

Neural correlates of syntactic movement: converging evidence from two fMRI experiments

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This paper studies neural processes of sentence comprehension, focusing on a specific syntactic operation—syntactic movement. We describe two fMRI experiments that manipulate this particular syntactic component. The sentences in each of the experiments are different, yet the structural contrast in both is syntactically identical, comparing movement and no-movement sentences. Two distinct Hebrew constructions, topicalization and wh-questions, were presented in an auditory comprehension task and compared to carefully matched baseline sentences. We show that both contrasts, presented in an auditory comprehension task, yield comparable activations in a consistent set of brain regions, including left inferior frontal gyrus (IFG), left ventral precentral sulcus (vPCS), and bilateral posterior superior temporal sulcus (pSTS). Furthermore, we show that these regions are not sensitive to two other syntactic contrasts. The results, considered in the context of previous imaging and lesion studies, suggest that the processing of syntactic movement involves a consistent set of brain regions, regardless of the superficial properties of the sentences at issue, and irrespective of task.

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Introduction

This paper investigates the neural substrate of syntactic processing—a focus of much research in current cognitive neuroscience. There is dense lesion-based body of data about it, a host of ERP studies, and more recently, a growing number of neuroimaging studies. The lesion literature suggests that—contrary to traditional views (e.g., Zurif, 1980)—gross distinctions between linguistic levels (e.g., syntax, semantics) do not correspond to cerebral loci (Broca's or Wernicke's region, respectively) in any obvious way (Grodzinsky, 2000). The language regions of the brain seem rather to be making finer functional distinctions. In particular, there are

certain components of syntax that appear to be localizable (e.g., Grodzinsky, 1986, 1995; Neville et al., 1991; Stromswold et al., 1996; Zurif et al., 1993), and they will be the focus of this paper.

Within the imaging literature, important series of studies have aligned with the more traditional view: With few exceptions (to which we will return below), most studies have concentrated on the cerebral substrate of 'syntax' as compared to 'semantics'. A survey of these returns mixed, somewhat inconsistent results: In some studies, syntactic conditions have activated both Broca's and Wernicke's regions (Dapretto and Bookheimer, 1999; Embick et al., 2000; Friederici et al., 2000; Keller et al., 2001; Luke et al., 2002; Roder et al., 2002). In other studies, syntactic conditions activated Wernicke's but not Broca's region (Kuperberg et al., 2000; Vanderberghe et al., 2002). In one study, syntax activated Broca's but not Wernicke's region; but then Broca's region was also activated by the semantic condition (Kang et al., 1999); in another study, Broca's region was activated more by syntax than by semantics (Dapretto and Bookheimer, 1999); but this pattern was not found in other studies directly comparing syntax with semantics (Kuperberg et al., 2000, 2003; Luke et al., 2002; Newman et al., 2001; Ni et al., 2000).

When syntax and semantics were crossed, an interaction between the two was found in several regions, including Broca's region (Keller et al., 2001; Roder et al., 2002), left cingulate (Roder et al., 2002), left posterior middle frontal gyrus, and left inferior parietal cortex (Keller et al., 2001).

Finally, regions beyond those traditionally known to neuropsychology as language areas also appear to be involved in syntactic processing, including the right homologue of Broca's region (Embick et al., 2000; Friederici et al., 2000; Luke et al., 2002; Moro et al., 2001; Ni et al., 2000 (Exp. 1)) and the right homologue of Wernicke's region (Friederici et al., 2000; Kuperberg et al., 2000; Luke et al., 2002; Ni et al., 2000). In a recent study (Kuperberg et al., 2003), Broca's and Wernicke's regions were activated by conceptual and not by syntactic violations, the latter activating bilateral inferior parietal lobule, bilateral parieto-occipital cortex, right middle frontal and precentral gyri, and other regions in the right hemisphere.

Little anatomical consistency is found, then, when all syntactic processing is lumped together and contrasted with semantics. This is so even when the analysis is restricted to a single task (e.g.,

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violation detection), a single modality, and so on. Moreover, a true organizing principle is expected to be indifferent to these factors. Realizing that, and in view of the shift from linguistic levels to subcomponents that lesion and ERP research had previously undergone, we manipulated a specific syntactic relation, in isolation from other syntactic factors, across different constructions and tasks.

Our choice was syntactic movement. A central concept in the theory of syntax (e.g., Chomsky, 1957, 1995; Haegeman, 1994), it is also a subcomponent of syntax most intensely studied in psycholinguistics (e.g., Kluender and Kutas, 1993; Tanenhaus and Trueswell, 1995). It is, moreover, closely linked to Broca's region, which has been claimed to house mechanisms that underlie movement (Grodzinsky, 1986, 2000).

Seeking an imaging perspective, we used fMRI to measure regional changes in brain activation sensitive to this syntactic relation. If the very same brain regions are consistently activated by syntactic movement, across tasks and particular sentence forms, then the imaging picture becomes consistent, and results would converge on those obtained through other research methodologies. Some imaging results (to which we return below) have provided suggestive, though inconclusive, indications that Broca's region (as well as other brain regions) is involved in the computation of syntactic movement. To further clarify the picture, we embarked on our experiment, which we describe below, beginning with a quick exposition of syntactic movement.

Syntactic movement is a special syntactic relation that features in a variety of constructions (including questions, relative clauses, etc.). To understand what syntactic movement is, consider first an active sentence like 'the horse kicked the rider'. In this sentence, the predicate kick determines the semantic roles of two arguments: one immediately preceding the verb ('the horse'), another immediately following it ('the rider'). Contrast this sentence with one that contains a relative clause: 'the nurse helped the rider that the horse kicked _'. Unlike before, there is now considerable distance between the two elements (kick, the rider); moreover, their sequential order is reversed. Still, semantic roles are preserved under this major change, and 'the rider' is the recipient of the kicking action like before. The properties of the verb also remain unchanged—'kick' still assigns a semantic role rightwards, namely, to the position marked by _. 'The rider' is phonetically present in one position, but its semantic role is in _. The two positions must therefore be related during processing to reach the correct interpretation.

Appearing in different guises, this relation features in virtually every linguistic theoretical framework (Haegeman, 1994; Kaplan and Bresnan, 1982; Pollard and Sag, 1994), including generative grammar (starting with Chomsky, 1957), where it was termed 'transformation' and later 'movement' (Chomsky, 1977). Within this framework, a sentence is considered as involving movement if its surface structure (roughly, the hierarchical structure of the sentence as it is overtly pronounced) is different from its deep structure (a hierarchical structure produced by a fixed set of simple derivation rules, in which, for instance, an English verb is immediately adjacent to the left of its object). Several different classes of movement have been defined, distinguished by the position to which an element was dislocated, and restricted by different sets of constraints (Chomsky, 1977). Our focus here is on one class of movement (known as 'A-bar' movement), which is evident in a variety of constructions including relative clauses, wh-questions, topicalization, and clefts.

Movement has been subject to extensive psycholinguistic research: It is computed on-line (Nicol and Swinney, 1989), and is a major contributor to the perceptual complexity of sentences in the performance of healthy subjects (Fodor et al., 1974; Neville et al., 1991). Moreover, neuropsychological research has shown that certain types of movement pose specific comprehension difficulties to aphasic patients suffering from a lesion in Broca's region (Grodzinsky, 2000; Grodzinsky and Finkel, 1998; Zurif et al., 1993). Movement is thus central to any approach to language perception.

Several functional neuroimaging studies have investigated aspects of syntactic movement under the general label of 'syntactic complexity' (see Caplan, 2001 for a review). Some have documented increased activation in left inferior frontal cortex (e.g., Caplan et al., 1999; Cooke et al., 2001; Indefrey et al., 2001; Inui et al., 1998; Just et al., 1996; Stromswold et al., 1996), and some have found activation in other regions as well, such as right inferior frontal gyrus, left and right posterior superior temporal cortex, left superior parietal, and left angular gyrus (Caplan et al., 1999, 2002; Cooke et al., 2001; Just et al., 1996). However, these results conflate movement with other complexity factors; therefore, it is impossible to determine which of these factors caused brain activation in specific regions. In most of these studies, object relatives (or clefts) were compared with subject relatives (or clefts), which according to standard linguistic assumptions (Haegeman, 1994), involve movement as well. In several studies (e.g., Stromswold et al., 1996 and other studies reviewed in Caplan, 2001), a further manipulation of the type of embedding (center vs. right branching) supplemented the above mentioned syntactic contrast. In yet another study (Cooke et al., 2001), the distance traversed by movement was independently manipulated, resulting in right posterior temporal activation. Finally, in one study (Roder et al., 2002), movement sentences (German scrambling) were contrasted with no-movement sentences, activating left inferior frontal cortex, left posterior superior temporal sulcus, left superior frontal gyrus, left cingulate gyrus, and right insula. However, this contrast collapsed together grammatical and ungrammatical sentences and pseudo-word strings, again complicating interpretation in terms of movement.

In a recent fMRI experiment conducted in our lab (Ben-Shachar et al., 2003), syntactic movement was dissociated from other complexity factors such as number of embeddings and verb complexity. By comparing minimal pairs of Hebrew sentences with and without movement in a grammaticality judgment task, we found movement-related left lateralized activation in left inferior frontal gyrus, and bilateral activations in posterior superior temporal cortex.

While this study distinguishes between movement and other sources of complexity, the results may still be specific to the construction used (object relatives). Given the difficulties in formulating a neurological generalization that we have witnessed with regards to the syntax-semantics dichotomy, it is not at all a trivial matter to find a consistent set of brain regions activated by syntactic movement, across different tasks and various syntactic constructions. Yet only in this case can we state a generalization about brain regions involved in the computation of syntactic movement.

