

Research Article

THE NEURAL REALITY OF SYNTACTIC TRANSFORMATIONS: Evidence From Functional Magnetic Resonance Imaging

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Abstract—The functional anatomy of syntactic transformations, a major computational operation invoked in sentence processing, was identified through a functional magnetic resonance imaging investigation. A grammaticality judgment task was used, presented through a novel hidden-blocks design. Subjects listened to transformational and non-transformational sentences in which a host of other complexity generators (number of words, prepositions, embeddings, etc.) were kept constant. A series of analyses revealed that the neural processing of transformations is localizable, evoking a highly lateralized and localized activation in the left inferior frontal gyrus (Broca's region) and bilateral activation in the posterior superior temporal sulcus. The pattern of activation associated with transformational analysis was distinct from the one observed in neighboring regions, and anatomically separable from the effects of verb complexity, which yielded significant activation in the left posterior superior temporal sulcus. Taken together with neuropsychological evidence, these results uncover the neural reality of syntactic transformations.

Natural language understanding is a hard combinatorial problem. In particular, the ability to comprehend sentences in real time requires fast and efficient analysis of complex linguistic objects (Clifton, Frazier, & Rayner, 1994; Gibson, 1998). Computational models that (psycho)linguists construct characterize the knowledge base and mechanisms that carry out this analysis, and neurolinguistics seeks to identify their neural substrate. We present the results of a neurolinguistic investigation into the cerebral localization of a critical aspect of sentence processing—syntactic transformations (Chomsky, 1957, 1995).

Many syntactic relations involve adjacent elements, yet in certain cases, “action at a distance” is required. In an active sentence like *The horse kicked the rider*, the verb *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 in the first sentence, there is now considerable distance between the two elements *kick* and *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, as before. Yet the properties of the verb are the same—*kick* still assigns a semantic role rightward, namely, to the position marked by ■. *The rider* is phonetically present in one position, but its semantic role is in a different position, ■. The two positions must therefore be related during processing if the correct interpretation is to be reached.

Appearing in different guises, this relation features in virtually every linguistic theoretical framework (Elman, 1993; Haegeman, 1994; Pollard & Sag, 1994), including generative grammar, where it is termed *transformation*. It is computed on-line (Nicol & Swinney, 1989), and is a major contributor to the perceptual complexity of sentences in the performance of healthy subjects (Fodor, Bever, & Garrett, 1974; Neville, Nicol, Barss, Forster, & Garrett, 1991). Moreover, neuropsychological research has shown that transformations pose specific comprehension difficulties to aphasic patients with a lesion in Broca's region in the left inferior frontal cortex (Grodzinsky, 2000; Grodzinsky & Finkel, 1998; Zurif, Swinney, Prather, Solomon, & Bushell, 1993). Transformations are thus central to any approach to language perception.

Sentence processing has been investigated intensely through functional imaging techniques like functional magnetic resonance imaging (fMRI) and positron emission tomography (PET). Several neuroimaging studies have found that Broca's region is activated by syntactically complex sentences (Dapretto & Bookheimer, 1999; Friederici, Wang, Herrmann, Maess, & Oertel, 2000; Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Stromswold, Caplan, Alpert, & Rauch, 1996). Some of these studies have found activation in other areas as well, including Wernicke's region and the right-hemispheric homologues of Broca's and Wernicke's areas. This variability may have resulted from the variety of complexity generators confounded in these studies, such as place and number of embeddings, propositional content, and various types of transformations collapsed together.

Our approach was different: Recognizing that the processing complexity of sentences is determined multifactorially (e.g., Gibson, 1998), we aimed to further break down the neural structure of the sentence-processing device into its parts. This we hoped to achieve by investigating a single potential generator of syntactic complexity and examining its neural implementation using fMRI. Syntactic transformations were a natural choice because of their centrality in linguistic theory, as well as in psycholinguistic and neuropsychological research, as discussed earlier.

We sought to isolate the neural correlates of the transformational component, while controlling for as many complexity generators as possible, and varying the transformation factor in an unconfounded manner. In our critical comparison, subjects attended to sentences that required transformational analysis and sentences that did not, while relative changes in blood-oxygenation-level-dependent (BOLD) signal were monitored with fMRI. In an attempt to set the effect of transformations apart from that of other complexity factors, we further manipulated the complexity of verbs embedded in these sentences and compared the effects of the two factors.

We used a grammaticality judgment task in which the transformation factor was crossed with grammatical status in a 2×2 factorial design. Crucially, a host of recognized complexity generators (such as number of words, verbs, embeddings, and propositions) were kept

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constant (see Fig. 1a). Minimal pairs of Hebrew sentences were used, so that we could compare sentences that contained embeddings with transformations (+T, Fig. 1a, condition a) against sentences that contained embeddings without transformations (−T, condition c). Our +T stimuli embedded object-relative clauses (the embedded clause is in square brackets): *azarti la-yalda še-[Mary ra'ata ■ ba-park]* ("I helped the girl who(m) [Mary saw ■ in the park]"). Our −T stimuli embedded sentential complements: *amarti le-Mary še-[ha-yalda raca ba-park]* ("I told Mary that [the girl ran in the park]"). This minimal contrast was possible because Hebrew permits the use of a single complementizer (i.e., embedding marker: *še-* = who, whom, that) in both relative clauses and sentential complements.

