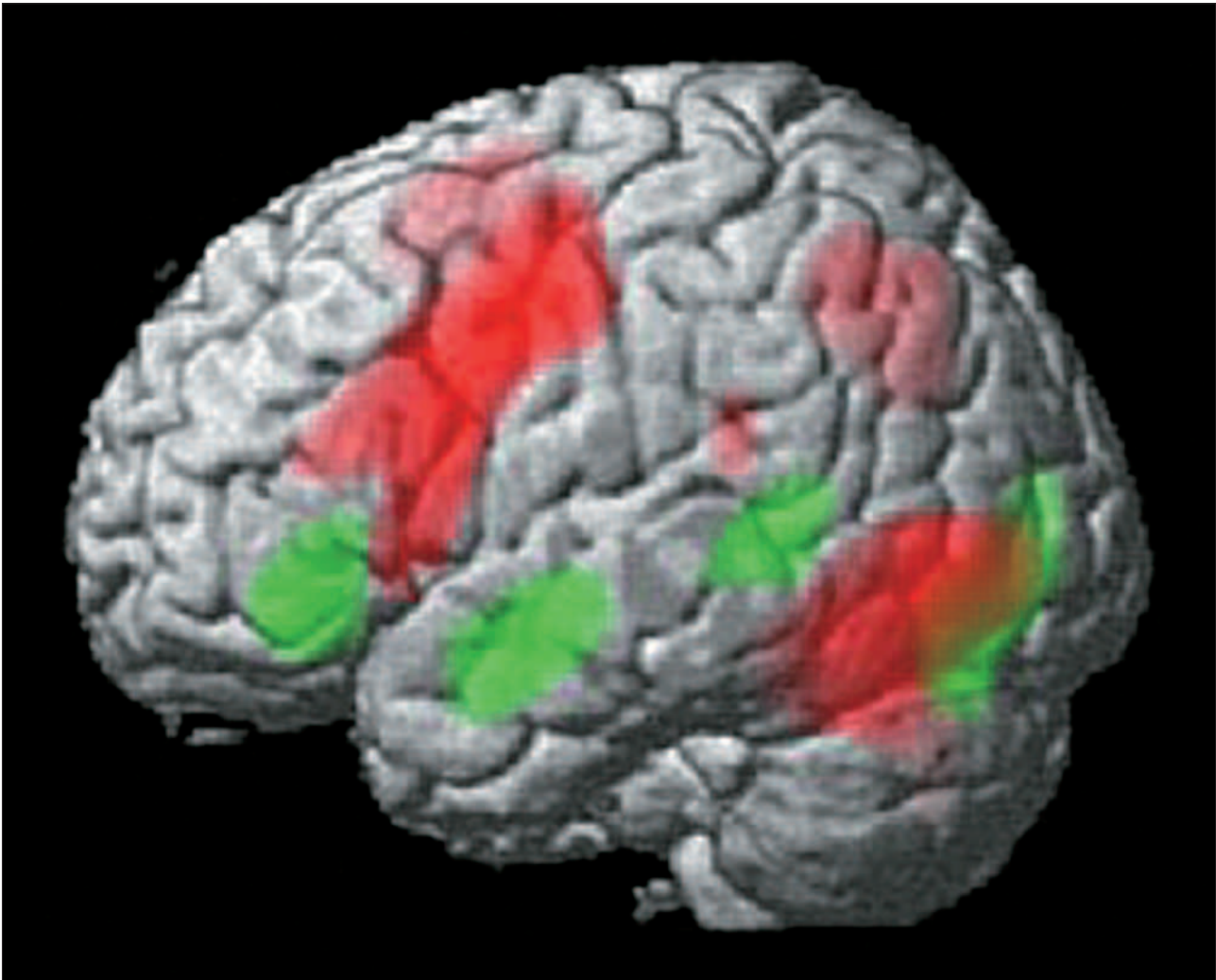


Fig. 5 – SPM rendering of activations obtained from the conjunction analysis, regions activated both for the sentence and the sequence judgement tasks (red) and from the subtraction sentence – sequence, showing areas with specific activation in the sentence comprehension task (green). Note that these two networks map respectively the dorsal and the ventral pathways and ‘end’ in the ventral prefrontal regions.