In the current paper, we present evidence from two new fMRI experiments, in which syntactic movement was manipulated using previously untested task and constructions. Our aims were twofold: (1) Generality: To test whether syntactic movement embodies a true neurological generalization, we used two new constructions

that involve movement: topicalization and wh-questions, and presented them in an original comprehension paradigm. (2) Restrictedness: To distinguish between movement and other syntactic effects, we included within each experiment an additional syntactic contrast. In Experiment 1, the effect of topicalization was compared with a change in the order of the objects. In Experiment 2, the effect of wh-questions was contrasted with the effect of object versus subject questions. As we will show, our movement-sensitive regions were insensitive to these syntactic contrasts. Thus, our movement effects can be related to movement in particular rather than to syntax in general.

Experiment 1

In this experiment, subjects were presented with a topicalization contrast. Hebrew topicalization sentences involve syntactic movement, as shown in example (1b) (Hebrew examples are given in Table 1):

- (1) a. John gave [_{O₁}the red book] [_{O₂}to the professor from Oxford].
 b. [_{O₁}The red book] John gave – [_{O₂}to the professor from Oxford].

Topicalization differs from object relatives (tested in many previous studies) both syntactically (for instance, topicalization does not involve ‘that’ insertion as in the object relative clause: ‘the book that John read’) and semantically (in topicalization, the moved element becomes the semantic ‘topic’ of the sentence). Still, both constructions relate an early appearing phrase to a later object position through movement. Thus, the topicalization contrast allowed us to test our hypothesis that regions activated by object relatives more than by no-movement controls (Ben-Shachar et al., 2003) are in fact sensitive to syntactic movement in general.

We aimed to dissociate the effect of movement from the effect of changing the order of the two objects. We therefore included two topicalization conditions: topicalized O₁ (see Table 1, condition C) and topicalized O₂ (Table 1, condition D). These topicalization conditions were compared to baseline conditions in which both objects followed the verb, in either order (Table 1, conditions A, B). This 2 × 2 design allowed us to focus on movement as our syntactic contrast of interest, distinct from another syntactic factor.

The manipulation of order introduced yet another experimental question pertaining to the difference between the two baseline conditions A and B. The English versions of these two constructions are given in (2):¹

- (2) a. John gave [_{O₁}the red book] [_{O₂}to the professor from Oxford].
 b. John gave [_{O₂}to the professor from Oxford] [_{O₁}the red book].

According to some linguistic accounts (e.g., Aoun and Li, 1989; Larson, 1988), (2a) and (2b) are related through movement, a phenomenon termed as ‘Dative shift’. However, dative shift involves a different type of movement than the one involved in topicalization (this is termed ‘A-movement’, in contrast with ‘A-bar movement’ found in topicalization, relative clauses, and wh-questions).² We therefore aimed to see whether the linguistic

¹ Note that in Hebrew, in contrast with English, dative shift does not involve the deletion of the preposition ‘to’. Thus, (2b) is perfectly grammatical in Hebrew.

² In fact, recent accounts hold that both constructions are independently generated, without any movement involved (see, e.g., Harley, 2003; Pesetsky, 1995, Ch. 3).

distinction between movement types is reflected in different patterns of brain activation, by comparing condition A versus condition B.³

Materials and methods

Participants

Twelve healthy, native Hebrew-speaking volunteers (five males, seven females) participated in the experiment. The data of one subject were excluded from analysis based on an anatomical abnormality that was found in the anatomical scan (a white matter lesion in the middle portion of the corpus callosum).

Participants’ age ranged from 21 to 32 (mean age 26, SD 3.1), and they were all right-handed, according to their own report and as measured by the Edinburgh Handedness Inventory (Oldfield, 1971). All participants reported normal hearing and no history of neurological or psychiatric illness or any cognitive deficit. Written informed consent was obtained from all participants according to protocols approved by the Sourasky Tel-Aviv Medical Center and by the Ethics committee of Tel-Aviv University.

Materials

Sixty-eight clusters of sentences (such as A–D in Table 1) were constructed, using 32 Hebrew double object verbs (i.e., verbs that take two objects such as ‘give [the book] [to John]’).⁴ Hebrew double object verbs were selected according to several linguistic tests (Ben-Shachar and Grodzinsky, 2002; Borer and Grodzinsky, 1986; Landau, 1994). The first object (O₁) was always inanimate and the second object (O₂) was always animate to satisfy semantic selection properties of double object verbs. Each object was modified by an adjective (O₁ and half of the O₂ cases) or a prepositional phrase (half of the O₂ cases). These modifiers made the sentences sound more natural, by creating the pragmatic setup for the topicalization of each object, and by decreasing the similarity between the sentences.

An additional ‘no-movement’ condition was included in the experiment, with sentences such as ‘John read [the red book] [with the professor from Oxford]’, but this condition was not included in the final ANOVA. In such sentences, there is only one true object (the red book), followed by an adjunct (an optional descriptive phrase that may be dropped; compare [John read the book] with *[John gave the book]). The aim of this condition was as follows: according to some linguistic theories (Aoun and Li, 1989), and in contrast with others (Larson, 1988), the basic order of the two objects is S V O₂ O₁ (condition B), as in ‘John gave Mary the book’. It is claimed that the other order (S V O₁ O₂, condition A: ‘John gave the book to Mary’) involves movement. Condition E was therefore included as a no-movement baseline to which both conditions A and B may be compared.

³ It could be argued that using both conditions A and B as our baseline for topicalization could diminish our effect, if indeed any of them involves movement, and if this type of movement is processed by the same brain regions. However, reducing the baseline to only one condition would result in a weaker statistical power. Moreover, based on linguistic evidence alone, it is not clear which of these conditions (A or B) involve movement (see Aoun and Li, 1989). We therefore used both as baseline, which also allowed us to contrast topicalization effects with order effects. Evidently, the topicalization effect survived this challenge.

⁴ The full list of sentences and verbs used may be obtained from the authors.

Table 1
Design of experiment 1

Condition	Schematic structure	Description	Example (top: Hebrew sentence; bottom: English word by word translation)
A	S V O ₁ O ₂	Baseline	John natan ['et ha-sefer ha-'adom] ₁ [la-professor me-oxford] ₂ John gave [the-book the-red] ₁ [to-the-professor from-Oxford] ₂
B	S V O ₂ O ₁ _	Dative shifted	John natan [la-professor me-oxford] ₂ ['et ha-sefer ha-'adom] ₁ John gave [to-the-professor from-Oxford] ₂ [the-book the-red] ₁
C	O ₁ S V _ O ₂	Topicalized direct object	['et ha-sefer ha-'adom] ₁ John natan _ [la-professor me-oxford] ₂ [the-book the-red] ₁ John gave _ [to-the-professor from-Oxford] ₂
D	O ₂ S V O ₁ _	Topicalized indirect object	[la-professor me-oxford] ₂ John natan ['et ha-sefer ha-'adom] ₁ _ [to-the-professor from-Oxford] ₂ John gave [the-book the-red] ₁ _
E	S V O ₁ adj	Baseline with adjunct	John kara ['et ha-sefer ha-'adom] ₁ ['im ha-professor me-oxford] John read [the-book the-red] ₁ [with the-professor from-Oxford]

Abbreviations: S = subject, V = verb, O₁ = first (direct) object, O₂ = second (indirect) object, adj = adjunct. 'et' is the Hebrew accusative case marker.

However, a preliminary analysis revealed that this condition yielded higher activations than both conditions A and B. This could be the result of the relative salience of this condition, as this was the only condition that included a different preposition ('im' = with, as opposed to 'le' = to in all other four conditions). Alternatively, activation for the control condition could be structurally related and may stand for a real difference in the processing of obligatory objects versus optional adjuncts (see Speer and Clifton (1998) for behavioral evidence in the same direction). The reason for this effect clearly warrants further investigation; however, in the current study, this condition could no longer serve as baseline for conditions A and B and was therefore excluded from the final ANOVA. It was still included in the 'all-sentences' functional localizer, yielding a more general localizer and minimizing the influence of the experimental effect on the localizer test (see Data analysis section of experiment 1).

Eleven sentences of each condition A–D and 17 sentences of condition E were recorded by a female native speaker of Hebrew, and concatenated into a single audio file in the final order and timing using standard voice editing software (Goldwave 4.01 Goldwave Inc., St. John's, Canada).

Paradigm

The task was auditory sentence comprehension, probed by comprehension questions that followed only part of the blocks (for example, the sentence 'John brought the shiny diamond to the anxious buyer' was followed by the question 'was the diamond big?'). Questions were recorded in a male voice, and scattered in the experimental protocol such that no more than two consecutive blocks appeared without a question. They were always presented at the end of a block and followed by silence, to allow their exclusion from further analysis. This was crucial in order to prevent the contamination of our fine syntactic contrast with a different construction (questions). To force subjects' constant attention and

prevent them from predicting the occurrence of questions, sentences were presented in blocks of one, two, or three items (of a single condition), with the questions following two-thirds (18/27) of the blocks (see Fig. 1). The probability that a question follows a sentence in a block was 0.2. This original 'Variable Length (VaL-) block design' allowed partial sampling of subjects' performance, with unpredictable occurrence of comprehension questions, but still retaining the statistical power of a block design (Friston et al., 1999).

For each condition A–D, sentences were presented in two triple blocks, two double blocks, and one single block. Eight additional blocks of various lengths were included in the experiment: seven blocks of condition E (see Materials section of experiment 1) and one 'dummy block' that started the experimental run but was not analyzed. The exclusion of the first block from analysis prevented statistical bias in favor of the first condition presented, since the first block usually evokes higher than normal activations. Overrepresentation of double and triple blocks was motivated by their enhanced statistical power. Each of the 5 single blocks was followed by a question, as well as 6 of the 10 double blocks and 7 of the 12 triple blocks. The order of presentation was pseudorandomized, so that conditions A–B or C–D never appeared consecutively.

