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Network dynamics of memory operations in language processing

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Abstract (244words < 250)

The order of words in a sentence often convey important information to determine its meaning. All word order variations are thought to be derived from base order sentences by application of a word displacement operation called movement, a key concept in generative grammar. The moved word (filler) leaves a silent copy at the extracted position (gap), and the filler is reactivated when the hearer passes over the gap. Consequently, memory operations are supposed in the processing of sentences with movement to establish the filler-gap link. For languages that allow relatively free ordering of words unlike English, a theoretically distinct linguistic operation called scrambling is proposed. In addition to the theoretical differentiation, the two operations were reported to activate distinct brain regions. Thus, free-word phenomena in some languages have challenged the theoretical universality of movement. To clarify whether scrambling is an instance of movement, we designed a functional magnetic resonance imaging study, in which we compared the effect of the memory load parameterized by the filler-gap distance in the two constructions. Here we show that the processing of sentences constructed by the two linguistic operations rely commonly on the inferior frontal gyrus and middle superior temporal sulcus in the left hemisphere. Furthermore, dynamic causal modeling analyses revealed that the memory load increases the interaction between the pars opercularis and inferior frontal sulcus. These results suggest that the same neural mechanism supports the memory operation necessary for the processing of sentences constructed by movement and scrambling.

Introduction (477 < 500)

The displacement of constituents in a sentence, or syntactic movement, is a key linguistic concept that accounts how variations of word order are generated from the base orders. On this view, the members of the question-answer pair <*Which student did John see* ◄, *John saw the chemistry student*> are related by a formal order-changing operation that derives the former from the latter, whose word-order is considered more basic. The underlined question expression (the moved "antecedent", or "filler") is related to its base post-verbal position (◄, *a k a* "trace" or "gap") by a formally established link (Chomsky 1981; Chomsky 1995). The establishment of the filler-gap link has been shown as a real psychological process. The moved word (a filler) is reactivated at the gap as the sentence is processed, as demonstrated by a priming effect at the gap position (Tanenhaus et al., 1985; Clifton and Frazier, 1988; McElree and Bever, 1989). Early imaging work roughly localized movement in Broca's region (Stromwold et al., 1996; Ben Shachar et al., 2003). Later, more refined studies focused on left pars triangularis (Brodmann Area (BA) 45) (Friederici et al., 2006a; Santi and Grodzinsky, 2007, 2010).

Movement is considered a universal syntactic operation that occurs by necessities and causes a change in the meaning. Therefore, it is not clear that it covers certain alternations in languages with relatively free word order such as German or Japanese. Members of the German pair <*Der Mann zeigte dem Kind den Onkel*, *Der Mann zeigte den Onkel dem Kind* ◄ – the man showed the child to the uncle> have a similar meaning, even though they differ in the order of the objects. Dubbed Scrambling (Ross, 1967), the similarity between this relation and Movement has been a subject of controversy among linguists (Fanselow, 1990; Müller and Sternefeld, 1993; Fanselow, 2001), even though psycholinguistic results are similar to the English ones (Clahsen and Featherston, 1999; Nakano et al., 2002). Imaging results suggest that the supporting neural mechanisms for scrambling may differ from those of movement (Friederici, Schlesewsky et al. 2000), and it activats the pars opercularis (BA 44)(Friederici, Fiebach et al. 2006). These divergent results may merely be due to cross-linguistic differences; alternatively, Movement and Scrambling may truly be different formal operations. Carefully controlled experiments using a single language are therefore needed, in order to clarify the issue. German has both.

The present functional magnetic resonance imaging (fMRI) study examined neural correlates for the processing of German sentences constructed by scrambling and movement. To overcome problems that arise when very different structures are compared directly, we parameterized memory load by nesting a distance parameter in each construction, that equally increased the number of noun phrases that intervened between the filler and the gap. This resulted in a within-subject 2 x 3 factorial design, with factors TYPE (Scrambling/Movement) and DISTANCE (3 levels of memory load), with 240 base order and derived sentences (Fig 1). Any significant interactions would indicate a difference in the neural bases for the two sentence types.

Methods

Participants

Twenty-two young, right-handed, healthy subjects were examined (eleven females). Handedness was assessed with the Edinburgh Inventory (Oldfield, 1971) (mean 93.9, range 80 - 100). The mean age was 25.0 years old and the range was 20 - 33 years old. All of the participants were native German speakers. Reading span was measured by a German version of the Daneman and Carpenter reading span test (Daneman and Carpenter, 1980) (mean 4.0, range 3 – 5.5). All had no history of neurological disorders. The experimental procedures were approved by the Research Ethics Committees of the University of Leipzig. Written informed consent was given by all subjects.

Experimental design

Stimuli

Our goal was to investigate the relationship between Movement (MOV) and Scrambling (SCR). Sentences (all in German) were divided accordingly into 2 conditions. In both instances, an displaced filler may or may not be separated from its gap by one or more NP interveners. Exploiting this fact, we introduced a 3-valued DISTANCE parameter, which was nested within each condition. DISTANCE took the value of the number of NPs that intervened in the linear sequence between the filler and its gap (Fig. 1).

The 3 levels of the MOV condition were created as follows: at the "base" were sentences that can be described schematically as "*I think that* NP_{NOM} *V* NP_{DAT} NP_{ACC} *Temporal Adverb*" (where NP_{NOM}, NP_{DAT} *and* NP_{ACC} denote noun phrases with case marked definite articles for nominative, dative, and accusative), e.g.:

(1) *Ich glaube, der Mann zeigte dem Kind den Onkel gestern abend*
I think, the_{NOM} man showed the_{DAT} boy the_{ACC} uncle yesterday night

Sentences for all 3 levels of Movement were derived from the base form by applying Movement to one of the 3 noun phrases, which moved it to the sentence-initial position, with the result of there being 0, 1 or 2 NP interveners between the filler and its gap (levels M0, M1, M2, respectively, Fig. 1, top). The execution of this operation had several consequences: a. the moved (or topicalized) NP became the focus of the sentence, which forced the definite article (*der/dem/den*) to become a demonstrative (*dieser/diesem/diesen* = $this_{CASE}$), similar to English (cf. *this man, I think, presented the uncle to the boy*). b. Movement left a trace behind. c. the main verb *glaube* was forced into the second position in the sentence (a specific rule of German).