al., 2005). However, other authors obtained contradictory results, with syntactic complexity implicating preferentially the portion BA 45tr of Broca’s area or both sub-regions (BA44/45) (Just et al., 1996; Caplan et al., 1998, 2001; Röder et al., 2002), so the evidencing of a differential function and the determining of the respective functions of BA 44 and BA 45 are still open. Recently, different authors have even hypothesised that Broca’s area (BA 44/45), could specifically be implicated in the processing of syntactic transformations as described in linguistic theory (Ben-Shachar et al., 2003, 2004), though this effect could not be replicated when different transformation classes were mixed together (Wartenburger et al., 2004). In the present study, the choice of whole brain data analyses, associated to the relying on a conjunction analysis, certainly constitutes a clear limitation that further experiments, relying on single-subject anatomical and/or functional ROI definition will try to overcome. However, it is possible that in our current experiment, the complexity of employed tasks may have been too low to implicate more

inferior portions of BA 44. In particular, our different fMRI acquisition sessions did not mix different complexity conditions, which could have pushed subjects to enter in routine-processing strategies, relying on more shallow processes than typically required to engage more inferior portions of left prefrontal cortex. Nevertheless, a region of the middle prefrontal cortex (BA 6/9/46), was identified as participating in both the sentence judgement and sequence processing task, suggesting an involvement of neural tissue in this area in the processing of sequential properties of sentences. In the accompanying theoretical paper (Dominey and Hoen, 2006, this issue), we describe a construction-based sentence comprehension model relying on a dual-path processing mechanism in which middle prefrontal structures (Ba 6/9/44/46) and posterior-inferior (BA 44op) regions within Broca’s area, are hypothesized to be engaged in manipulating construction structures in a transformation processing network. In the context of sentence comprehension, middle and posterior inferior prefrontal regions would thus be engaged

preferentially in sequential, structure-related computations, with increasing structural complexity or task demands progressively involving more inferior regions (see Love et al., 2006, this issue for data and discussion about the same topic). However, further investigations will be needed to clarify this hypothesis (see for example Wartenburger et al., 2004 for contradictory results).

Brain Regions specifically Engaged in Sentence Comprehension

When we subtracted activations observed for sequence processing from those obtained for sentence processing, we could identify different brain regions specifically implicated in sentence comprehension compared to sequence processing. These regions mainly included bilateral middle temporal gyrus (BA 21) in the medial/anterior portion of the temporal cortex and the left inferior and middle temporal gyrus (BA 21/22) in the posterior portion of the left temporal cortex, Wernicke's area. These regions are classically associated with sentence comprehension, related to meaning extraction in both modalities (see Bookheimer, 2002; Scott and Johnsrude, 2003; Scott and Wise, 2004 for reviews). Left anterior temporal regions were associated to the processing of early syntactic information, related to lexical category information identification (Friederici, 2002; Friederici et al., 2000, 2003). Sentence processing specific regions also included the left middle and inferior frontal gyri (BA 45/47/11). This observation is in agreement with various functional imaging experiments that have shown activations of the anterior part of the ventral-prefrontal cortex related to semantic or thematic processes in sentence comprehension (Dapretto and Bookheimer, 1999; Cooke et al., 2001; Hashimoto and Sakai, 2002; Pilgrim et al., 2002; Newman et al., 2003), as well as in semantic aspects of verbal fluency (Amunts et al., 2004).

These different observations, as well as our own observation argue in favour of an involvement of anterior left-inferior frontal regions (BA 47/45/11) in semantic aspects of sentence processing. In the accompanying theoretical paper (Dominey and Hoen, 2006, this issue), we argue that these regions are implicated on the mapping of lexical/semantic information onto constraining structural information.

Hemispheric Asymmetries and Right-Hemisphere Activations

When comparing the sentence- and abstract sequence- judgement tasks, a first observation regarding hemispheric specialization can be made. In both tasks, the activations engage large neural networks throughout the left hemisphere but also homologous regions in the right hemisphere. This

seems to be less true for the sentence judgement task, in which a clear preference for the left language dominant hemisphere can be observed, whereas the sequence judgement task seems to engage regions in both hemispheres almost equally. This could be related of course to the existence of a functional specialization in the left hemisphere for the processing of meaningful linguistic stimuli, as revealed by the network activated specifically for the judgement of sentences alone (Figure 5). However, even in this last contrast, some activation still remains in the right hemisphere.