Stimuli presentation. Mean length of the sentences was 3.4 s (SD = 0.27 s). Within a single block, sentences were presented every 5 s, experimental blocks lasting 5, 10, or 15 s. Comprehension questions added 2.5 s to the overall block length and were appended 1 s after the last sentence. Double and triple blocks were interleaved within silent blocks of 10 s. Single blocks were followed by 5 s of silence (due to the reduced signal expected in those blocks). In addition, 20 s of silence were inserted at the beginning of the experiment and 12.5 s of silence ended the experiment. Overall, the experiment lasted 625 s (10 min and 25 s).

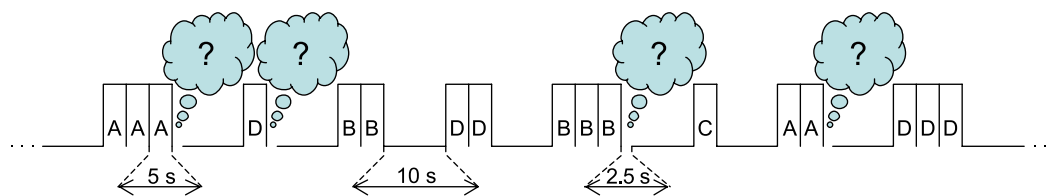


Fig. 1. Variable Length block design with sample questions. A schematic representation of the design and timing parameters used in experiments 1 and 2. Blocks of one, two, or three sentences of the same condition (identified by an upper case letter) are plotted as boxcars. Question marks denote comprehension questions that followed some of the blocks.

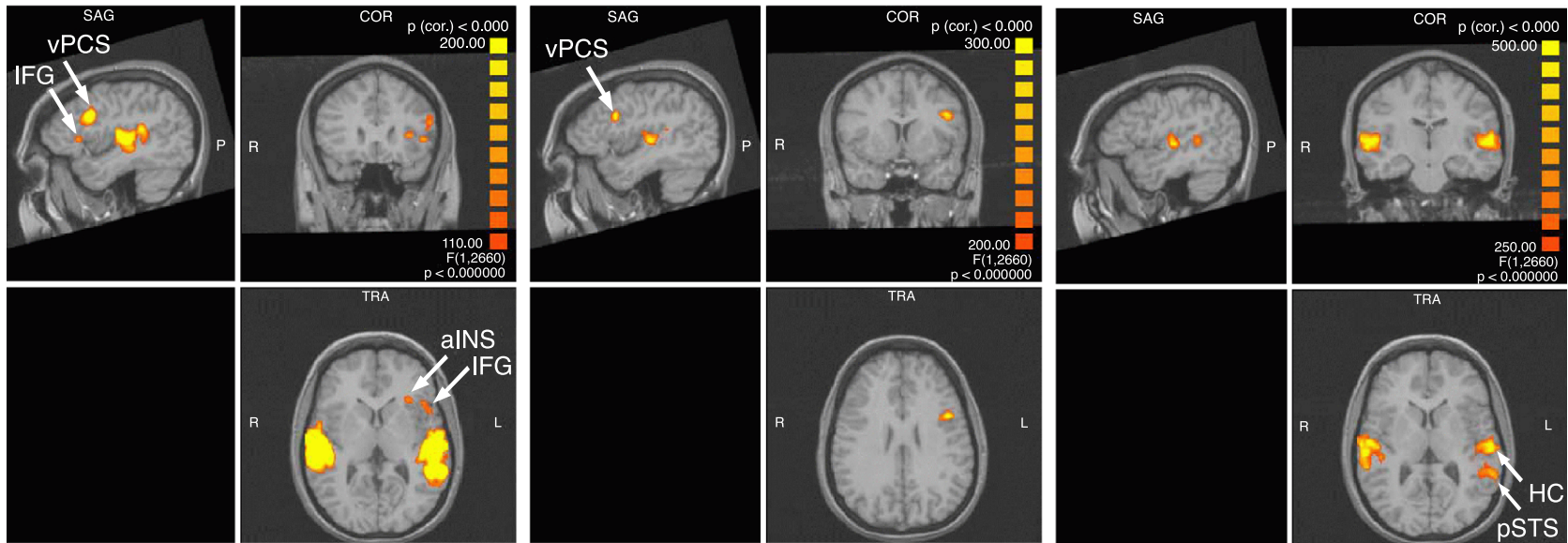


Fig. 2. Regions of Interest. A statistical parametric map (11 subjects) of left hemisphere ROIs (right hemisphere homologues were also analyzed, using lower thresholds). The maps show the contribution of the localizer predictor (all-sentences vs. silence) in a fixed effects analysis. For visualization purposes, maps were thresholded to yield clear separable activations in adjacent regions (all $P < 0.001$, corrected). The actual definition of ROIs was performed on the single subject activation maps (see Individual subject analyses section of experiment 1). Note the relatively small extent of the two inferior frontal regions (IFG, aINS) compared to the other three ROIs (left panel). This difference gave rise to the different sizes defined for these regions (300 activated voxels in IFG, aINS; 500 activated voxels in all other ROIs).

Table 2
Mean Talairach coordinates of ROIs

ROI	BA	Exp. 1: Mean Talairach coordinates (SD)			Exp. 2: Mean Talairach coordinates (SD)		
		x	y	z	x	y	z
LIFG	44, 45	−43 (4)	21 (6)	7 (3)	−44 (5)	21 (4)	8 (6)
RIFG	44, 45	48 (5)	19 (5)	9 (4)	47 (5)	22 (9)	12 (8)
LvPCS	6/9	−41 (6)	11 (5)	27 (3)	−45 (5)	8 (5)	25 (2)
RvPCS	6/9	44 (6)	12 (5)	32 (5)	42 (8)	10 (7)	27 (3)
LaINS	13	−27 (2)	22 (4)	9 (3)	−28 (3)	20 (6)	9 (4)
RaINS	13	32 (4)	23 (6)	7 (4)	32 (2)	19 (7)	12 (6)
LpSTS	39/22, 37	−56 (4)	−42 (6)	7 (4)	−55 (5)	−41 (4)	6 (3)
RpSTS	39/22, 37	58 (5)	−31 (8)	6 (4)	56 (5)	−34 (6)	6 (3)
LHC/mHC	41, 42	−54 (3)	−18 (7)	10 (5)	−46 (3)	−21 (5)	8 (4)
RHC/mHC	41, 42	57 (5)	−15 (5)	9 (4)	51 (4)	−17 (5)	8 (4)

Abbreviations: L/RIFG = left/right inferior frontal gyrus; vPCS = ventral precentral sulcus; aINS = anterior insula; pSTS = posterior superior temporal sulcus; mHC = medial Heschl's complex (gyrus and sulcus). BA= Brodmann Area: 44, 45 = including both BA 44 and BA 45. 6/9 = BA 6 bordering BA 9.

Procedure and experimental setup

Subjects were instructed to listen carefully to each sentence, and when yes/no comprehension questions are presented, to answer them using a response box (two alternatives forced choice). Sentences were presented to subjects within the scanner through pneumatic headphones (Newmatic Sound Systems, Petaluma, CA). The presentation of the stimuli was controlled by an external computer, using Goldwave 4.01. Subjects' responses were issued using a response box (Compumedics Neuroscan, El Paso, TX) held in their left hand, and the responses were collected by homemade software.

Instructions were given to the subjects both outside and inside the scanner just before the beginning of the experiment. The experiment was preceded by a practice run conducted within the scanner, where subjects listened to sentences in variable block lengths similar to the experimental design. Ten sentences, of all five conditions, were mixed in the practice period, to minimize prior expectations as to the similarity of structure within adjacent sentences. Two comprehension questions were also included in this run to make the subjects familiar with the voice of both readers and also to familiarize them with the response box. The practice period was accompanied with MR image acquisition using the same sequence as the experiment, to adjust subjects to the noises of the scanner. Following the practice run, necessary adjustments in volume were made and the experimental run began.

fMRI data acquisition and analysis

Data acquisition. Blood oxygenation level dependent (BOLD) contrast was obtained with gradient-echo echo-planar imaging (EPI) sequence ($T_R = 2500$ ms, $T_E = 55$ ms, flip angle = 90° , imaging matrix size: 80×80 , FOV = 24 cm) on a 1.5 T Signa-horizon LX 8.25 GE echo-speed scanner (General Electric Medical Systems, Milwaukee, WI). Fourteen functional (T_2^* weighted) and anatomical (T_1 weighted) axial slices of 5-mm thickness with 1-mm gap were acquired. Two hundred and fifty volumes were collected during a single functional run for each subject. Functional data was automatically reconstructed from k-space off-line. In addition, three-dimensional, high resolution spoiled gradient-echo (SPGR) sequence was acquired for each subject, allowing volume-based statistical analyses of signal changes along time.

Data analysis. Data analysis was performed using BrainVoyager 4.4 software (Brain Innovation, Maastricht, The Netherlands), complemented by Matlab (The Mathworks, Natick, MA; used to prepare individual time courses for group ANOVA) and STATISTICA (StatSoft, Tulsa, OK; performing group ANOVA). It included (1) preprocessing and normalization; (2) ROI analysis on individual subject data; and (3) group analysis.

Preprocessing and normalization. Individual 3D anatomical scans were resampled and interpolated yielding volume repre-

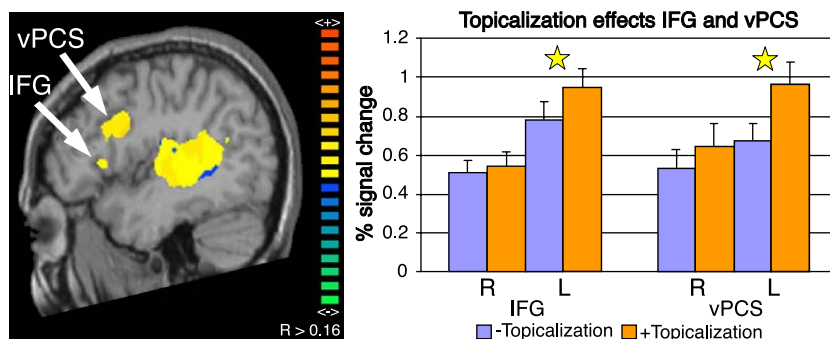


Fig. 3. Topicalization effects in IFG and vPCS. On the left, a statistical parametric map (11 subjects) of left frontal ROIs sensitive to the topicalization contrast. The map shows relative contribution of +topicalization conditions (yellow) vs. -topicalization conditions (blue). The graph on the right shows mean % signal change in left and right IFG and vPCS. Blue bars for -topicalization sentences, orange bars for +topicalization sentences (error bars represent standard error of the mean). Stars denote significant differences between the conditions in a given ROI ($P < 0.05$).