In the Scrambling condition (SCR), that featured a syntactic rule that does not manifest in English, the displacement operation was similarly applied, and 3 levels – S0, S1, and S2 – were also created, with 0,1, and 2 intervener NPs, respectively. The base form (which was S0 here) was similar to the base of MOV, except the position of the temporal adverb, which was sentence-initial (Fig. 1, bottom):

(2) *Gestern abend glaube ich, dieser Mann zeigte dem Kind den Onkel*
yesterday night think I, this$_{NOM}$ man showed the$_{DAT}$ boy the$_{ACC}$ uncle

Note that the leftmost NP is focused, and appears with a demonstrative. Note also that SCR leaves a trace, and that the verb is in second position, similar to MOV.

In both MOV and SCR, all nouns were masculine and animate, and were case marked unambiguously (i.e., *der*, *dem*, and *den*, for nominative, dative, and accusative respectively). All verbs (V) were ditransitive, obligatorily taking 2 objects, which were all human (*beschreiben* = describe; *empfehlen* = recommend; *nennen* = name; *vermitteln* = mediate; *zeigen* = show). The temporal adverbs were *heute/gestern/morgen/mittag/abend* (today/yesterday morning/noon/evening)".

In sum, the experiment comprised of six conditions derived from a 2 x 3 factorial design with factors TYPE (scrambling/movement) and DISTANCE (0/1/2 NPs between the filler and the trace).

Stimuli presentation

The stimuli presentation was programmed with Presentation 10.3 software (Neurobehavioral Systems, Inc., Albany, California, USA) on a Windows PC. Stimuli were projected through an LCD projector (PLC-XP50L, SANYO, Tokyo, Japan) onto the back of a screen. Subjects viewed the images on the screen above their heads through a mirror attached to the head-coil.

Procedure

Several days or weeks before, the candidate participants performed the same task in the laboratory. We recruited participants who performed with mean accuracy of more than 75 % for the fMRI experiment. An event-related design was adopted and the sentences of the six conditions were presented in a pseudo-random order. In a trial, a sentence was visually presented word by word with a duration of 500 ms and inter-word-interval of 100 ms, so that one sentence was presented with 9 frames in 5.3 s. Fixed expression of the matrix subject and verb "glaube ich" (I think) and temporal adverbial such as "*gestern abend*" (yesterday morning) were presented in one frame (e.g., a sentence was segmented as "*Gestern abend*,| *glaube ich*,| *zeigte*| *dieser* |*Mann*| *den*| *Onkel* | *dem* | *Kind*."). The beginnings of the presentation of the first word/phrase were jittered against the scanning with 0 and 800 ms. Mean sentence onset asynchrony was 11.2 s. Forty distinct sentences per condition were presented, resulting in a total of 240 trials which were performed in one session that lasted approximately 45 minutes. In 20 % of the trials, short probe sentences to test the participants' comprehension followed 100 ms after the end of the final word of the sentence and remained on the screen for 3 s. Half of the probe sentences restated part of the content of the sentence presented previously. The probes were constructed with the subject, the verb (V), and the object of the correct combination, namely either NP_{NOM} V NP_{DAT} or NP_{NOM} V NP_{ACC}. The other half was similarly made with a subject, the verb, and an object, but did not match the sentence previously given. For example, we swapped the case marking from dative to accusative, or vice versa. Alternatively, one of the objects was presented as the subject. The probes were given in a pseudo-random manner to ensure that they processed all of the sentences presented. The participants were requested to judge whether the probe sentence expressed the same content or not and to report it as soon as possible by pressing MRI-compatible response buttons using the index and the middle finger of the right hand.

Image acquisition

Functional MRI data were acquired with a whole-body 3 Tesla Magnetom TRIO operating at 3 T (Siemens Medical Solution, Erlangen, Germany) with a gradient-echo EPI sequence. The brain was covered with 2.5 mm thick 24 axial images with 0.5 mm gaps (TR = 1.6 s, TE = 30 ms, Flip angle = 90°, FOV = 19.2 x 19.2 cm^2, 64 x 64 matrix). The resulting voxel size was 3 x 3 x 3 mm^3. The slices were aligned to the AC-PC plane and placed to cover the whole Broca's and Wernicke's area. The same slices were scanned with a T1-weighted MDEFT sequence (TR = 1300 ms, TE = 7.4 ms, 256 x 256 matrix) for the spatial coregistration of EPI images to high-resolution anatomical images. The subjects had one session of fMRI scanning with 1682 volumes per session in about 45 min. Structural high-resolution images of the participants were also collected on a different day with a three-dimensional MDEFT sequence (TR = 1300 ms, TE = 3.93 ms, TI = 650 ms, Flip angle = 10°, FOV = 25.6 x 24 cm^2, 256 x 240 matrix, sagittal 128 slices, 1 mm thick, 2 NEX). A stabilization cushion was laid under and to the sides of the head to reduce head motion.

Analysis

Behavioral data

Mean reaction times (RTs) and accuracy rates were calculated for each condition of each subject and were analyzed using a two-way within-subject ANOVAs with factors

TYPE and DISTANCE.