Our design, in fact, was richer: On the one hand, it crossed the transformation variable with grammaticality (still allowing for the exclusion of ungrammatical sentences in the analysis; see our discussion

of the hidden-block design later in the introduction). On the other hand, the transformation variable was crossed with verb complexity (VC), manipulated in both the main and the embedded clause of each stimulus sentence. Verb complexity is known to affect the perceptual complexity of sentences (Gibson, 1998; Shapiro, Gordon, Hack, & Killackey, 1993; Shapiro, Zurif, & Grimshaw, 1987) and is measured by the number of arguments a verb takes, or by the number of possible argument-structure representations it enters into.

In our stimuli, the main verbs of the +T sentences (dyadic verbs, as in *X helped Y*; VC = 2) were simpler than those in the −T sentences (triadic verbs, as in *X told Y that P*; VC = 3). The embedded verbs also varied in complexity (*X saw Y*, VC = 2, vs. *X ran*, VC = 1), yet this complexity was balanced by the ungrammatical versions of the +T and −T sentences (note that ungrammaticality was due to the switching of embedded verbs between these sentences). The resulting overall

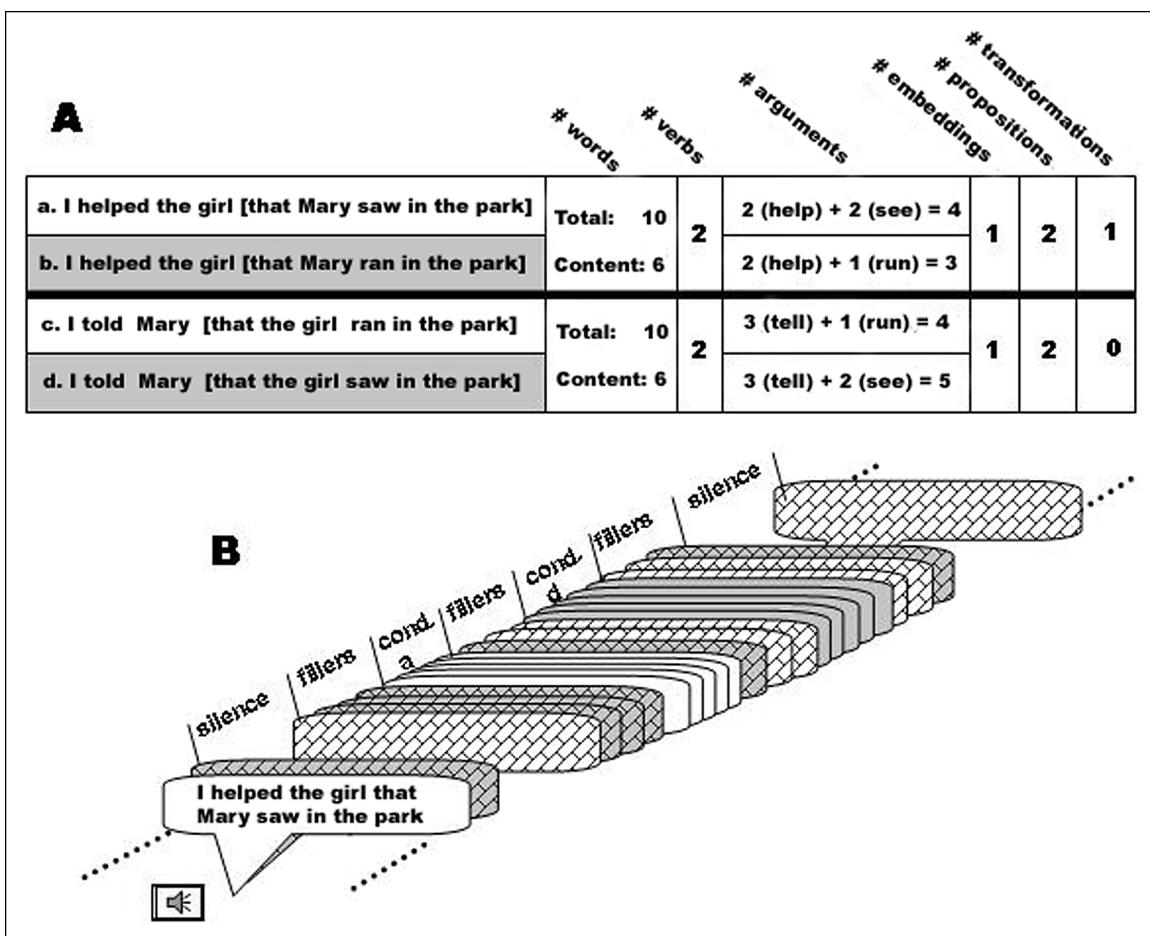


Fig. 1. Experimental stimuli and design. Panel (a) shows examples of the stimulus materials (translated to English): Condition a included grammatical sentences containing transformations (+T sentences); condition c included grammatical sentences without transformations (−T); in the ungrammatical version of each condition (conditions b and d, in gray), an embedded transitive verb (*saw*) was replaced by an intransitive (*ran*) and vice versa. Five other complexity generators were balanced as indicated. The experimental contrast compared +T sentences (conditions a + b) with −T sentences (conditions c + d), across grammaticality. As shown in panel (b), stimuli were presented in a hidden-block design: Each experimental block consisted of five sentences from the same condition (nontextured balloons—grammatical sentences in white, ungrammatical in gray). These blocks were hidden within sequences of fillers (brick-textured balloons). This design resulted in a sequence of sentences with same-response clusters of variable length (1–5 sentences) appearing in a pseudorandom order. Color versions of the figures in this article can be viewed on the Web at <http://freud.tau.ac.il/~yosef1/PsychSci-Images/>.

complexity metric in the $\pm T$ contrast (conditions a + b vs. c + d) thus worked against our experimental contrast (see Fig. 1a).