Table 3
Experiment 1: ANOVA results

ROI	Topicalization (main)	Hemisphere (main)	Topicalization × hemisphere (interaction)	Topicalization (simple effects)	
				Left	Right
IFG	$F(1,10) = 6.64, P < 0.05$	$F(1,10) = 18.4, P < 0.005$	$F(1,10) = 7.86, P < 0.05$	$F(1,10) = 21.76, P < 0.001$	$F(1,10) = 0.345, P = 0.57$
vPCS	$F(1,10) = 9.72, P^* < 0.05$	$F(1,10) = 6.03, P^* < 0.05$	$F(1,10) = 6.59, P^* < 0.05$	$F(1,10) = 19.74, P^* < 0.005$	$F(1,10) = 1.77, P^* = 0.213$
aINS	$F(1,8) = 2.68, P = 0.14$	$F(1,8) = 1.47, P = 0.26$	$F(1,8) = 0.12, P = 0.73$	$F(1,8) = 2.67, P = 0.14$	$F(1,8) = 1.3, P = 0.29$
pSTS	$F(1,10) = 20.52, P < 0.005$	$F(1,10) = 1.14, P = 0.31$	$F(1,10) = 2.98, P = 0.12$	$F(1,10) = 8.49, P < 0.05$	$F(1,10) = 23.29, P < 0.001$
HG	$F(1,10) = 29.34, P < 0.001$	$F(1,10) = 2.69, P = 0.13$	$F(1,10) = 3.25, P = 0.1$	$F(1,10) = 23.59, P < 0.001$	$F(1,10) = 23.43, P < 0.001$

P^* = post hoc probability given by the Tukey's HSD test. Bold cells contain significant Ps.

sensation with $1 \times 1 \times 1$ mm resolution. This 3D volume was transformed into the standard coordinate system of Talairach and Tournoux (1988). Functional 2D data were manually coregistered with 3D data using the alignment tool provided by BrainVoyager 4.4. This procedure involves reslicing (achieved by resampling and trilinear interpolation of the high resolution anatomical data) until a good correspondence is reached between functional slices and their corresponding anatomical slices. This generated a volume time course consisting of the activation level over time for each three-dimensional voxel. The first six functional volumes were excluded from analysis. Individual volume time courses were subject to 3D motion correction and highpass filter (filtering out the lowest three frequencies). The rest of the analysis was performed on these preprocessed volume time courses.

Individual subject analyses. Most of our results were obtained in an ROI analysis performed on individual subject data. We chose this method of analysis for two reasons: First, we are looking for very subtle effects of syntactic structure, comparing linguistically motivated minimal pairs. This minimal comparison is expected to yield much smaller effects on brain activation than, for example, faces versus houses. It is therefore very unlikely that these effects will survive the (corrected) significance threshold in a whole brain analysis. Secondly, we expected movement to activate high-level language regions. Large individual variability in the localization of cytoarchitectonic borders as well as gross anatomic borders was previously documented for one such region (Broca's region; see Amunts et al., 1999; Tomaiuolo et al., 1999), and these findings may generalize to other high-level language regions. It is therefore expected that movement-related activations in these regions may not overlap across subjects, thus precluding their detection in standard whole brain group analysis.

Our investigation focused on three ROIs: left inferior frontal gyrus (IFG, BA 44, and 45, including pars opercularis and pars triangularis), left and right posterior superior temporal sulcus (pSTS, BA 39 bordering BA 37, 22, including the posterior third of the superior temporal sulcus). These regions were chosen based on available lesion data (see Grodzinsky, 2000) and on our previous study with relative clauses (Ben-Shachar et al., 2003). In order to examine lateralization of function, we analyzed the activation in both homologues of these regions. For each ROI, we further defined a 'control region', an adjacent region that was also activated by the task, to test the restrictedness of our movement effects. Anterior insula (aINS, including the anterior third of the insular cortex, medially bordering IFG) served as control for IFG, and Heschl's complex (HC, BA 41, 42, including Heschl's gyrus and sulcus) as the control region for pSTS. Finally, a fifth region, ventral precentral sulcus

(vPCS, BA 6 bordering BA 9, including the part of precentral sulcus that borders the middle frontal gyrus) was analyzed. This region was found to be activated by the task in the group analysis (see Group analysis section of experiment 1 below) and was consistently activated in each of our individual subjects. We therefore decided to include it in our ROIs. A visualization of the anatomical locations of the ROIs is given in Fig. 2.

Within these anatomical borders, ROIs were functionally defined independently for each participant, using the 'all-sentences' predictor as a functional localizer test. This general localizer test included all experimental conditions (as well as condition E, which was not included in the overall ANOVA, as explained in the Materials section of experiment 1), to define ROIs for each participant separately, in a way that will be minimally biased by the experimental effects we were looking for.⁵ A general linear model (GLM) was computed for each subject, with two predictors: (1) all-sentences and (2) comprehension questions, both defined against a baseline of silent blocks. Boxcar predictors were convolved with a standard hemodynamic response function (HRF) used by BrainVoyager 4.4 ($\Delta = 2.5$, $\tau = 1.5$). An individual statistical parametric map was computed for the 'all-sentences' predictor, and average time course was computed for a cluster of voxels activated within each anatomical ROI.

An activity threshold was determined for each ROI so that a fixed number of voxels passed the threshold in this region (300 voxels in IFG and aINS, 500 voxels in the other ROIs; minimum activity threshold was set to $P < 0.01$ [uncorrected]). These cluster sizes reflected the relative sizes of activations in each region in the group activation map of the localizer test. The relatively small size of inferior frontal regions was also guided by their anatomical adjacency: if larger clusters were chosen, it was impossible to separate IFG and aINS.

Time courses were collected and shifted individually for each ROI. Shifts were determined in a manner that maximized the correlation between the time course and the 'all-sentences' predictor.⁶ After shifting, the data were transformed into percent

⁵ Naturally, by using a functional localizer we may be missing relevant brain regions that are involved in movement but are not activated by our localizer. In particular, we are prone to miss brain regions that are activated in rest as well as in sentence comprehension (we thank a NI reviewer for pointing this out). Unfortunately, this issue may not be resolved in the current experiment.

⁶ This definition proved highly robust: the same shifts also maximized two other related measures reflecting amount of 'localizer' activation: (a) One-sample t test over percent signal changes in activation blocks; (b) The integral of the average activation function.

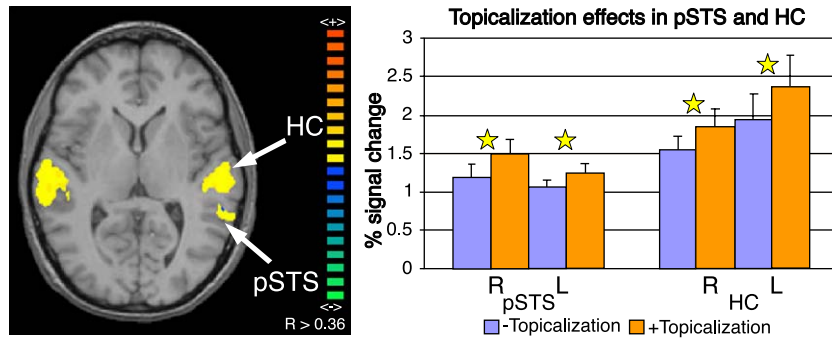


Fig. 4. Topicalization effects in pSTS and HC. On the left, a statistical parametric map (11 subjects) showing relative contribution of the +topicalization conditions (C, D; in yellow) vs. -topicalization conditions (A, B; in blue) in posterior temporal ROIs. On the right, blue bars show mean % signal change for -topicalization conditions and orange bars show +topicalization conditions, in bilateral posterior STS and Heschl's complex. Stars denote significant differences ($P < 0.05$) between adjacent bars in a given ROI. Error bars denote the standard error of the mean.

signal change scores, using the preceding silent period as a baseline for each activation block. In order to reduce each block (2, 4, or 6 time points) to a single number reflecting activation, a weighted average of the time points within each block was calculated. This way, no data points were ignored, but the inverted U shape of the HRF was taken into account. The weights were determined separately for each ROI, by calculating the average activation function in that ROI across all subjects and blocks. This average activation function served as the weighting function for that ROI; for instance, the first time point in each block (usually showing a low signal) was given a relatively small weight, while the third time point (and the second time point in Heschl's gyrus) was given a higher weight. Block activation scores were inserted into a multiple ANOVA as described in Group analysis.

Group analysis. We conducted two analyses on the group level: (a) A multi-subject activation map was created for our localizer test, to guide us in choosing our ROIs. (b) A multi-subject ANOVA was performed on ROI data, to test the significance of our experimental effects.

(a) A group GLM was computed with two predictors (all-sentences, questions), and a multi-subject SPM was generated for the 'all-sentences' predictor. Both fixed effect and random effect analyses were performed. In the absence of significant activation in the random effects analysis,⁷ we used the fixed effect map of the localizer test: (i) to define the cluster size for each ROI (see Individual subjects analysis) and (ii) to note a very high activation in a region that was not analyzed in our previous study (vPCS). Consequently, this region was included in our ROI analysis to test its sensitivity to movement.