Imaging data

Preprocessing of structural and functional MRI data

The first five volumes of each fMRI session were discarded to eliminate magnetic saturation effects, and a total of 1682 volumes per session were used. The data analysis was carried out using SPM8 (available at http://www.fil.ion.ucl.ac.uk/spm/) on Linux PC workstations. Structural images were corregisterd to individuals' T1 and functional images and normalized using the DARTEL procedure (Ashburner, 2007), in which individual structural images are segmented into gray and white matter, and mean images of all individual's images serve as templates. The DARTEL normalization proceeds in 6 steps with increasing spatial resolution with the final step for the linear transformation into MNI space. For functional data preprocessing, EPI images were realigned to the first image and resliced with correction for geometrical warping using a deformation field map scan. Subsequently, the difference in the slice acquisition time was corrected and the all volumes were resliced again. The first-level statistics were computed with the not-normalized and not-smoothed images, and the resulting statistical images were normalized using the DARTEL parameters with voxel resampling at 3 x 3 x 3 mm^3 and smoothing of 8 mm FWHM and fed into the second-level ANOVA. We also normalized individual structural and functional data using the individual structural images normalized by DARTEL as the target images. Using these data, the first level statistics (SPM{F}) were computed in order to exploit in the extraction of the volume of interest (VOI) time series data for dynamic causal model (DCM) analysis.

Within-subject ANOVA

Each subject's haemodynamic responses induced by the trials were modeled with a box-car function with the duration of 5.3 s for sentence and 3.0 s for probe short sentence (comprehension task) and convolved with a haemodynamic function that reaches the peak 6.0 s after the stimuli onset. The global mean intensity of each session was normalized to 100. Confounds by global signal changes were removed by applying a high pass filter with a cut-off cycle of 128 s. Signal increase relative to the baseline in each condition of each participant was estimated according to the general linear model. The resulting individual contrast images were normalized using the DARTEL parameters, smoothed with 6 mm HWFM Gaussian kernel, and submitted to the second level (group) analysis, a 2 x 3 within subject ANOVA with factors TYPE (SCR/MOV) and DISTANCE(3 levels) with correction for nonsphericity. Main effects were tested with t tests since we were interested in a positive linear effect by DISTANCE. The interactions were examined with an F test. Statistical inferences were drawn at $p < 0.05$ at cluster level: the statistical maps (SPM{T/F}) were thresholded at $p < 0.01$ (not corrected) for intensity, and then thresholded by the cluster size (50 contiguous voxels).

Trial time course plot and its correlation with accuracy

To inspect the main effects in detail, trial time courses of the activated foci were plotted. First, the volumes of interest (VOI) were defined as 6-mm radius spheres with the individual local maxima nearest to the group maxima for the pars opercularis (PO), inferior frontal sulcus (IFS), and middle superior temporal sulcus (mSTS) for the linear effect of DISTANCE, and inferior and superior occipital gyri (IOG and SOG) for the main effect of TYPE (see Table 2). Second, time series data were extracted as eigenvariates (without adjustment) and the trial time courses were estimated for each participant's preprocessed time series data. In practice, the trial time courses for each condition were modeled with 21 variables representing the BOLD signal every 0.8 s from 0 to 16.0 sec and the simultaneous equation was solved against the time series data of VOIs under the assumption for the linear time invariant system. Paired t-tests were carried out (S1>S0, S2>S1, S2>S0, M1>M0, M2>M1, M2>M0) on the BOLD signal between conditions on each time point.

To examine which regions are associated with the performance, correlation coefficients between the BOLD signal intensity and accuracy across the participants were calculated in each VOI in each time point along the trial time course. For this analysis, we estimated trial time courses in the PO, IFS, mSTS, FG, IOG, SOG and other activated foci namely, the right pars opercularis (RPO), inferior parietal sulcus (IPS), right inferior parietal sulcus (RIPS), precuneus (Prec) (see Table 2) using the same procedure described above. Since we observed significant difference in accuracy only in the SCR condition, we applied this analysis to the SCR conditions. Mean time courses of the three level of DISTANCE were used for the calculation of the correlation coefficients.

Dynamic causal modeling analysis

To understand the dynamic causal relation between the activated regions revealed as the main effect of DISTANCE in the ANOVA, we performed the dynamic causal model (DCM) analysis. Four VOIs, IFS, PO, mSTS, and FG in the left hemisphere were selected to construct DCMs (Fig 5). First, we reanalyzed the functional data with new design matrices that explicitly encode the input and the two modulatory effects, to follow the framework of the DCM analysis. In this analysis, the experimental events were regrouped into the input (all sentences that were not followed by the probe sentence were encoded with 1 and the others were 0), the modulatory effect by DISTANCE (S1, S2, M1, and M2 were encoded with 1 and S0 and M0 were with 0), and the modulatory effect by TYPE (SCR 1 and MOV 0). The sentences with probe were modeled as a distinct condition to avoid complication in estimation of BOLD signal for sentence segregated from the probe, and six motion parameters were also modeled as covariates of no interest in the design matrices. The 'effect of interest' contrast was calculated as the F contrast (SPM{F}) of the input and the two modulatory effects. Then, the individual local maxima were picked up in IFS, PO, STS, and FG in the left hemisphere from individual SPM{F}s as the closest individual maxima to the group maxima (Fig 5). The spherical VOIs of a 6 mm radius were created with the individual local maxima as the centers. SPM{F}s were thresholded with $p < 0.05$ without correction and the VOI time series data were extracted as eigenvariates (the first principal component) of the supra-threshold voxels' time series data in the spherical VOI. The VOI time series were adjusted for the effect of interest; the contributions from the sentence with probe condition and the motion parameters were subtracted from the time series data.

