Rearranging the world: Neural network supporting the processing of temporal connectives

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ABSTRACT

Temporal connectives (*before*/*after*) give us the freedom to describe a sequence of events in different orders. Studies have suggested that '*before-initiating*' sentences, in which events are expressed in an order inconsistent with their actual order of occurrence, might need additional computation(s) during comprehension. The results of independent component analysis suggest that these computations are supported by a neural network connecting the bilateral caudate nucleus with the right middle frontal gyrus, left precentral gyrus, bilateral parietal lobule and inferior temporal gyrus. Among those regions, the caudate nucleus and the left middle frontal gyrus showed greater activations for '*before*' than '*after*' sentences. The functional network observed in this study may support sequence learning and processing in a general sense.

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Introduction

Temporal connectives, in particular '*before*' and '*after*', give us the freedom to describe a sequence of events in different linguistic orders. In sentences beginning with '*after*', events are mentioned in their actual order of occurrence (e.g., *After the scientist submitted the paper, the journal changed its policy.*). By contrast, in sentences beginning with '*before*', events are expressed out of chronological order (e.g., *Before the journal changed its policy, the scientist submitted the paper.*). Behavioral evidence indicates that '*before*' sentences are more difficult to understand, in particular for young children (Natsopoulos and Abadzi, 1986; Trosberg, 1982) and patients with Parkinson's disease (Natsopoulos et al., 1991) or aphasics (Sasanuma and Kamio, 1976).[1] Such processing difficulty likely arises from the engagement of additional computations for '*before*' sentences.

Listeners and readers alike use both real-world and linguistic knowledge to create a mental model about who, when, where and why during language comprehension (Ferstl and von Cramon, 2007; Ferstl et al., 2005; Hagoort and van Berkum, 2007; Hagoort et al., 2004). In case of the description of temporally successive events, world knowledge leads us to expect the order of event mention to be similar to the order of actual event occurrence (the order of event mention strategy in Natsopoulos et al., 1991), because in the real world time unfolds sequentially and current events are often caused by prior events. On the other hand, linguistic knowledge tells us that temporal conjunctions may be used to express events in their order of occurrence as well as to re-order them: The sentence initial '*after*' signals that events are expressed in their actual order of occurrence, whereas the sentence initial '*before*' signals the reverse order. For '*before*' sentences, consequently, additional computations would seem to be required to rearrange the mental representation structured by real-world knowledge of temporal sequence. If this process of re-ordering is defective, over-application of the world-knowledge-driven heuristic strategy may lead to the misinterpretation of '*before*' sentences, as has been reported for patients with Parkinson's disease (Natsopoulos et al., 1991).

Taking advantage of the exquisite temporal resolution of event-related brain potentials (ERPs), Münte et al. (1998) compared the online processing of '*before*' and '*after*' sentences. Remarkably, the electrical brain responses to these two sentence types diverged within approximately 300 ms after the presentation of one or the

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[1] We explicitly acknowledge that there are more differences to the semantics of temporal connectives than just the temporal ordering of events. The most important difference is that sentences beginning with after signal that the subordinate clause is true while before allows for the subordinate clause to be either true or false (Before I decline a beer, I rather die). However, in the current study care was taken in selecting sentence materials for which the veridicality of the subordinate clause was not an issue. In particular, the use of the past participle throughout the materials in both clauses signals that both clauses are true.

other of the sentence-initial temporal connectives. A sustained relative negativity characterized the response to '*before*' vs. '*after*' sentences, focused over the left frontal scalp. The size of this slow negative effect was highly correlated with individual working-memory spans, with individuals with higher spans showing a larger negativity. This ERP finding was consistent with the hypothesis that temporal connectives invoke the engagement of a left frontal working memory system to deal with the temporal re-ordering of events expressed in '*before*' sentences. However, by its nature, the ERP technique could not identify the exact brain systems implementing these computations.