(b) A group ANOVA was performed within each ROI, with hemisphere, topicalization, order of objects, and activation block as within subject variables. Post hoc comparisons were performed in vPCS using Tukey's HSD test. The effect of

datave shift was further tested as a planned contrast between conditions A and B (see Table 1).

Experiment 1: results

Behavioral results

Subjects performed the behavioral task successfully, with a mean of 17.3 correct responses out of 18 questions (SD = 0.65; percent correct responses: 96.3%, SD = 3.6%). The errors

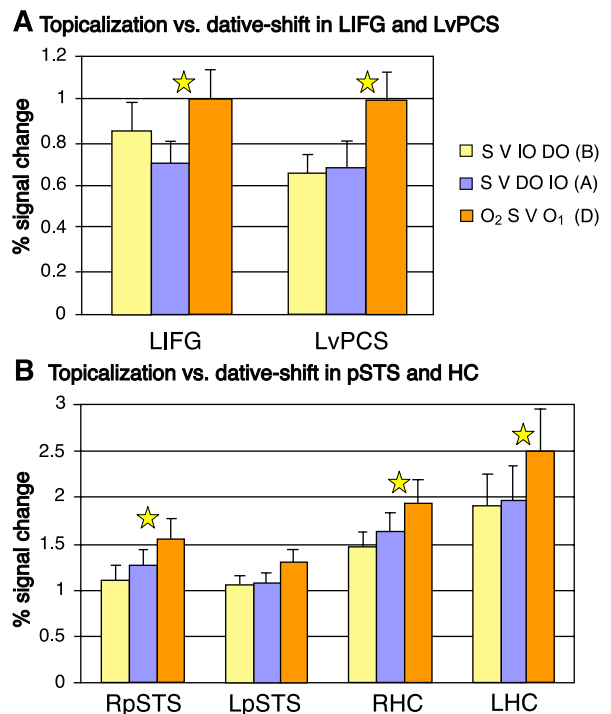


Fig. 5. Topicalization vs. datave shift. Bars show mean percent signal change for conditions A (blue), B (yellow), and D (orange) (error bars denote standard error of the mean). The topicalization contrast remains significant in the reduced comparison (D vs. A) in all but LpSTS (stars denote significant differences between conditions D and A). The datave shift contrast (B vs. A) is not significant in any of the topicalization sensitive ROIs.

⁷ This possibly resulted from the fact that we did not apply spatial smoothing to our data. As our main analysis focused on predefined ROIs, spatial smoothing was not necessary, and could diminish small and localized effects by averaging across neighboring voxels. Without spatial smoothing, focused activations may not overlap across subjects.

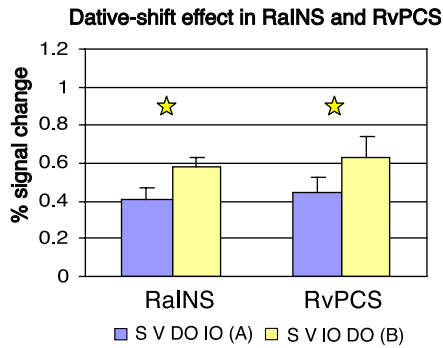


Fig. 6. Dative shift effects in right frontal regions. Bars show mean percent signal change for experiment 1, condition A (in blue) and condition B (in yellow). Stars denote significant difference between conditions in both right anterior insula and right ventral precentral sulcus. Error bars denote standard error of the mean.

were distributed evenly and did not involve any one specific question.

Imaging results

Group analysis: a fixed effect analysis on all 11 subjects found significant [$F(11,2640) = 25$; $P < 0.001$, corrected] task-related activation (for the ‘all-sentences’ predictor) in the following regions: bilateral posterior superior temporal gyrus and sulcus, bilateral Heschl’s complex, left ventral precentral sulcus. Group activation in aINS and LIFG did not reach significance, even though these regions were activated by the localizer test in most individual subjects. This result most likely reflects low signal levels in these regions (also reflected in the smaller cluster size used in their definition), as well as high inter-subject variability in the exact anatomical location of the activation within these regions (see Individual subject analyses section of experiment 1).

Individual data in ROIs: Above threshold activation was documented in IFG in 10/11 subjects and in aINS in 9/11 subjects. Other ROIs were activated by all 11 subjects. Mean Talairach coordinates of the activations in each ROI are given in Table 2. Below are the results of the group ANOVA conducted with *topicalization*, *hemisphere*, *order of objects*, and *block* as within subject variables.

Movement effects

The focus of this experiment was on the effects of syntactic movement evident in topicalization sentences (conditions C, D vs. A, B; see Table 1) within ROIs predefined by the functional localizer (see Materials and methods of experiment 1).

Within anterior regions, a left lateralized topicalization effect was found in both IFG and vPCS (post hoc in the latter; see Data analysis section of experiment 1): topicalization sentences evoked significantly higher activations in left, but not right, IFG and vPCS. The lateralization of these effects was manifested in significant interactions between topicalization and hemisphere (see Fig. 3 and Table 3).

No such effect was found in the anterior insula, our frontal ‘control region’ medially adjacent to IFG: neither an effect of topicalization or hemisphere, nor an interaction between the two was found in this region. An inter-regional analysis comparing left IFG and left aINS yielded a significant region \times topicalization interaction [$F(1,8) = 5.36$, $P < 0.05$], showing that the topicalization effect in LIFG was indeed significantly larger than the one in LaINS.

Posteriorly, bilateral topicalization effects were found in both pSTS and HC (see Fig. 4). In contrast with the topicalization effect found in frontal regions, the posterior topicalization effects did not interact with hemisphere. Moreover, there was no lateralization in the overall task-related activation in these regions, as shown in a nonsignificant main effect of hemisphere (see Table 3).

Dative shift

Our design involved yet another contrast, given by the different order of the objects in no-topicalization sentences (condition B vs. A, Table 1), which may reflect movement of one object across the other, a phenomenon known as ‘dative shift’ (see Introduction to experiment 1). We found that none of the regions activated by the topicalization contrast showed a significant effect for the dative shift contrast. The contrast between topicalization and dative shift effects persisted in most regions when we equated the power of the effects by reducing the topicalization test to a comparison of two conditions (D vs. A, rather than C, D vs. A, B; condition D is equivalent to condition B in the order of O_1 and O_2 and was therefore chosen as the representative topicalization condition in the reduced contrast). This reduced comparison (Fig. 5) yielded a significant effect of topicalization ($D > A$) and a nonsignificant effect of dative shift ($B > A$) in LIFG, LvPCS (post hoc), LHC, RHC, and RpSTS (but not in LpSTS).

Surprisingly, the dative shift (DS) contrast ($B > A$) yielded a significant effect in two right frontal regions: right aINS [$F(1,8) = 11.8$, $P < 0.01$] and right vPCS [$F(1,10) = 4.99$, $P = 0.049$] (see Fig. 6). This effect approached significance in right IFG as well [$F(1,10) = 4.47$, $P = 0.061$]. Interestingly, RaINS also showed a significant effect of linear order [$F(1,8) = 16.84$, $P < 0.005$], with higher activations for the [O_2 , O_1] order, across topicalized and non-topicalized sentences. Thus, the DS effect found in this region may not be specifically related to dative shift, but could be a special case of the sensitivity to linear order in this region.

Intermediate summary—experiment 1

Experiment 1 showed that the comprehension of topicalization sentences is associated with brain activation in left inferior frontal gyrus, left ventral precentral sulcus, bilateral Heschl’s complex, and bilateral posterior superior temporal sulci. These regions were not sensitive to the dative shift contrast, which activated right frontal regions—right anterior insula and right ventral precentral sulcus.

Experiment 2: wh-questions

In this experiment, syntactic movement was manipulated using wh-questions, which are considered a classic case of syntactic movement (Chomsky, 1973). It is assumed within linguistic theory that the wh-phrase (such as [which tourist]) is generated in the canonical position (e.g., subject or object position) and moves backward to form a question (see example 3).

- (3) (a) subject Q: the waiter asked [which tourist] [_ ordered salad for lunch].
 (b) object Q: the waiter asked [which salad] [the tourist ordered _ for lunch].

Thus, wh-questions and topicalization sentences may be viewed as instances of a single generalization, syntactic movement, even though they differ in many other aspects (e.g., prosodic, semantic). If the regions activated by topicalization indeed respond to syntactic movement, they are expected to be activated by wh-questions as well.

We presented Hebrew embedded questions of three types: subject and object wh-questions (see Table 4, conditions B and C), and yes/no questions as in (4) (Table 4, condition A):

(4) yes/no Q: the waiter asked if [the tourist ordered salad for lunch].

Note that the embedded yes/no question in (4) forms a declarative sentence, so there is actually no movement involved. Moreover, given that all question types were embedded within declarative sentences, there was no difference in the type of response triggered by each of these question conditions. Thus, our movement contrast compared embedded wh-questions (subject and object) with embedded yes/no questions.

Finally, we also compared between subject and object wh-questions. Though both involve movement according to standard linguistic theory (Haegeman, 1994), note that the subject wh-questions we tested (Table 4, condition B) lack two main features of object movement: the order of the subject, verb and object does not change, and there are no words separating the wh-phrase from its original (subject) position. By contrasting these two types of questions, we aimed to examine whether this distinction is reflected in the activation of movement-sensitive regions.

Materials and methods

Participants

Ten healthy volunteers (three males, seven females) participated in experiment 2. Four of them took part in experiment 1 as well, but this experiment was run in separate sessions, a year after experiment 1 took place. Participants' age ranged from 21 to 30 (mean age, 25.9; standard deviation, 3.1). The selection criteria and protocol were the same as in experiment 1.