The rational to select these four VOIs are as follows. Since the sentences were given visually, we reasoned that the FG receives the external input that drives the system. The FG VOI was selected to hit the visual word form area (Cohen et al., 2000; Cohen et al., 2002) on the basis of the activation coordinates reported in a metaanalysis study ($x = -44 \pm 4$, $y = -58 \pm 5$, $z = -15 \pm 6$) (Jobard et al., 2003). Although the ANOVA did not reveal FG activation for the main effects or interaction, the SPM{F} for the effect of interest in individual analysis with the new model for DCM detected consistent activation in this region. In the left inferior frontal gyrus cluster, we defined two distinct VOIs namely the PO and IFS. The reason for taking two VOIs was twofold: 1) a previous study (Makuuchi et al., 2009) indicated that the PO and the IFS are functionally dissociable in the processing of sentences with syntactically complex structures and 2) that the most significant focus was located in the IFS and the second one was found in (the lateral aspect of) the PO (Table 2). The mSTS is included in the model as it was revealed by the ANOVA and it has been shown to be anatomically and functionally connected to the left inferior frontal gyrus as a part of the language network (Friederici et al., 2006b; Lohmann et al., 2009).

A total of seven DCMs were constructed, estimated, and compared (Fig 5). In all models, the connections IFS-PO, PO-STS, IFS-STS were supposed to exist. All connections were modeled as bidirectional (i.e., IFS-PO means IFS→PO and PO→IFS), and modulation by the factors DISTANCE and TYPE was allowed on all connections except recursive ones. The first model was the full connection (six connections) model. The second to fourth models were five connection models, which lacked IFS-FG, PO-FG, and STS-FG connections respectively. The fifth to seventh models were 4 connection models. In these models, the connection from/to FG was either to/from one of the three regions. One subject was excluded from the DCM analysis because this subject showed activation in not all four VOIs at the given threshold ($p < 0.05$ not corrected). Therefore, twenty subjects' DCM results were submitted into the Bayesian model comparison. The DCM estimates of connection strengths of the winning model were evaluated by one-sample t-tests with statistical threshold corrected by the false discovery rate at $q < 0.05$ (Benjamini and Hochberg, 1995).

Results

Behavioral results

Accuracy and reaction times (RT) to the probe sentence are summarized in the Table 1. One subject, who performed at 50 % (chance level) on S2, M1, and M2 conditions, was excluded from the behavioral and fMRI analyses. A 2 x 3 within subject ANOVA with factors TYPE (SCR/MOV) and DISTANCE (3 levels) were performed on accuracy and RT. For accuracy, interaction was significant ($F(2, 40) = 5.06$ ($p<0.05$)). An analysis of simple main effect revealed a significant effect of TYPE at DISTANCE 2 ($F(1, 20) = 14.01$ ($p < 0.01$)) and a significant effect of DISTANCE at SCR, $F(2, 40) = 11.47$ ($p<0.01$). These results indicate that S2 is significantly more difficult than the other conditions. The RT did not show any significant main effect or interaction. Correlation coefficient between accuracy and RT were -0.26.

Imaging results

A 2 x 3 within subject ANOVA with factors TYPE (SCR/MOV) and DISTANCE (3 levels) were performed on the fMRI data. Firstly, no significant interaction was found. Secondly, the main effect of TYPE (as t contrast) was only found in the bilateral occipital regions, including inferior and superior occipital gyri (IOG and SOG) (Fig 2, 3 and Table 2). Crucially, the main effect of DISTANCE (as a t contrast for S/M0<S/M1<S/M2) involves the left inferior frontal gyrus (IFG) involving the pars opercularis (PO, BA 44) and posterior portion of pars triangularis (BA 45) and extends to the left inferior frontal sulcus (IFS). Moreover, activation was found in the middle superior temporal sulcus (mSTS) in the left temporal cortex, as well as the left globus pallidus, the right pars opercularis (RPO) and the bilateral intraparietal sulci (IPS/RIPS). Although the activation is identified as the main effect of DISTANCE for both sentences types, a parametric increase of activation with the level of DISTANCE is found only for the SCR conditions (Fig. 3). For MOV conditions no significant difference was found between M1 and M2 in PO and IFS. In the mSTS, all three levels showed a similar activation (Fig. 3). The trial time course plots for the occipital activation in the superior occipital gyrus (SOG) and the inferior occipital gyrus IOG reflect the difference in the TYPE of the sentences. Of note are the two peaks of the trial time course plots of the occipital activation for the MOV conditions (Fig. 3).

Since the accuracy of the probe judgment was significantly lower in the S2 condition compared to the other conditions, we explored which regions are sensitive to the individual difference in accuracy in the SCR conditions. By plotting correlations between the mean trial time courses of three SCR conditions (i.e., S0, S1, and S2) and mean accuracy, we found that the bilateral PO show higher correlation with the accuracy (Fig 4). The correlation plot of the PO shows most positive correlation at 6 s and most negative at 10 s, which indicates the leftward horizontal shift of the TTC plot for high performers. The RPO has peak at 8 s but lacks highly negative correlation in the later period, indicating the BOLD signal peak height increase in high performers but not the temporal shift of the TTC.

DCM results

The Bayesian model comparison revealed that the model 1, which is a full connection model, is the best among seven models (Fig 5). The model expected probabilities of the winning model were 0.252, while those for the rest were 0.124, 0.124 0.125, 0.125, 0.126, and 0.125. The model exceedance probabilities of the winning model were 0.378, while those of the other 6 models were 0.102, 0.103, 0.104, 0.104, 0.106, and 0.103. One sample t tests were performed on the connection strength estimates. The significant (FDR correction $q < 0.05$) intrinsic connections and modulatory effects are as shown in the Fig 5 and Table 3.