In all our different contrasts, some important activation loci were observed in the right cerebral hemisphere. In particular, the sentence/sequence conjunction analysis revealed a large network of right hemisphere regions activated by both tasks, including occipital (fusiform and middle occipital gyri, BA 19/37), parietal (superior parietal lobule, BA 40/7, postcentral parietal gyrus, BA 3), supplementary motor area (BA 6), central sulcus (BA 4) and frontal (middle frontal gyrus, BA 46, inferior frontal gyrus, BA 44) regions, as well as the right cerebellum, suggesting a participation of right hemisphere regions in both tasks. The right cerebellum activation is not surprising as it has been shown that hemispheric dominance for language processing is usually reversed between cortex and cerebellum (Jansen et al., 2004). Right intraparietal (BA 7/40) as well as occipital (BA 17/18/37) activations have been reported in experiments testing the difference between modality-specific working memory networks. In a recent experiment, Crottaz-Herbette et al. (2004), observed activations in the mentioned regions specifically when subjects performed a verbal working memory task on visually presented stimuli compared to when they performed the same task with auditory presented stimuli. This occipital parietal visual working memory network is certainly recruited quite extensively both by the abstract sequence judgement task and the sentence judgement task, as both require the processing of visual verbal stimuli presented item by item, that certainly taxes the verbal working memory quite heavily. It is thus possible that right hemisphere activation observed in the conjunction analysis might reflect some non specific and hence shared verbal working memory components, present in both tasks.

The right hemisphere, though generally considered as the non dominant language hemisphere was shown to participate in different aspects of language processing as reasoning or inference making on linguistic material (Mason and Just, 2004; Noveck et al., 2004), semantic integration during discourse comprehension (St George et al., 1999; Robertson et al., 2000). These experiments suggested that part of the temporal and frontal cortices in the right hemisphere may be implicated in contextual meaning mapping. In our