The design, moreover, allowed a separate test of the VC effect itself, taking advantage of the way complexity of embedded verbs was set up. The complexity of the embedded verbs was manipulated orthogonally to the $\pm T$ contrast. This enabled the grouping of experimental conditions either according to the T contrast (with grammaticality and the complexity of embedded verbs balanced—conditions a + b vs. c + d) or by the VC contrast (with grammaticality and transformation balanced—conditions b + c vs. a + d). We could thus compare the two contrasts, in order to see whether transformations can be set apart neurologically from other complexity factors.

In order to implement a grammaticality judgment task while maintaining the statistical efficiency of a block design (Friston, Zarahn, Joesphs, Henson, & Dale, 1999), we employed a novel *hidden-block* design, in which blocks of experimental stimuli were interleaved within pseudorandom sequences of filler sentences (see Method and Fig. 1b). Stimuli of a single experimental condition were blocked in order to magnify the BOLD effect triggered by the subtle syntactic contrast of interest. The blocking of each experimental condition separately also allowed separate analyses of grammatical and ungrammatical sentences. Response prediction was prevented by hiding these blocks within sequences of filler sentences (not belonging to any experimental condition); the filler sequences were of variable length, and their grammatical status and syntactic structure was assigned pseudorandomly.

METHOD

Subjects

Twelve healthy right-handed volunteers gave written informed consent to participate in the experiment. All had a college education and were native speakers of Hebrew (7 females, 5 males; mean age = 27, $SD = 3$). The experimental protocol had been approved by the ethics committees of Tel-Aviv University and Tel-Aviv Sourasky Medical Center.

Materials

We have already discussed the structure of the grammatical sentences (+G; Fig. 1a, conditions a and c) in the introduction. An ungrammatical counterpart of each condition ($-G$, conditions b and d) was created by replacing an embedded transitive verb in each sentence (e.g., “saw”) with its intransitive counterpart (e.g., “ran”) and vice versa. The inclusion of $-G$ sentences balanced the choice of embedded verbs (e.g., *ra’atal/raca* = “saw/run”), which featured in both $\pm T$ sentences. The matrix verbs (e.g., *azartil/amarti* = “I helped/I told”) could not be balanced. The resulting systematic bias was conservative, as it biased the materials in a direction opposite to our expectation: The less complex, dyadic (two-argument) verbs, such as “help,” were included in the putatively more complex $+T$ sentences. Conversely, the more complex, triadic (three-argument) verbs, such as “tell,” were included in the less complex $-T$ sentences (Shapiro et al., 1987).

The manipulation of grammaticality served to balance the choice of embedded verbs in the comparison of $\pm T$ sentences. Other complexity generators were kept constant as follows: All sentences had an equal number of (content and function) words, verbs, embeddings, and propositions. The number of verbal arguments per sentence was

the same for the grammatical sentences, and even greater for $-G$, $-T$ sentences (condition d). If number of arguments increases complexity, it would work against the experimental expectation. Our main experimental contrast compared $+T$ sentences (Fig. 1a: conditions a + b) with $-T$ sentences (conditions c + d), across grammaticality. We also tested a different contrast, regrouping the conditions according to the complexity of the embedded verb. In this case, $+VC$ sentences (conditions b + c) were compared with $-VC$ sentences (conditions a + d), across grammaticality and transformation.

The Hidden-Block Design

Blocks of five consecutive sentences of the same condition (Fig. 1b, nontextured balloons) were hidden within sequences of filler sentences (Fig. 1b, brick-textured balloons), whose number and grammaticality were systematically varied, to prevent response prediction. All filler sentences were $-T$ sentences and contained embeddings as either noun phrase complements (English: “John heard the rumor [that the woman left town]”) or adjuncts (English: “John listened to the radio after [that the woman left town]”). Embeddings were on the subject or the object of the matrix clause. Ungrammatical fillers contained a violation (in either matrix or embedded clause) of either subject-verb agreement or subcategorization requirements of the verb. This controlled variability in filler structure served to maintain subjects’ attention, while hiding the experimental blocks within superficially similar sentences.

Each subject was presented 160 sentences: 80 filler sentences (half of them grammatical) and 80 experimental sentences, 20 items per experimental condition, in four separate blocks. Prior to testing, sentences were rated by three independent judges, to ensure high level of agreement on correct responses.

Sentences lasted 3.5 to 4.5 s (stimulus onset asynchrony = 6 s), with 30-s silent epochs at the beginning of the run and after each sequence of 20 sentences. The experiment was separated into two equal runs, presented in a random order, each lasting 642 s.

fMRI Data Acquisition

BOLD contrast was obtained with gradient-echo echo-planar imaging (EPI) sequence ($T_R = 3,000$ 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. Seventeen functional (T_2^* weighted) and anatomical ($T1$ weighted) axial slices of 5-mm thickness with 1-mm gap were acquired. Three-dimensional (3-D), high-resolution spoiled gradient-echo (SPGR) sequence was acquired for each subject, allowing volume-based statistical analyses of signal change over time.