Materials

Sixty clusters of sentences were constructed (see examples in Table 4). We used embedded questions because they allow a straightforward comprehension task (such as the one used in experiment 1), and yield a clean comparison with no-movement questions. Simple wh-phrases (e.g., 'which tourist' rather than 'which fat tourist') were used in all conditions. The NP in the embedded clause (the embedded object in condition A–B, the embedded subject in condition C) was modified by a single adjective.⁸

In sentence construction, five Hebrew verbs that take embedded questions as their complements were used: *sha'al* (asked), *badak* (checked), *berer* (found out), *shaxax* (forgot), *hit'anyen* (was interested to know). Each verb repeated three times in all conditions. All verbs and embedded questions were in past tense. The referential nouns (waiter, tourist) were not repeated throughout the experiment—only one version of each cluster was presented in the experiment. For each condition, 15 sentences of

different clusters were chosen, such that the mean length of the sentences in each condition was identical (eight words, average length = 21.4 syllables).

Sentences were recorded by a female native speaker of Hebrew, and processed as in experiment 1. Thirteen comprehension questions were composed, referring either to the adjective, the verb, the embedded subject, or the object. A couple of representative sentence–question pairs are given in (5):

(5) a. The boxer asked if the athlete received an honorable prize in the ceremony.

Question: did the boxer receive a prize?

b. The artist checked which dealer purchased plastic paint in Sweden

Question: did the dealer buy oil paint?

c. The banker found out which stocks the heavy investors bought in the stockmarket.

Question: did the banker find out about the stocks?

Questions were recorded in a male voice and interleaved in the experimental protocol as in experiment 1.

Paradigm

The task and experimental paradigm were the same as in experiment 1.

For each condition, 15 sentences were presented in 2 triple blocks, 4 double blocks, and 1 single block. The overrepresentation of double blocks was motivated by the relatively high signal documented in experiment 1 for these blocks, and by timing considerations. A dummy block of two sentences was used as in experiment 1. Comprehension questions followed 13 out of 22 blocks.

Stimuli presentation: Mean length of the sentences was 3.6 s (SD = 0.2). Within each block, sentences were presented every 5 s. Blocks were separated by silent blocks of 12.5 s each. Comprehension questions added 5 s to the overall block length, appended 1 s after the last sentence. In addition, 30 s of silence were inserted at the beginning of the experiment and 17.5 s of silence ended the experiment.

Overall, the experiment lasted 610 s (10 min and 10 s).

Procedure, experimental setup, data acquisition

The same as in experiment 1.

Data analysis

Data analysis procedures were identical to those used in experiment 1, except for the following sections.

Localizer test. The use of a functional localizer test was adopted in experiment 2 as well. However, in this case, we did not use the all-sentences predictor as a localizer test. This is because two of our three conditions included wh-questions, which could have biased the localizer in favor of our contrast of interest (movement vs. no-movement). We therefore defined a localizer test that included only two of our experimental conditions—yes/no questions and subject questions (Table 4, conditions A, B). Subject questions were chosen since they do not involve a filler-gap distance, which could bias the localizer in yet another direction.

The localizer predictor was constructed as a boxcar with zeros in all silent blocks, and 1 s in blocks of conditions A and B. Separate predictors were defined for condition C, the dummy block, and comprehension questions. As in experiment 1, all predictors were convolved with a standard HRF model (with $\delta = 2.5$, $\tau = 1.25$).

⁸ The adjectives in condition C were shorter to compensate for the extra syllables introduced by the determiners ('*ha-*' = *the*) in the embedded subject.

Table 4
Design of experiment 2

Condition	Description	Example (top: Hebrew; middle: English word by word translation; bottom: English)
A	Embedded yes/no Q	ha-meltzar sha'al im [EMB [NP ha-tayar] hizmin [NP mashke alcoholic] [PP baboker]] The waiter asked if [EMB [NP the-tourist] ordered [NP drink alcoholic] [PP in-the-morning]] The waiter asked if the tourist ordered an alcoholic drink in the morning
B	Embedded subject Q	ha-meltzar sha'al [wh 'eize tayar] [EMB _ hizmin [NP mashke alcoholic] [PP baboker]] The waiter asked [wh which tourist] [EMB _ ordered [NP drink alcoholic] [PP in-the-morning]] The waiter asked which tourist ordered an alcoholic drink in the morning
C	Embedded object Q	ha-meltzar sha'al [wh 'eize mashke] [EMB [NP ha-tayar hashamen] hizmin _ [PP baboker]] The waiter asked [wh which drink] [EMB [NP the-tourist the-fat] ordered _ [PP in-the-morning]] The waiter asked which drink the fat tourist ordered in the morning

Abbreviations: wh = wh-phrase, EMB = embedded clause, NP = noun phrase, PP = prepositional phrase.

To make sure that the choice of a particular localizer test did not bias the results, we compared the results in a single ROI (LIFG) functionally defined by each of the two possible localizers (<yes/no + subject Q>, <yes/no + object Q>; see footnote 9).

Definition of ROIs. The same ROIs were analyzed as in experiment 1. However, the anatomical definition of the low-level auditory region changed. Recent functional and cytoarchitectonic studies (Morosan et al., 2001; Rademacher et al., 2001) have shown that low level auditory functions may be limited to the medial two-thirds

of HG, whereas the lateral third is more similar in structure and in function to the superior temporal gyrus. Consequently, we hypothesized that the topicalization-related activations we found in HC in experiment 1 could be attributed to the inclusion of this higher level lateral cortex in our definition of HC. Therefore, in experiment 2, we limited this ROI to include only activated clusters in the medial two-thirds of Heschl's complex, according to the following procedure (the data from experiment 1 was later reanalyzed according to these guidelines): (a) Heschl's sulcus (HS) was anatomically identified in the para-sagittal view, and served to find Heschl's gyrus (see Morosan et al., pp. 695). (b) The statistical map of the functional localizer test was overlaid on the 3D brain. In contrast with the localizer test that defined all other regions, HC was defined with a boxcar predictor (without smoothing by an HRF model) shifted in one image. The reason for this difference is that only in this region, a boxcar predictor yielded consistently higher activations as measured by the number of activated voxels for any given threshold. (c) Clusters activated by the localizer within the medial two-thirds of HC were captured (since most of the activations within this region fell in HS, we could not limit our definition to HG). However, this extension of the borders is hardly misleading, since HS is generally included within the same cytoarchitectonic region (Te1; see Fig. 2 in Rademacher et al., 2001). Cluster choice was also guided by the probability map given in Rademacher et al. (2001; pp. 675).

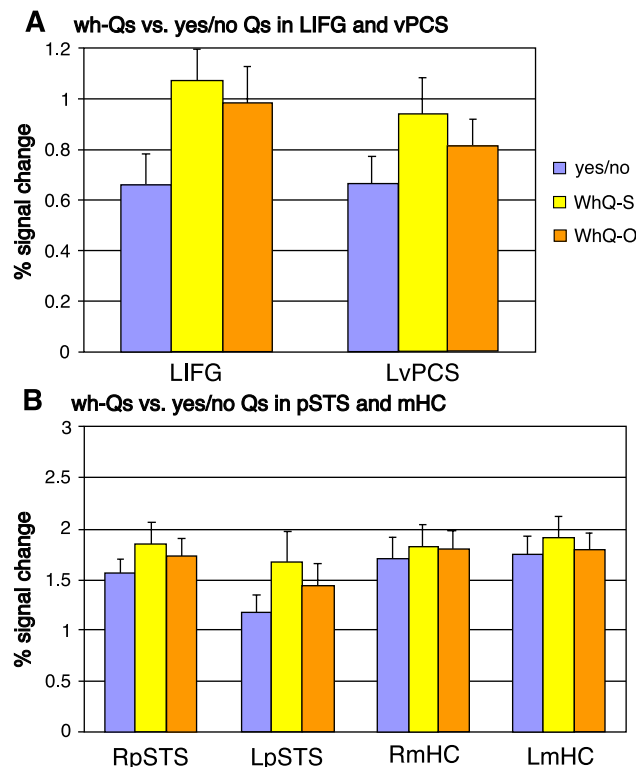


Fig. 7. Wh-Qs vs. yes/no Qs in frontal and temporal ROIs. Bars show mean percent signal change for yes/no questions (blue), subject wh-questions (yellow), and object wh-questions (orange), in left frontal (A) and bilateral posterior temporal (B) ROIs. A significant effect of wh-questions (subject and object) vs. yes/no questions is found in LIFG, LvPCS, and LpSTS. A marginally significant effect is found in RpSTS ($P = 0.051$). No significant difference is found between subject and object wh-questions in any of the ROIs. Error bars denote standard error of the mean.

Group analysis. Individual time courses were weighted and averaged as in experiment 1. These individual scores were subject to a group ANOVA with *condition*, *hemisphere*, and *block* as within subject variables. In addition, two planned contrasts were carried out: (1) A planned contrast between both wh-questions conditions (conditions B and C; see Table 4) compared to yes/no questions (condition A). Naturally, this contrast was balanced so that each of the conditions B–C were given a weight of 1/2, while condition A was given a weight of –1. (2) A planned contrast between object and subject questions (C vs. B).