Discussion (1278 <1500)

Main results

The present 2 x 3 factorial design fMRI study compares the neural activities caused by the memory operation at the three levels (factor DISTANCE) in the movement and scrambling constructions (factor TYPE). The ANOVA revealed a main effect of DISTANCE in the left inferior frontal gyrus (IFG) encompassing the pars opercularis (PO), posterior portion of pars triangularis (PTr), and inferior frontal sulcus (IFS), and the middle temporal sulcus (mSTS). A main effect of TYPE is found in the inferior and superior occipital gyri (IOG and SOG) predominantly in the left hemisphere. Crucially, an interaction is not significant. Hence, these results suggest that the brain network for the processing of scrambling constructions is similar to that of movement construction when one focuses on the operation of the memory defined by the filler-gap distance (Tanenhaus et al., 1985; Clifton and Frazier, 1988; McElree and Bever, 1989; Clahsen and Featherston, 1999; Nakano et al., 2002). By comparing the two constructions within a single language, the present study dissolve the previous dichotomy that movement activates the PTr in English (Santi and Grodzinsky, 2007, 2010), while scrambling does the PO in German (Friederici et al., 2006a). We conclude that the two constructions require both the PO and PTr for the processing of the filler-gap dependency. With respect to the linguistic question about the relation between the two constructions, the present study supports the position that views scrambling as an instance of movement (Fanselow, 1990; Müller and Sternefeld, 1993; Fanselow, 2001).

The language network dynamics by memory load

In the previous study, we found that the processing of syntactically more complex hierarchical structures activates the left PO, while concomitant increased verbal working memory processes activates the left IFS (Makuuchi et al., 2009). The functional connectivity between the two regions (revealed by psycho-physiological interaction (PPI) analysis) increases when the sentence is syntactically complicated and at the same time the distance between obligatory dependent pairs is elongated. Using DCM, another analysis to detect the change in the effective connectivity, the present study replicates the increased interaction between the PO and IFS when the sentence taxes more memory load by the longer distance between the linguistically dependent pairs. The intrinsic connection pattern indicates that the PO receives input from the FG and sends outputs to the IFS and mSTS, suggesting that the PO plays a role as the hub of the network. The centrality of the PO in the sentence processing is demonstrated also by the direct association between the sentence comprehension accuracy and the neural activity in the area (Fig 4). The plot for the left PO indicates that the higher performer's BOLD responses start and end earlier than the lower performers'. This means that earlier PO activation is linked to more correct processing of the sentences. Taking these findings together, the present study corroborates the view that the left PO is a locus for syntactic computations in the neural language network (Friederici et al., 2006b; Friederici et al., 2006a; Makuuchi et al., 2009), and the PO interacts with other regions including the IFS (Makuuchi et al., 2009) that supports memory that is additionally needed in the processing of sentences of longer distance between dependent pairs or of complicated structures.

Difference between the processing of movement and scrambling constructions

A closer look of trial time course plots (Fig 3) allows one to describe that the activation in the left PO increased systematically as a function of the number of intervening noun phrases (NPs) between the filler and the gap for scrambling sentences, whereas the difference between the two non-base order sentences (M1 and M2) was squeezed in the movement conditions (Fig 3). The former finding replicates the results previously reported for reading scrambled German sentences (Friederici et al., 2006a). On the other hand, the latter is a novel observation. In the movement construction, one case-marked NP moves out from the clause to the sentence initial position, which is a special position that makes the constituent salient. Indeed, topicalization can be viewed as emphasizing a constituent by moving it to such a special position. The sentence initial position is advantageous in terms of verbal short term memory for a sequence: the short term memory for a sequence is most robust for the items given at the start and the end positions, but deteriorated at the middle positions (Henson, 1999). From this perspective, topicalization construction is an efficient way to impress the NP at the sentence initial position for better encoding and processing. Intensive encoding of a filler may establish a robust link to the gap regardless of the direct or indirect object NP, thereby reducing the difference in the processing cost between M2 and M1. In contrast, scrambling in the present study moves the constituent into the middle of the sentence (Fig 1), which is an unfavorable region to put an important item in terms of short term memory encoding. This positional difficulty will make the processing of filler-gap dependency more prone to the interveners in S2 than in S1 conditions, resulting in the parametric activation increase with the distance.

Topicalization has another vital cognitive aspect, which may have impact on the processing. That is the syntactic predictability of the sentence structure. The object (i.e., non-subject) NP at the sentence initial position signals a movement construction, allowing to predict the gap in the forthcoming sequence and to prepare for the processing of the filler-gap dependency. In other words, the brain keeps the filler 'active' until the gap appears (Clifton and Frazier, 1989; Frazier and Flores D'Arcais, 1989). We speculate that the prediction of the forthcoming gap drives visual attention, which activates the occipital regions (Fig 2B). This syntactic prediction will facilitate the filler-gap processing. On the other hand, a temporal adverbial is topicalized and raised to the sentence initial position in the scrambling constructions. Since the temporal information is orthogonal to the task (i.e., thematic role assignment), the topicalized construction is not helpful for the task execution.

Other regions

The middle superior temporal sulcus (mSTS) also revealed a significant main effect of DISTANCE, suggesting this region is a constituent of the sentence processing network, as documented in other studies for the processing of movement (Ben-Shachar et al., 2003; Fiebach et al., 2005; Santi and Grodzinsky, 2010) and scrambling (Roder et al., 2002; Kinno et al., 2008). Notably, these mSTS activations are always accompanied by the left IFG activation.

The bilateral intraparietal sulcus (IPS) activation is revealed by the main effect of DISTANCE. Since this region is not activated in the previous scrambling and movement studies, we interpret this activation may reflect memory processes which are requested specifically by the current task, rather than by the syntactic processing of the sentence per se. One interpretation is phonological working memory (Jonides et al., 1998). It is plausible that the on-line processing of the sentence cannot follow the rate at which words are coming because of processing delay due to the complexity of the structure, thereby driving a temporal storage of the sentence in phonological form. Alternative interpretation of the function of this region is episodic memory retrieval (Rugg et al., 2002; Wagner et al., 2005; Cabeza et al., 2008). The task requires a judgment of whether the probe sentence correctly depicts the agent and recipient of the action (i.e., thematic roles), orienting the participants to remember and to recall all persons in the sentence with their appropriate thematic roles. Since the sentences always involve three persons who lack any implications for their relations (e.g., a policeman and a thief), the grasping as well as the remembering of the thematic roles are demanding. The unique association of each person with their thematic may urge the participants to form an episodic memory. The precuneus activation is also suggestive of episodic memory retrieval (Wagner et al., 2005).