Procedure

Participants listened to Hebrew sentences presented through MRI-compatible headphones (Newmatic Sound Systems, Petaluma, CA) and judged the grammaticality of sentences by pressing a yes/no response button with their left hand at the end of each sentence. Elaborate instructions and practice were administered prior to the imaging session, to make sure that the participants understood the task and performed it well (Grodzinsky & Finkel, 1998).

Behavioral responses were recorded during scanning to ensure that subjects were attending throughout the experiment. Behavioral data

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from only 8 subjects were available for later analysis (no data of the remaining 4 subjects were available because of technical failure). One subject was excluded from further analysis because of a high error rate (30% errors), which suggested a low level of attention. The average accuracy of the other 7 subjects was 93% correct.

Functional data of the remaining 11 subjects were projected on their 3-D anatomical scan transformed to Talairach space (Talairach & Tournoux, 1988), by manually realigning the 2-D anatomical images with the 3-D scan.

Data Analysis

The first stages in data analysis were performed using BrainVoyager software (version 4.1, 4.4; Brain Innovation, Maastricht, The Netherlands). Boxcar predictors were defined for each condition, shifted by 6 s to compensate for the delayed hemodynamic response. A general linear model (GLM) was calculated twice for the group of 11 subjects—for both fixed and random effects analyses. A specific planned contrast was tested on these models: +T conditions (a, b) against −T conditions (c, d).

Next, a region-of-interest (ROI) analysis was performed. ROI definition was both anatomical and functional: Four bilateral ROIs were defined anatomically per subject, using anatomical markers (discussed later in this section). ROIs were then defined functionally as follows: Statistical parametric maps were calculated for the fillers GLM predictor (against the baseline of silent blocks) for each subject. For each anatomical region, an individual threshold was selected such that at least 100 suprathreshold voxels (of $1 \times 1 \times 1$ mm) remained in each hemisphere.¹

The average time course of activation within these regions was transformed (using Matlab—The Mathworks, Natick, MA) into percentage signal change scores² and subject to a multiple analysis of variance (using STATISTICA—StatSoft, Tulsa, OK), with region, hemisphere, transformation, and grammaticality as within-subjects independent variables.

Based on previous neuropsychological and neuroimaging data (Damasio, 1992; Grodzinsky & Finkel, 1998; Just et al., 1996; Wise et al., 2001), the analysis focused on the left inferior frontal gyrus (LIFG; Brodmann Area, BA, 44/45) and the left posterior superior temporal sulcus (LpSTS; BA 22/39). We further analyzed two additional ROIs: left anterior insula (LaINS; BA 13/14, medially adjacent to IFG) and left Heschl's complex (LHC; BA 41/42, dorsally and anteriorly adjacent to LpSTS). These regions served as control regions, to examine the anatomical specificity of our effects. Finally, right-hemisphere homologues of all these ROIs were also included in the analysis, to examine the degree of lateralization of function in each.

1. This value allowed segregation between distinct neighboring clusters, especially inferior frontal gyrus and anterior insula. High variability among subjects and brain regions disallowed the setting of a fixed threshold for all subjects. We therefore used the minimum number of voxels as a functional index to determine a threshold separately for each region and for each individual subject.

2. Percentage signal change, PSC, was calculated as follows:

$$PSC = 100 \times \frac{\text{signal} - \text{baseline}}{\text{baseline}},$$

where baseline was the mean signal in the two images preceding the experimental block. As the baseline was always measured during the presentation of a filler sentence, negative PSCs show below-filler activation rather than pure inactivation.

The anatomical borders of each region were defined individually on the 3-D reconstructed brain according to the following guidelines:

IFG: the two posterior foldings of the IFG—pars opercularis and pars triangularis;

pSTS: the posterior third of the STS;

aINS: the anterior third of the insula, bordering the IFG;

HC: Heschl's gyrus and sulcus

RESULTS

Our first analysis, motivated by the neuropsychological and neuroimaging literature, focused on Broca's and Wernicke's regions. A significant transformation effect was found in the left pars triangularis, where a higher BOLD signal was detected for +T sentences relative to −T sentences. A cluster of 91 voxels in LIFG (peak activity at Talairach coordinates ($-47, 18, 7$), fixed effects analysis on 11 subjects) passed the threshold ($p < .005$, uncorrected) for the T contrast. At this threshold, only one more significant cluster was found, located at LpSTS (121 voxels, peak activity at Talairach coordinates ($-37, -47, 20$)). Testing for the inverse effect ($-T > +T$) did not reveal significant activation in either region.

A parallel random effects analysis revealed a much smaller transformation effect in LIFG (14 voxels at $p < .05$, uncorrected), and no significant effect in LpSTS. The change in activation may be attributed either to functional intersubject variability (only a small subset of the subjects activating Broca's and Wernicke's regions) or to high intersubject variability in the anatomical boundaries of cytoarchitectonic regions (most subjects activating Broca's and Wernicke's regions but without overlap in Talairach coordinates). Indeed, such anatomical variability was documented with regards to Broca's area (Amunts et al., 1999; Tomaiuolo et al., 1999).