Experiment 2: results

Behavioral results

Subjects responded correctly to 10.7/13 questions on the average (SD = 1.2; mean percent correct responses: 82.3%, SD = 8.9%). The reduced accuracy in this experiment relative to experiment 1 may be attributed to the difficulty of answering a question regarding an embedded question. For instance, in a sentence such as ‘the man asked which tourist ordered the salad’, answering the question ‘did the tourist order salad’ raises a logical problem: can we assume that

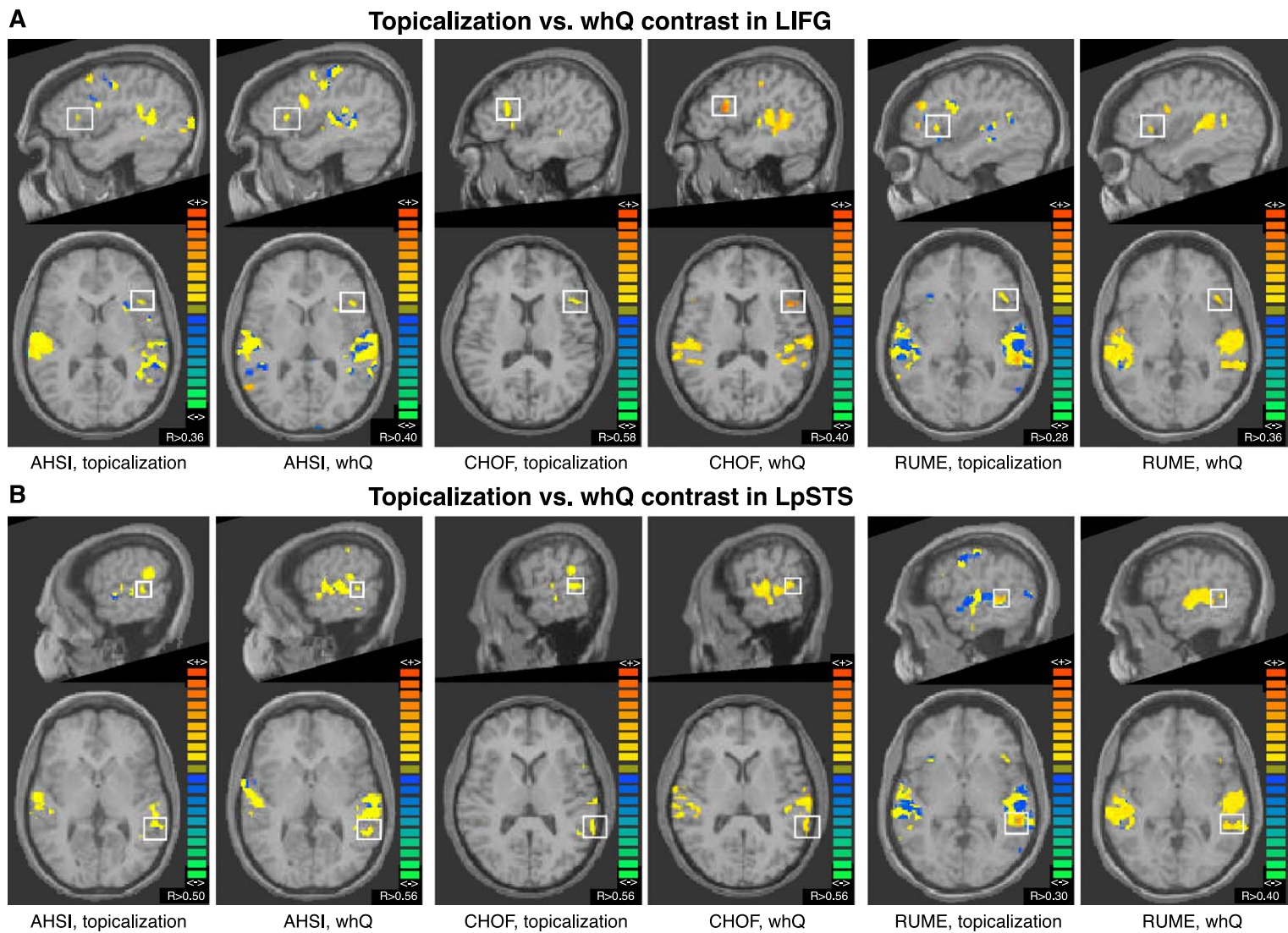


Fig. 8. A comparison of topicalization and wh-Q effects in LIFG (A) and LpSTS (B). For each of the three subjects that took part in both experiments, maps show relative contribution of + movement conditions (yellow) vs. - movement conditions (blue) in each experiment. Maps are thresholded to maximally equate the number of activated voxels in the relevant ROI.

the tourist indeed ordered salad simply by the fact that someone asked about it? Such logical conflicts probably contributed to the lower levels of performance in this experiment.

Imaging results

Group analysis. A fixed effects analysis on all 10 subjects found significant [$F(1,2366) = 31$; $P < 0.001$, corrected] task-related activation (for the functional localizer) in the following regions: bilateral posterior superior temporal gyrus and sulcus, bilateral Heschl's complex, left IFG, bilateral vPCS, bilateral aINS.

Individual data in ROIs. Above threshold activation was documented in IFG in 9/10 subjects, and in aINS in 8/10 subjects. Other ROIs were activated by all 10 subjects. Mean Talairach coordinates of the activations in each ROI are given in Table 2. Below are the results of a group ANOVA and planned comparisons (see Data analysis section of experiment 2).

Movement effect

The focus of this experiment was on the effects of syntactic movement evident in wh-questions [conditions (B, C) vs. (A)] within ROIs predefined by the functional localizer (see Materials and methods of experiment 2).

Within anterior regions, wh-questions yielded significantly stronger activations than yes/no questions in both left IFG [$F(1,8) = 9.85$, $P < 0.015$] and left vPCS [$F(1,9) = 6.62$, $P < 0.05$] (see Fig. 7A). This effect was neither significant in the right homologues of these regions nor in bilateral aINS [right IFG: $F(1,8) = 1.32$, $P = 0.284$; right vPCS: $F(1,9) = 2.33$, $P = 0.16$; left aINS: $F(1,7) = 3.42$, $P = 0.11$; right aINS: $F(1,7) = 3.16$, $P = 0.12$]. No main effect of hemisphere was found in either of these regions (IFG: $F(1,8) = 1.22$, $P = 0.3$; vPCS: $F(1,9) = 0.24$, $P = 0.63$; aINS: $F(1,7) = 0.98$, $P = 0.36$).⁹

In posterior regions, a significant effect of wh-questions relative to yes/no questions was found in left pSTS [$F(1,9) = 10.7$, $P < 0.01$] and a marginally significant effect was found in right pSTS [$F(1,9) = 5.06$, $P = 0.051$] (see Fig. 7B).

No such effect was found in mHC [left: $F(1,9) = 1.71$, $P = 0.22$; right: $F(1,9) = 2.5$, $P = 0.15$]. No main effect of hemisphere was found in posterior regions (pSTS: $F(1,9) = 2.29$, $P = 0.16$; HC: $F(1,9) = 0.04$, $P = 0.85$).

Reanalysis of mHC data from experiment 1

In view of the above findings in mHC, we hypothesized that limiting the definition of this region to the medial two thirds of Heschl's complex would eliminate the movement effect that we found in this region in experiment 1. We therefore conducted a reanalysis of HC data from experiment 1, following the same anatomical guidelines that were employed in experiment 2 (see Definition of ROIs section of experiment 2). We found a nonsignificant effect of topicalization in mHC [main effect: $F(1,10) = 3.38$, $P = 0.1$; left: $F(1,10) = 1.18$, $P = 0.3$; right: $F(1,10) = 4.13$, $P = 0.07$].

⁹ The activations in LIFG were also captured with a different localizer test (based on object Qs and yes/no Qs). The results showed a similar effect of wh-questions compared to yes/no questions [$F(1,8) = 10.27$, $P < 0.015$]. The individual time courses captured with each localizer were highly correlated (mean correlation coefficient $r = 0.98$, $SD = 0.04$). In general, individual GLM maps produced by both localizers showed considerable overlap. Thus, it is hardly likely that the results were systematically influenced by the choice of one localizer over the other.

Object versus subject questions

Object questions did not yield higher activation than subject questions in any of the ROIs ($P > 0.1$; see Fig. 7). To further test this effect, we compared condition C (object questions) with conditions B and A together (subject and yes/no questions). Here too, there were no significant effects in any of the ROIs analyzed ($P > 0.1$).¹⁰

Results summary—wh-questions

Wh-questions compared to yes/no questions yielded a stronger fMRI signal in left IFG, left vPCS and left pSTS, and a marginally significant effect in right pSTS. Other regions, including right IFG and vPCS, bilateral anterior insula and bilateral HC, were not sensitive to the experimental contrast. Object wh-questions did not show significantly stronger activation than subject wh-questions in any of the ROIs.

A comparison between the two experiments

Fig. 8 compares the activation maps acquired for the wh-Q contrast and for the topicalization contrast in three subjects who performed both experiments. Activation is compared in two ROIs: LIFG and LpSTS. This individual comparison shows very similar voxels activated by these two different contrasts in each individual, regardless of the different syntactic constructions used. The figure also demonstrates between-subject variability in the exact anatomical focus of activation within ROIs.

General discussion

We have shown a consistent pattern of activation for two cases of syntactic movement: topicalization-sentences and embedded wh-questions. Both activated left inferior frontal gyrus, left ventral precentral sulcus, and bilateral posterior superior temporal sulcus. These regions were sensitive neither to the subject object contrast (experiment 2) nor to the dative shift contrast (experiment 1), which in turn activated right frontal regions. Other task-related regions, such as anterior insula and medial Heschl's gyrus, were not sensitive to the movement contrasts.

A neurolinguistic generalization

The fMRI activations associated with topicalization and wh-questions are consistent with those found in yet another case of syntactic movement—object relatives tested earlier in our lab (Ben-Shachar et al., 2003). These three experiments, though differing in task, materials, and design, all manipulated syntactic movement. In all three, left inferior frontal gyrus was activated, as well as bilateral posterior superior temporal cortex. In all three, the left inferior activation was dissociable from the left anterior insular cortex, and

¹⁰ It could be argued that this null effect (object vs. subject wh-questions) reflects low statistical power. However, note that in both LIFG and LpSTS, the other two simple comparisons (subject wh-Qs vs. yes/no Qs, object wh-Qs vs. yes/no Qs) were significant [LIFG: $F(1,8) = 7.26$ and 5.51 , respectively, $P < 0.05$; LpSTS: $F(1,9) = 10.64$ and 8.69 , respectively, $P < 0.05$]. Thus, the design seems powerful enough to detect simple effects between single conditions.

the bilateral posterior temporal activations were dissociable from medial Heschl's complex, both representing neighboring regions activated by the task but indifferent to the linguistic contrast. Taken together, the combined results of these studies suggest that syntactic movement constitutes a neurally relevant linguistic generalization, processed by this consistent set of brain regions.