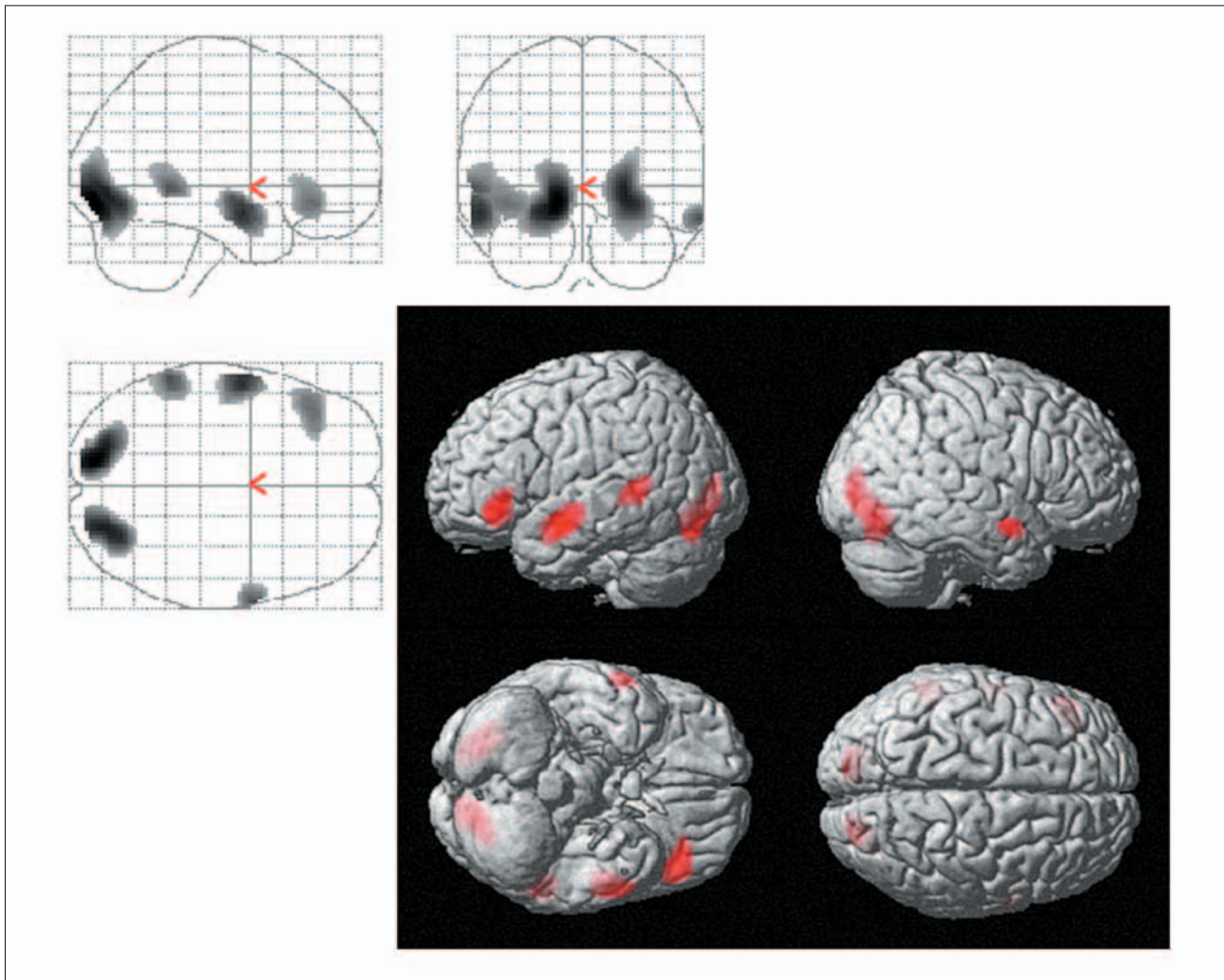


Fig. 4 – SPM{t} maps obtained for the subtraction sentence – sequence (up-left) and the same activations mapped on a template brain (down-right). p uncorrected, $k > 50$ voxels and volumes survive small volume correction. Network of areas activated only during the sentence judgement task.

particular sentence judgement task, the fact that subjects had to judge sentences that could be either correct or contain semantic or syntactic violations may have put a stress on meaning integration what may have caused increased participation of right hemisphere regions to the processing of our sentences.

The Role of Broca's Area in Sentence Comprehension

All these observations argue in favour of a functional segregation inside the left prefrontal cortex, including Broca's area proper in two information processing gradients. Superior and posterior regions, including BA 6/9/46/44, would be preferentially engaged in sequential and structural aspects of sentence comprehension, with more shallow parses or canonical structures processed in upper parts of this network, whereas deeper, more complex or working-memory demanding parses would implicate more inferior regions. Anterior and inferior regions, including BA 11/47/45, would be implicated in content

information insertion into structural matrixes selected in upper regions. Again, an increase in the complexity of mapping semantic information onto the selected sentence structures or increases in task demands, reflexive consciousness or memory load of required tasks, would progressively implicate more posterior regions along a second information processing gradient. This hypothesis is supported by numerous imaging experiments now and is in line with modern models of sentence comprehension based on the segregation of two main information processing streams the dorsal- and the ventral-pathway (Ungerleider and Mishkin, 1982; Goodale and Milner, 1992). Always more imaging studies argue in favour of this separation both in the visual (see Ungerleider et al., 1998 for review; Haxby et al., 2000; Goodale and Westwood, 2004, for recent considerations on that issue) as well as auditory system (Arnott et al., 2004). Even if the discussion is still largely open as to determine exactly what type of information is coded in those two auditory streams in humans (Recanzone, 2000; Rauschecker and Tian, 2000; Tian et al., 2001; Zatorre et al., 2002) it is now

widely admitted that two main information streams exist and that they underlie different types of auditory information inputs to the prefrontal cortices (Romanski and Goldman-Rakic, 2002; Schubotz et al., 2003).

Recently, these observations have been related to models of speech comprehension (Scott and Johnsrude, 2003) or more generally to the mapping of language comprehension on two memory systems in humans, the declarative (ventral) and procedural (dorsal) ones (Ullman, 2001a, 2001b and see Ullman, 2004 for recent extensions). According to this last view, the syntactic and semantic parts of language (e.g., sentence) comprehension would be treated separately and respectively by the procedural memory system, embodied in neural networks comprising structures in the dorsal pathway and the declarative memory system, contained in neural structures belonging to the ventral pathway. The procedural memory system is implicated in the acquisition of new and usage of well trained motor 'habits' or skills. Interestingly, it has also been demonstrated that the dorsal/procedural system is implicated in the acquisition and usage of context-dependent stimulus-response rule-like relations (Ullman, 2004). This system would be especially important for learning and processing these relations in the context of real-time sequences – whether the sequences are serial, abstract, sensori-motor or cognitive (Aldridge and Berridge, 1998; Schubotz et al., 2000; Boecker et al., 2002; Schubotz and von Cramon, 2002a, 2002b).

From all these observations one could propose that Broca's area could be considered anatomically as being in a position similar to that of the ancient roman god "Janus" the god of gates and bridges represented with two faces. Broca would have one face turned to a content-processing pathway, implicating structures from the ventral, recognition and declarative pathway and a second face turned to a structural/positional and syntactic processing pathway, implicating structures from the dorsal, localization and procedural pathway. Various recent observations in monkey anatomy as well as direct comparisons between monkey and human cortical cytoarchitecture and anatomical connections tend to support this view (Petrides and Pandya, 1988, 2002; Romanski et al., 1999).

Acknowledgments. The first author was granted during his thesis work by the French research minister (Bourse MRT). Authors would like to thank J.B. Poline and C. Fiebach for there very helpful comments and suggestions regarding ER-fMRI data analysis.

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