We therefore conducted a second, more conservative type of analysis, by defining ROIs on the basis of an independent functional contrast and looking for inter- and intraregional contrasts in the transformation effect. We used fMRI activation in filler sentences (relative to silent blocks) as a functional marker for task-activated voxels within each anatomical ROI for each subject (see Fig. 2). Only clusters activated by the functional localizer were included in the analysis. Notably, experimental blocks were not included in the localizer contrast, to avoid bias in cluster selection in favor of transformation-activated regions.

Mean Talairach coordinates for the centers of activation of the ROIs in the left and right hemispheres, respectively, were as follows—IFG: ($-45, 23, 7$) and ($47, 23, 6$); pSTS: ($-53, -42, 7$) and ($55, -33, 8$); aINS: ($-31, 24, 6$) and ($34, 23, 8$); and HC: ($-51, -20, 6$) and ($55, -11, 7$).

The results of the ROI analysis showed a robust transformation effect in IFG that was highly lateralized to the left, $F(1, 9) = 8.379, p < .05$, on the left and $F(1, 9) = 0.249, p = .629$, on the right; the Hemisphere \times Transformation interaction was significant, $F(1, 9) = 7.12, p < .05$ (Fig. 3a).

The transformation effect in LIFG remained significant even when analyzed within +G sentences only (Fig. 3b). The hidden-block design enabled separate analyses of the +G and −G sentence blocks. A significant Hemisphere \times Grammaticality \times Transformation interaction, $F(1, 9) = 5.68, p < .05$, resulted from a higher transformation effect in LIFG in grammatical sentences than in ungrammatical sentences.

A main effect of transformation was also found in pSTS bilaterally, $F(1, 10) = 5.168, p < .05$. This effect resulted from higher signal in

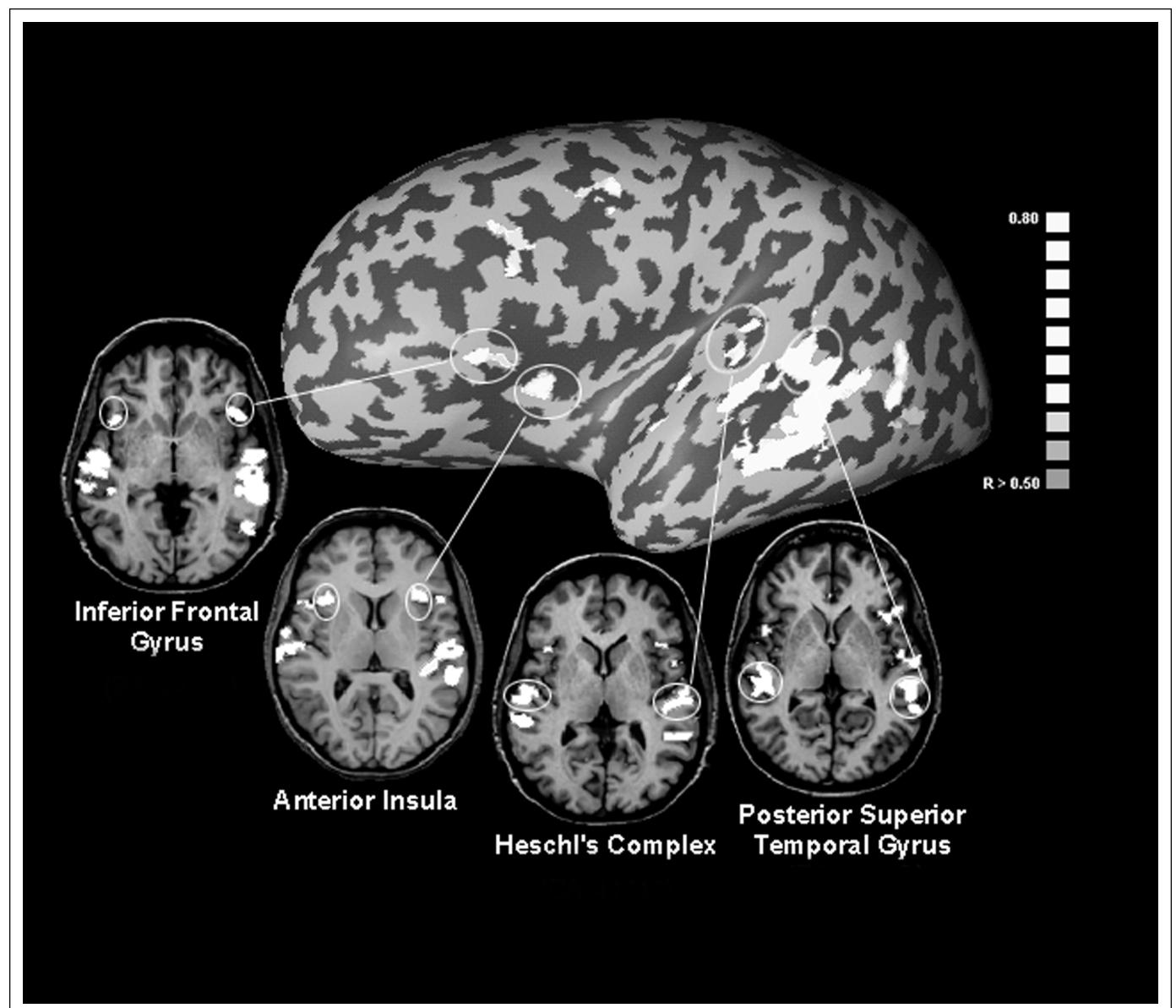


Fig. 2. Location of regions of interest (ROIs), presented on an inflated brain (dark sulci, light gyri). The circled bright regions show functional activation (threshold: $R > .5$) for the localizer contrast: filler sentences versus silent blocks in individual subjects. Average time courses of activated clusters were analyzed in four bilateral ROIs: inferior frontal gyrus, anterior insula, posterior superior temporal sulcus, and Heschl's complex. Note that left temporal activations are shifted posteriorly relative to their right-hemisphere homologues. This shift matches known asymmetries of temporal language areas (Geschwind & Levitsky, 1968).