Our results converge on a previous ERP study (Kluender and Kutas, 1993) that compared English object wh-questions ('what have you forgotten . . .') with yes/no questions ('have you forgotten . . .'). The authors report: 'ANOVAs restricted to individual electrodes thus showed main effects of sentence type only for Broca's area [$P < 0.001$; right hemisphere homologue of Broca's .. nonsignificant], left temporal regions (T5) [$..; P < 0.001$], and right temporal regions (T6) [$..; P < 0.001$]' (pp. 199). These results, while lacking the anatomical precision provided by fMRI, supply converging evidence to our conclusion that cuts across imaging technologies, syntactic constructions, task and language.

With regard to lesion studies, the results are in agreement with many findings demonstrating agrammatic (Broca's) aphasics' selective comprehension difficulties in various constructions involving movement (reviewed in Grodzinsky, 2000). Our results supply finer anatomical characterization of the regions involved in the computation of movement, distinguishing, for example, between Left IFG and Left anterior insula with respect to their sensitivity to movement. However, based solely on our fMRI results, we cannot determine which of the activated brain regions is indeed critical for processing movement sentences. Results from lesion studies make a strong case for the critical role of Broca's region in this respect.

As for Wernicke's region, the evidence from lesion studies is mixed (Grodzinsky and Finkel, 1998; Swinney et al., 1996). Our findings, showing bilateral activations in a part of Wernicke's region (pSTS, see Figs. 4 and 7B), suggest that a more homogeneous deficit in the processing of movement may show up in patients with bilateral posterior temporal damage. Further behavioral studies with patients may also clarify the different roles sustained by each of these homologues in the processing of movement sentences.

The exact division of labor between the regions activated by movement cannot be specified based on this study alone. One interesting interpretation comes from the study of control processes in memory, where it was suggested that frontal regions are engaged in selecting the appropriate representation while excluding context inappropriate ones (Buckner, 2003; Thompson-Schill et al., 1997). These anterior regions maintain interactions with posterior regions in temporal and parietal cortex that may serve as storage sites (Buckner, 2003). In this context, activation in left frontal regions could be related to the reactivation of the moved element in an appropriate sentential position, whereas posterior temporal activations could reflect maintenance of the moved element in memory.

Task-related and construction-specific activation

Some differences should be noted between the current experiments and our previous study of object relatives. First, the activation of the left vPCS (see Figs. 3 and 7A) was not recorded previously for the movement contrast. In fact, this region was not analyzed in our previous study since it was not activated by the functional localizer (grammaticality judgment on neutral sentences) in all subjects. This suggests that the activation of this region

may be task-related, and given the appropriate activating task (comprehension), its sensitivity to movement is evident.

The activations we found in LvPCS relate to two separate lines of research. Within the imaging literature concerning memory, LvPCS (termed as pLIPC, anterior portion) showed relative activation in phonologically related encoding tasks (Gold and Buckner, 2002; Poldrack et al., 1999), as well as in semantic tasks on single words (Wagner et al., 1998). In these studies, too, LvPCS usually coactivated with LIFG (termed aLIPC). In our movement sentences, LvPCS may have been involved in searching for a semantically appropriate element to be linked, while LIFG was performing a more syntactically guided search for this element. This hypothesis can be tested by manipulating syntactic and semantic plausibility of association orthogonally during functional imaging.

Secondly, LvPCS activation fell within the caudal ventral premotor cortex (see Picard and Strick, 2001; Rizzolatti et al., 2002). There is some preliminary evidence to suggest that this region may correspond to monkey area F4 (Rizzolatti et al., 2002), but the functional homology between monkey F4 and human ventral premotor is controversial (Grezes and Decety, 2001; Picard and Strick, 2001). It is hard to see at this point how the activation documented for our fine syntactic contrasts in the left vPCS could be related to the motor planning functions attributed to monkey F4 (cf. Rizzolatti et al., 2002). However, attempts have been made to relate monkey 'mirror neurons' in the adjacent F5 to language functions in human BA 44 (Rizzolatti and Arbib, 1998). In the future, this link between high motor functions in the monkey and specific language functions in human may be further pursued in caudal ventral premotor.

Another difference between the current study and our previous study of object relatives pertains to the activation of HC by the topicalization contrast (Fig. 4). This region was not sensitive to movement in our previous study, and was not expected to show up here due to its known lower level functions. One possible reason for its activation by topicalization is stress changes that take place in topicalized sentences (reflecting focus changes, see Introduction to experiment 1).

Another possible explanation for the topicalization effect in HC is that its anatomical delineation was not fine enough. Indeed, when this region was carefully defined using better anatomical guidelines published recently by Rademacher et al. (2001), there was no movement-related activation found there for both wh-questions and topicalization (see the reanalysis of HC data in Experiment 2: results section). Thus, we suggest that the definition of HC in experiment 1 included parts that are functionally related to STG, a higher level auditory region that might be involved in movement analysis or in stress changes characteristic of topicalization. Better functional discrimination is needed between these two regions to address this issue more precisely.

Linguistic distinctions in movement-sensitive regions

Having shown that several regions are activated by syntactic movement, it is no less important to ask to which syntactic contrasts these regions are *not* sensitive. An important result of the current study is that regions activated by topicalization did not show a comparable effect for dative shift (Fig. 5), which involves a different class of movement (if any, see footnote 2). Furthermore, regions activated by embedded wh-questions were not sensitive to the subject-object contrast (Fig. 7). These results

underline the selectivity of these regions and show that within the syntactic realm, their activation cannot be attributed to just any deviation from the canonical word order to which the listener expects. The current evidence thus allows us to restrict our neurolinguistic generalization to (A-bar) syntactic movement rather than to syntax as a whole.

Dative shift effects

In contrast with topicalization and wh-questions, the dative shift contrast activated right frontal regions. This effect is important for two reasons: first, it shows that our manipulation was strong enough to trigger activation in some part of the brain, and therefore supports a true distinction between dative shift and topicalization in left inferior frontal and bilateral posterior superior temporal regions. Secondly, it supports a dichotomous distinction between movement types, as opposed to a parametric measure of the amount of movement. A parametric view would predict increased activation in movement-sensitive regions that correlates with increased amount of movement (no-movement < dative shift < topicalization). Instead, we found that A-bar movement contrasts and the dative shift contrast split, giving rise to different patterns of brain activation. This is in agreement with a linguistically based approach that views each of these phenomena as belonging to different classes of movement (Larson, 1988).

The activation of right frontal regions in itself is hard to interpret, as little is known about these regions from neuroimaging and lesion studies. Still, it generates an interesting prediction regarding aphasic patients' ability to comprehend such sentences. In particular, we would expect Broca's and Wernicke's aphasics to process sentences with dative shift correctly, and right hemisphere frontal patients to show a different pattern of behavior. These predictions are not easily tested, however, due to the irreversible nature of the semantic roles of the two objects, among other things (but see Caplan and Futter, 1986 for one such attempt). Further evidence from English and Hebrew speaking aphasics with well-localized lesions may shed more light on this issue.

Subject versus object questions

The fact that the subject–object contrast in wh-questions did not turn out significant in any of the analyzed ROIs contrasts with neuroimaging findings in English relative clauses and clefts (reviewed in Caplan, 2001). These studies showed higher activation in Broca's region (and sometimes in other regions as well, e.g., Just et al., 1996) for object relatives and clefts compared to subject relatives and clefts. The reasons for this contradiction remain unclear. Note, however, that subject–object contrasts failed to yield significant activations in these ROIs (and particularly in Broca's region) in several other studies as well, including Fiebach et al. (2001; contrasting subject vs. object wh-questions), Indefrey et al. (2001; contrasting all-subject vs. subject/object relative clauses), Cooke et al. (2001), and Caplan et al. (2002; contrasting subject and object relatives). Some possible reasons for this variability are given in Caplan et al. (2002, pp. 36–37).

We suggest that both subject and object movement constructions are processed in movement-sensitive regions. This could only be seen if an appropriate no-movement baseline is used. Further contrasts between object and subject movement may stem from the difference in word order and/or in the distance between the moved element and its original position (see Cooke et al., 2001, for

a clean manipulation of this variable). These may activate a partially overlapping group of brain regions, as some of the movement-sensitive regions are in fact involved in holding the moved element in working memory, and therefore would work harder when the distance is greater. The critical distance required for these effects is likely to be influenced by the specific language and the task used (see Baddeley, 1997, Chap. 4). Since our study was not oriented toward this question, it is very likely that our contrast between object and subject questions did not involve the required distance to result in a significant effect.

Our interpretation is further corroborated by psycholinguistic and lesion data showing that (a) healthy subjects show movement-related (so-called 'gap-filling') effects in both object and subject relative clauses (Balogh et al., 1998; Nicol and Swinney, 1989); and (b) Broca's agrammatic aphasics (Swinney et al., 1996; Zurif et al., 1993) fail to show this effect in both subject and object relative clauses. These findings suggest that Broca's region is involved in processing syntactic movement in both subject and object relative clauses.

Finally, other types of movements were characterized within linguistic theory, such as A-movement (as in passive constructions) and head-movement (as in: 'are you listening?'). A neuropsychological dissociation has been documented between 'head-movement' and other types of movement (Grodzinsky and Finkel, 1998), but not between A-movement and A-bar-movement (evident in relative clauses, clefts, topicalization, and wh-questions). fMRI may be more sensitive to this latter distinction, since it usually finds activations in a wider set of brain regions that contribute to a given cognitive process, and since it allows the detection of gradual changes in activity. For instance, we may witness different patterns of fMRI activation for A- versus A-bar movement, or a relative difference in the amount of activation triggered by these types of movement in a specific brain region. Future findings of this kind will better our understanding of the relation between fine linguistic distinctions and language processing in the brain.

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