Tables

Table 1 Accuracy and RT of the probe sentence judgment

	S0	S1	S2	M0	M1	M2
Accuracy (%)	90.8 (SD 9.96)	91.5 (10.0)	77.2 (17.9)	94.5 (9.53)	92.8 (10.2)	90.9 (11.4)
RT (ms)	2173 (320)	2060 (382)	2044 (403)	2021 (341)	2051 (404)	2051 (412)

The results are of 21 subjects. One participant is excluded because of the low performances.

Table 2 Activation revealed by the within subject ANOVA

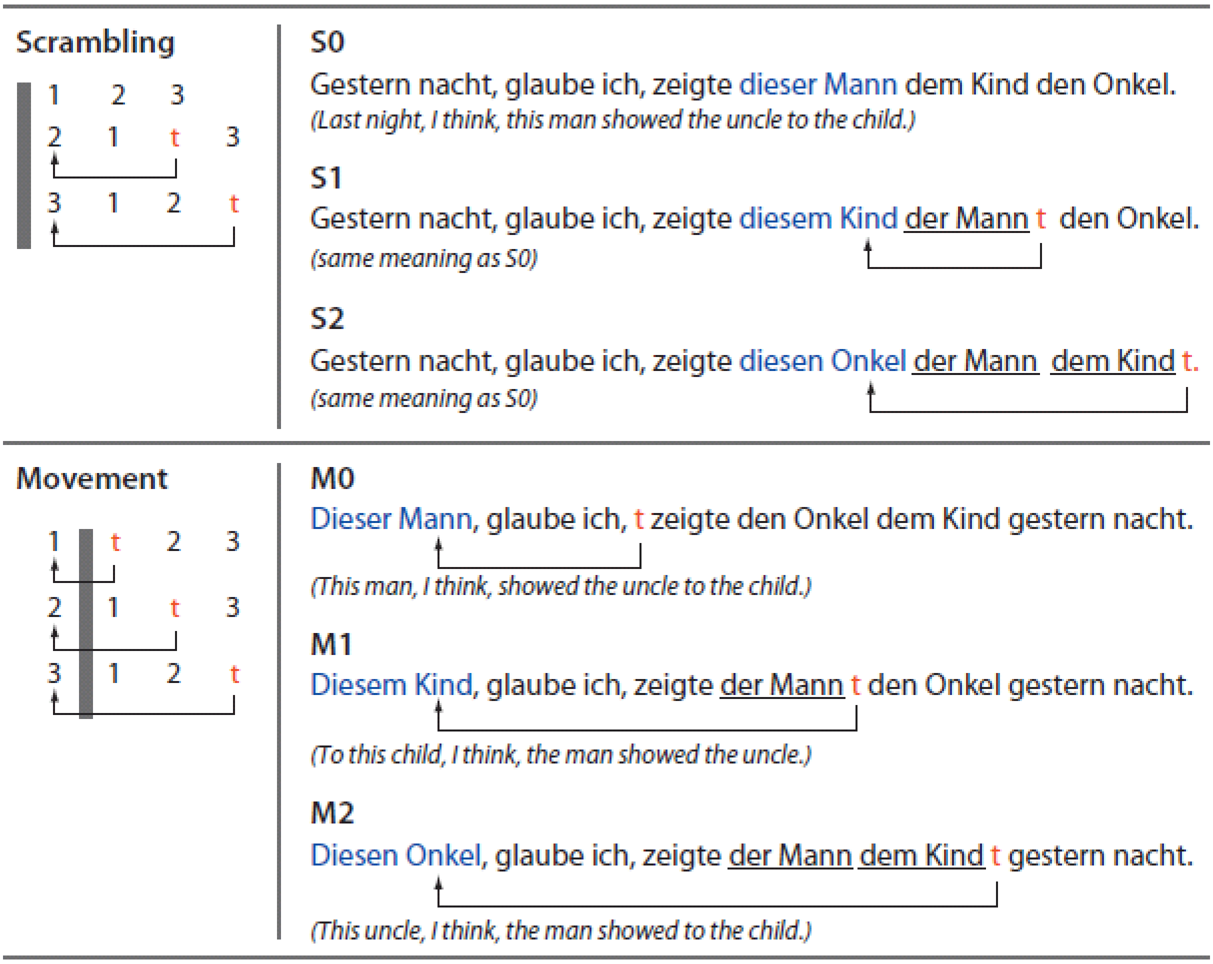
Anatomical region	cluster p	cluster size (voxels)	peak Z	coordinates
Main effect of TYPE				
MOV > SCR				
Left				
Inferior occipital gyrus	0.000	813	5.77	-18 -93 -6
Superior occipital gyrus	0.017	67	4.15	-33 -78 21
SCR > MOV				
n.s.				
Main effect of DISTANCE (as the linear effect S/M0 < S/M1 < S/M2)				
Left				
Inferior frontal sulcus	0.000	653¶	5.50	-36 6 33
Pars opercularis	0.000	653¶	5.47	-51 15 18
Intraparietal sulcus	0.000	171	5.21	-33 -51 36
Precuneus	0.020	64	4.41	-9 -66 42
Middle superior temporal sulcus	0.031	57	4.30	-54 -36 -6
Grobus pallidus	0.033	56	3.86	-21 -15 6
Right				
Intraparietal sulcus	0.031	57	4.18	33 -45 39
Pars opercularis	0.001	127	4.17	45 21 21

¶, the same cluster.