$+T$ conditions relative to $-T$ conditions (Fig. 3c). No significant Transformation \times Hemisphere interaction was found, $F(1, 10) = 0.001, p = .978$. Although no lateralization was found for the transformation effect in pSTS, an overall left lateralization was observed in this region, manifested as a main effect of hemisphere, $F(1, 10) = 5.335, p < .05$. Although overall performance in the grammaticality judgment task relies more heavily on LpSTS than on right pSTS (RpSTS), transformational analysis activates both sides.

The bilateral transformation effect persisted when the analysis was limited to grammatical ($+G$) sentences, $F(1, 10) = 6.637, p < .05$ (Fig. 3d). However, the effect of confining the analysis to $+G$ sen-

tences alone was different in left and right pSTS: Whereas the effect in LpSTS increased, $F(1, 10) = 8.473$ for the $+G$ analysis and $F(1, 10) = 3.993$ for the $\pm G$ analysis, the effect in RpSTS decreased, $F(1, 10) = 1.235$ for the $+G$ analysis and $F(1, 10) = 4.985$ for the $\pm G$ analysis. This interhemispheric difference caused a significant Hemisphere \times Grammaticality \times Transformation interaction, $F(1, 10) = 7.457, p < .05$, suggesting that the source of the transformation effect in the two pSTS homologues may be different.

To test whether transformations are distinct from other complexity generators, we examined the VC effect in the same regions activated by transformations. We thus compared the activations of conditions b

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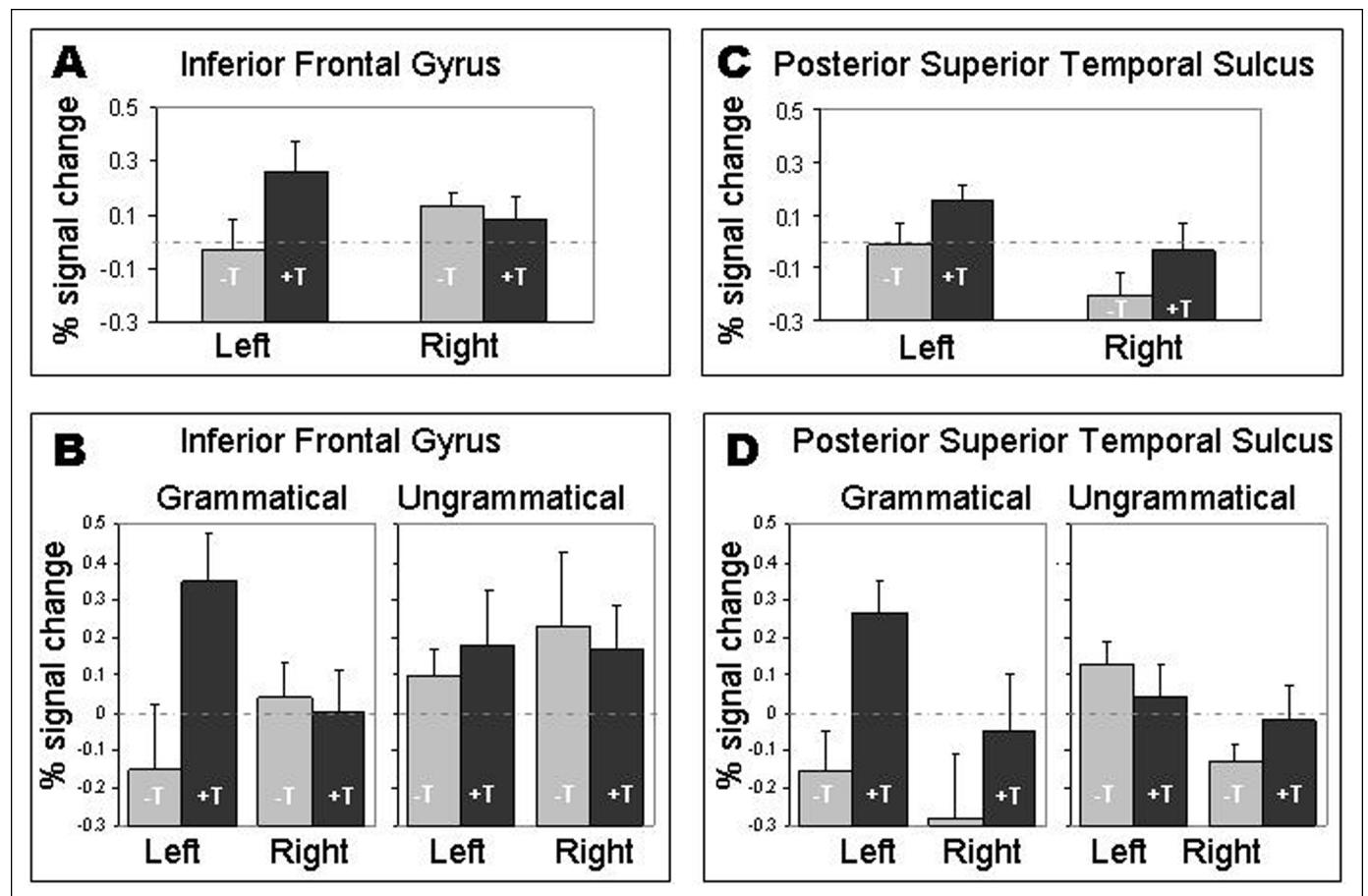


Fig. 3. Intraregional interactions in inferior frontal gyrus (IFG) and posterior superior temporal sulcus (pSTS). The graphs show the mean percentage signal change (PSC) for sentences that contained transformations (+T, dark bars) and sentences that did not contain transformations (-T, light bars). The graphs on the left show results for IFG across grammaticality (a) and separately for grammatical and ungrammatical sentences (b). Error bars represent standard error of the mean, computed for the 10 subjects who showed activation for the localizer contrast in both right and left IFG. The graphs on the right show results for pSTS across grammaticality (c) and separately for grammatical and ungrammatical sentences (d). Error bars represent standard error of the mean, computed for all 11 subjects. The dashed lines mark zero PSC, calculated relative to preceding filler activation (see footnote 2).

and c versus a and d in LIFG, LpSTS, and RpSTS. We found a significant VC effect only in LpSTS, $F(1, 10) = 11.563, p < .001$; this effect was higher than the transformation effect (see Fig. 4).³ In LIFG and in

RpSTS, by contrast, no VC effect was found, $F(1, 9) = 3.009, p = .117$, and $F(1, 10) = 0.569, p = .468$, respectively. These results demonstrate the specificity of the transformation effect.

The anatomical specificity of these effects was further tested by comparing the activation in transformation-sensitive regions with the activation in adjacent regions consistently activated by grammaticality judgment on filler sentences. We found that the transformation effect in IFG was highly localized, showing clear dissociation from the medially adjacent aINS, where no transformation effect was found, in either the left or the right hemisphere. The significant Region \times Hemisphere \times Transformation interaction across IFG and aINS, $F(1, 9) = 14.09, p < .005$, was the result of a significant left-lateralized transformation effect in IFG and no transformation effect in either left or right aINS (Fig. 5a).

No such dissociation was found in posterior regions: In an analysis of the transformation effects in pSTS and HC, no significant interaction involving region was found. Finally, a direct interregional comparison between the transformation effect found in IFG and in pSTS revealed a highly lateralized effect in IFG against a bilateral effect in

3. Effect size was calculated as the difference between the means divided by the standard error of this difference. This measure allows a comparison between transformation effects and VC effects in each ROI. For example, the size of the VC effect in LIFG and in

$$\text{effect size} = \frac{(\bar{B}, \bar{C}) - (\bar{A}, \bar{D})}{\sqrt{\frac{\text{Var}(B, C) + \text{Var}(A, D)}{N}}}$$

As this score is assumed to be t distributed, significance is determined with respect to the critical t with $N - 1$ degrees of freedom ($p < .05$, one-tailed). For simplicity, in Figure 4 we present the more conservative critical t ($df = 9$) in both regions, although a slightly lower threshold holds for pSTS (activated by all 11 subjects). Standard error of the effect size was estimated using Tukey's jackknife method (Sokal & Rohlf, 1981, chap. 18), which calculates the score on every subgroup of size $N - 1$ of the sample, and then uses the variability among these values to estimate the standard error of the statistic.

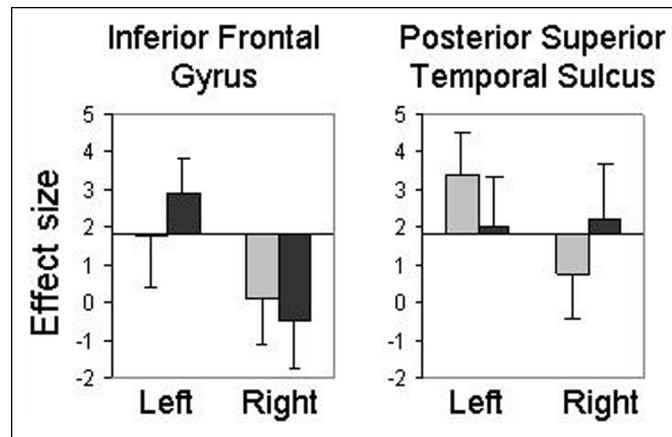


Fig. 4. Comparison of the effect size for transformations (dark bars) versus verb complexity (light bars) in the left and right inferior frontal gyrus and posterior superior temporal sulcus. The x -axis crosses the y -axis at the critical t value ($p < .05$; $df = 9$ for both regions of interest). Upward bars represent significant effect sizes; downward bars represent nonsignificant effect sizes. Error bars were calculated as jackknife estimation of the standard error of effect sizes (see footnote 3 for the computation of effect sizes and their standard errors).

pSTS: A clear difference in the pattern of the transformation effect in these two language areas was manifest as a significant Region \times Hemisphere \times Transformation interaction, $F(1, 9) = 7.97$, $p < .05$, resulting from a left-lateralized transformation effect in IFG and a bilateral transformation effect in pSTS (Fig. 5b).