1 voxel is 27 mm^3.

Figures

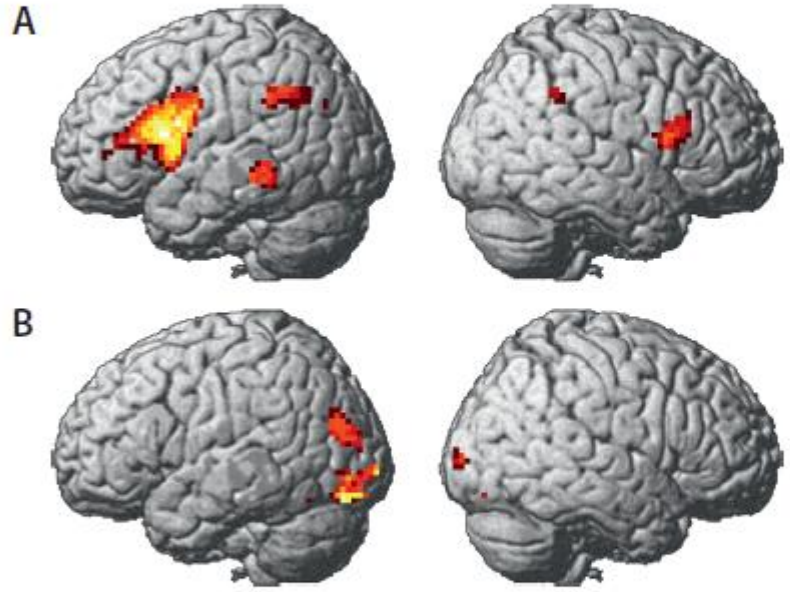
Fig 1 Schematic representation of scrambling and movement and the sentence examples



Left panel: Sentences are derived by a displacement of one of the NPs of the base order sentence. 1, 2, and 3 stand for NP_{NOM}, NP_{DAT}, and NP_{ACC}, and 1-2-3 is the base order. In the SCR conditions, when NP_{DAT} (2) moves to immediately before the NP_{NOM} (1), one NP (NP_{NOM}) exists between the filler (2) and the trace (t). When NP_{ACC} (3) moves to immediately before the NP_{NOM} (1), two NPs (NP_{NOM} (1) and NP_{DAT} (2)) intervene the filler (3) and the trace (t). The distance is measured by the number of the intervening NPs between the moved NP and the trace (t). The displacement of NPs and the definition of the distance is the same in The MOV condition, but NPs move beyond the clause boundary (the gray bars).

Right panel: Sentence examples. The distance was denoted as 0, 1, and 2. In the MOV condition, the NPs travel over the clause boundary "glaube ich". The traces (t) are not pronounced, but the dislocated NPs (blue, connected with t by arrows) are reactivated at the position of t (the gap).

Fig 2 ANOVA results

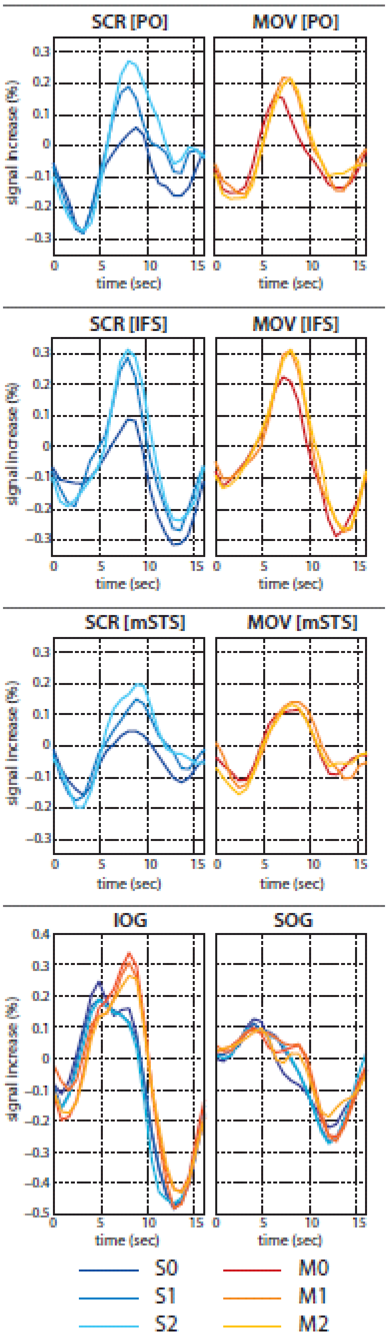


A. Main effect of DISTANCE (S/M2>1>0)

B. Main effect of TYPE (MOV>SCR)

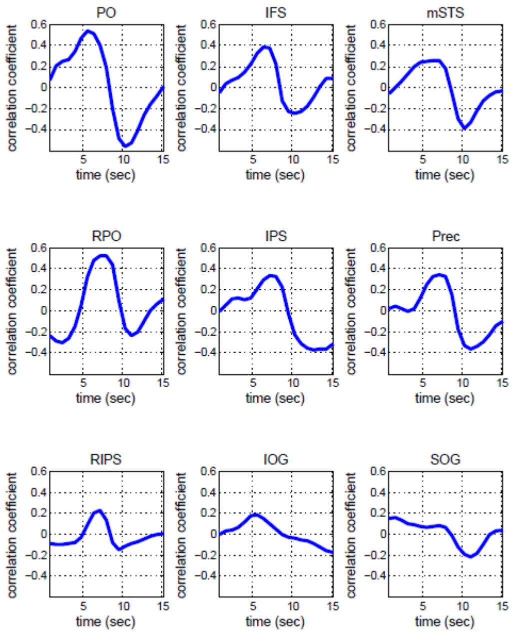
T contrast, $p < 0.05$ (corrected).