DISCUSSION

The results show transformation-related activation in Broca's region (LIFG), as well as in bilateral pSTS. Of these regions, only LpSTS was activated by verb complexity. In both LIFG and LpSTS, the transformation effect increased when ungrammatical sentences were excluded from analysis, suggesting that the effect reflects natural processing, rather than violation detection that ungrammatical sentences may have triggered. Finally, the anatomical specificity of the transformation effect in LIFG was demonstrated as an interregional interaction in an analysis including the neighboring LIFG and LaINS.

The results are important because they constitute the first clear-cut imaging evidence for the neural reality of syntactic transformations: The neural activity evoked by transformational analysis sets this process apart from other putative sources of computational complexity during sentence perception. Moreover, the results begin to depict the relationship between transformational operations and the anatomical basis of certain lexical entries. Transformational analysis—an abstract theoretical concept—is region-specific, and dissociable from other sources of linguistic complexity such as the argument structure of verbs. This finding not only confirms classical linguistic claims regarding the distinctness of transformational rules, but also provides fine-grained anatomical information regarding their localization in the brain, which has thus far been based on results concerning the difficulties Broca's aphasics have in comprehending transformationally derived sentences (Grodzinsky, 2000; see also Roeder, Stock, Neville, Bien, & Roesler, 2002, for recent converging imaging results from a

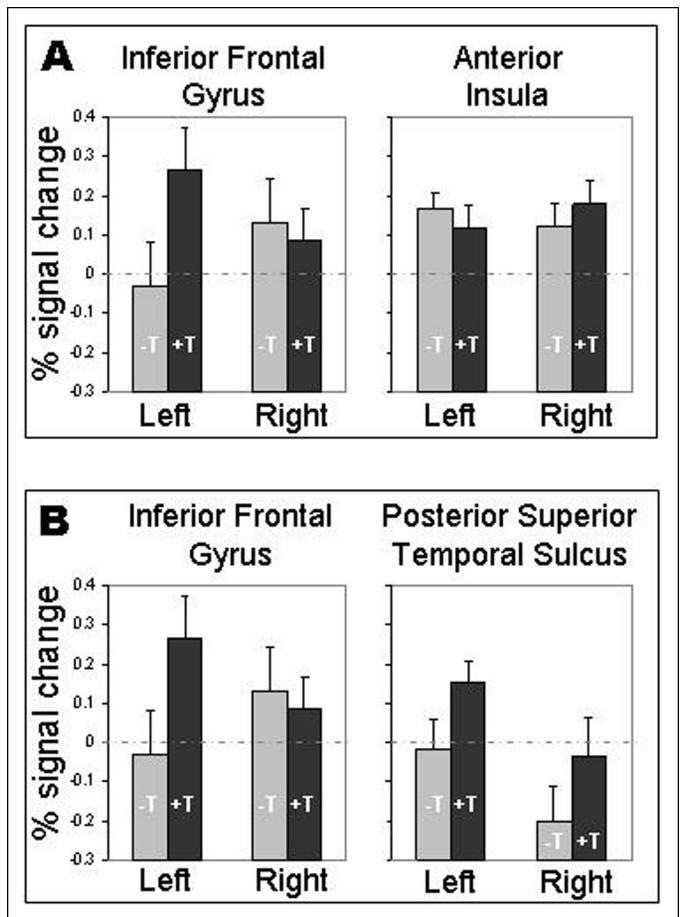


Fig. 5. Interregional interactions in the transformation effect. The graphs show the mean percentage signal change (PSC) for sentences that contained transformations (+T, dark bars) and sentences that did not contain transformations (-T, light bars), across grammaticality. Results for inferior frontal gyrus (IFG) and anterior insula (aINS) are compared in (a). Results for IFG and posterior superior temporal sulcus (pSTS) are compared in (b). Error bars represent standard error of the mean, computed in each panel for the 10 subjects who showed activation for the localizer contrast in both regions. The dashed lines mark zero PSC, calculated relative to preceding filler activation (see footnote 2).

set of very different structures in German). The high-resolution capacity of fMRI separates LIFG from its medially adjacent neighbor—aINS, usually included in Broca's region (Mohr, 1976). Although both regions were activated by the task, only LIFG was engaged in processing transformations.

Finally, our study provides some clues regarding syntactic analysis in the posterior language regions—Wernicke's area and its vicinity. The functional picture for these regions has thus far been blurred, with results from both lesion studies (Caplan, Baker, & Dehaut, 1985; Grodzinsky & Finkel, 1998; Zurif et al., 1993) and neuroimaging studies (Caplan, 2001; Just et al., 1996) being mixed. Juxtaposing three sets of findings may clarify the picture to some extent: First, transformations lead to bilateral activation in pSTS. Second, verb complexity activates only the LpSTS (a result consistent with lesion

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data: Wernicke's aphasics' performance on complex verbs is markedly different from the performance of healthy subjects, e.g., Shapiro et al., 1993). Third, bilateral activation in Wernicke's region grows when the distance between the positions linked by transformation is increased (Caplan et al., 2002; Cooke et al., 2002). Thus, linking between distant positions may be performed bilaterally in pSTS; if so, such processing contrasts with two lateralized processes: structural analysis of sentences containing syntactic movement, which may take place in LIFG, and access to predicate argument structure (Stowe, Tanenhaus, & Carlson, 1991), which occurs in LpSTS.

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