Fig 3 Trial time course plots for the activated regions revealed by ANOVA



The trial time courses in the PO, IFS, and mSTS are shown.

Fig 4 Correaltion between trial time course and accuracy



Correlation between the trial time courses and accuracy of the probe judgment for the SCR condtions (mean of the 3 levels of DISTANCE) are plotted. Only the PO and RPO exhibit a high correlation (r > 0.5, -0.5 < r). The positive correlation around 6 s and negative one aound 11 s in PO can indicate the leftward shift of the trial time courses of the high accuracy participants. This means that the higher performances are accompanied with faster increase and faster drop of the BOLD signal change.

Fig 5 Dynamic causal model analysis

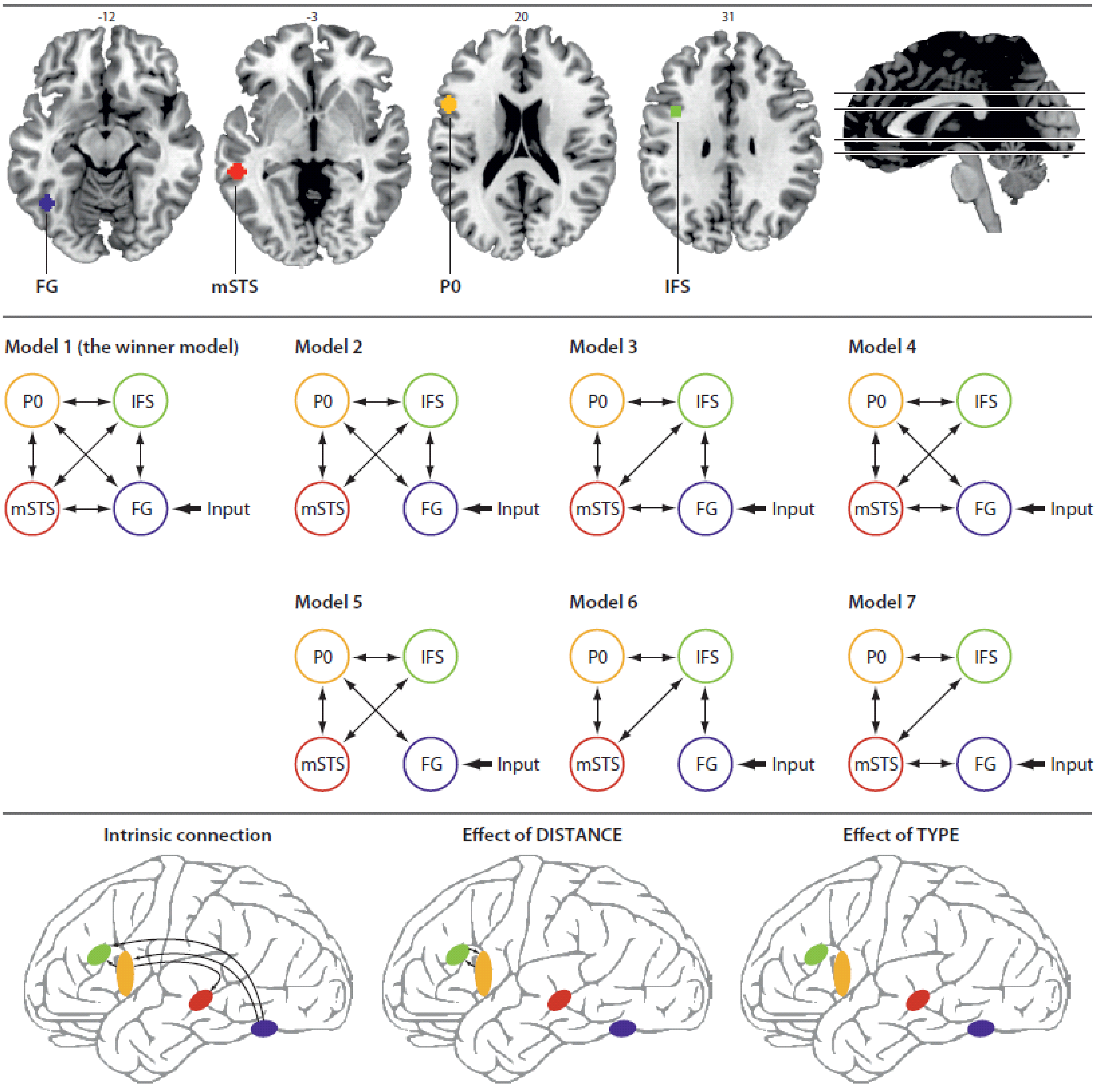


Fig 5

Top panel: VOIs used in the DCM analysis.

The VOIs are shown at the mean coordinates of the individual maxima. The radii represent the largest starndard deviation (SD) of the coordinates among x, y, and z directions. The group statistics maxima, the mean of the individual maxima, and the SD of the individual maxima are as follows: PO(-51 15 18),(-52.8 12 19.2),(6.3 5.2 4.5), IFS(-36 6 33),(-38.6 6.9 31.1),(3.1 4.6 4.2), mSTS(-54 -36 -6),(-56.3 -36.8 -2.9),(4.0 6.2 5.5), and FG(-44 -58 -15),(-43.1 -59.0 -12.2),(5.1 4.9 4.8).

Middle panel: Seven dynamic causal models.

Bottom panel: The winning model (the model 1) in the Baysian comparison among 7 models.
Statistically significant effective connectivity (FDR correction $q < 0.05$) and the modulatory effect are shown by arrows. The TYPE does not show any significant modulatory effect on the connection strength (right).
Blue: FG, Red: mSTS, Yellow: PO, Green: IFS.

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