We thus turned to functional MRI to answer this question. The learning and processing of temporal sequence are subserved by a distributed set of cortical and subcortical structures. One region being constantly observed is the caudate nucleus (particularly the caudate head), which shows more activations for learning a given sequence successfully vs. unsuccessfully (Peigneux et al., 2000), for processing sequences following vs. violating a learned rule (Schubotz et al., 2004), for generating complex vs. simple sequences (Forkstam et al., 2006; Lehéricy et al., 2006), and for learning sequences determined by a hierarchical vs. non-hierarchical dependency rule (Bahlmann et al., 2008, 2009). Although it did not show up for the integration of temporal information in text comprehension (Ferstl and von Cramon, 2007; Ferstl et al., 2005), the caudate head is active for reasoning which requires the detection and application of a sequence rule (Christoff et al., 2001; Melrose et al., 2007). The caudate activity is usually accompanied by activations of the middle frontal gyrus (MFG, BA9/46), the supplementary motor area (SMA, BA6) and the premotor cortex in such tasks (e.g., Bahlmann et al., 2008, 2009; Forkstam et al., 2006; Lehéricy et al., 2006; Peigneux et al., 2000; Schubotz et al., 2004). The MFG (BA9) and the medial superior frontal gyrus (mSFG/pre-SMA, BA8) are also involved in organizing temporally successive actions (e.g., 'get dressed' and 'take a shower', see Crozier et al., 1999; Sirigu et al., 1998). Moreover, a meta-analysis suggested that BAs 6, 8, 9 support working memory especially when temporal order must be maintained (Wager and Smith, 2003). It is reasonable to assume that the caudate nucleus and the prefrontal cortex (PFC) work together as a dynamic brain network which is called upon relatively early (within 300 ms, Münte et al., 1998) during the processing of '*before*' and '*after*' sentences. This assumption is consistent with previous proposals that loops from the PFC, through the caudate nucleus, the globus pallidus and the thalamus, and back to the PFC are crucial for encoding the temporal order of sensory events and for sustaining the resulting representation in working memory (Alexander et al., 1986; Beiser and Houk, 1998).

In the present investigation, we used functional MRI in a group of healthy young adults while they read sentences beginning with '*before*' or '*after*'. We conducted a regular univariate analysis to examine brain regions differentially activated, and then an independent component analysis (ICA) to determine brain networks dynamically modulated in the processing of '*before*' vs. '*after*' sentences. Different from the univariate analysis which is heavily based on hypothesis, the data-driven ICA reveals a set of spatially independent networks (the so-called components), with each component presented as a spatial map of functionally connected brain regions along with a time-course highly correlated with the real fMRI time-courses. We expected to observe a functional network connecting caudate nucleus with prefrontal regions in both analyses.

Material and methods

All procedures were cleared by the ethical review board of the University of Magdeburg, the affiliation of the senior author at the time of the experiment.

Participants

Eighteen native German speakers (9 women, mean age 25 years, age range 20 to 34 years) participated in this study. They were right-handed and had normal or corrected-to-normal vision. None of them had a history of neurological or psychiatric disorder. All of them gave written informed consent before scanning.

Stimuli and task

Participants read German sentences for comprehension during scanning and completed a recognition test after scanning. They were informed about the recognition test before scanning to make sure they would read the sentences attentively. Note, that German is very similar to English with regard to the '*before*'/'*after*' distinction. Each sentence consisted of two clauses, with each clause describing a distinct event happening to a distinct person (or persons). One event was not logically, causally or referentially related to the other. These clauses were connected by temporal ('*after/before*', German: '*nachdem/bevor*') or coordinating conjunctions ('*and*', German: '*und*'). The '*and*' sentences were used as a neutral condition in which two events did not occur successively. The behavioral and fMRI results of the '*and*' condition are shown in the Supplemental materials. Here are examples.

a) Nachdem der Zauberer das Kaninchen beseitigt hat, hat der Kameramann den Film gewechselt. [After the magician removed the bunny, the cameraman changed the film.]
b) Bevor die Tänzerin die Vorstellung abgesagt hat, hat der Direktor den Dirigent gefeuert. [Before the female dancer canceled the show, the director fired the conductor.]
c) Die Kinder haben den Ball verschossen und der Trainer hat den Schiedsrichter beleidigt. [The children kicked the ball and the trainer offended the referee.]

We created 120 sets of sentences (see Supplementary materials for the full set of materials) and split them into three lists so that the '*after*' version, the '*before*' version and the '*and*' version for any pair of clauses did not appear in the same list. For each pair of clauses, linguistic orders were the same across conditions. Thus, three sentences of each set had not only the same clauses but also the same clause order. Each participant read only one list comprising 40 sentences per condition. Each list was used for six participants. Sentences were presented clause-by-clause. Each clause was displayed for 2.5 s. Then a fixation cross stayed on the screen for 15 s. In other words, each trial had a fixed length of 20 s. There were two sessions, each lasting 20 min. The interval between two runs was defined by personal preference. The second run would start only if participants said they were ready to continue.

A recognition test was conducted after scanning to assess whether participants had read the sentences attentively. Each participant read 30 old sentences, all from the list he/she used. One half of these sentences had been presented in the first run; the other half had been presented in the second run. Participants were asked to indicate whether a particular sentence had occurred in the first or in the second run.

fMRI data acquisition

Data were collected on a 3-T Siemens Trio system in two sessions. Functional images were acquired using a T2*-weighted echo planar imaging (EPI) sequence, with 2000-ms time repetition (TR), 30-ms time echo (TE), and 80° flip angle. Each functional image consisted of 32 axial slices, with 64×64 matrix, 224 mm×224 mm field of view, 4-mm thickness, no gap, and 3.5 mm×3.5 mm in-plane resolution. Structural images were acquired using a T1-weighted magnetization-prepared rapid-acquired gradient echo (MPRAGE) 3D

sequence, with 2500-ms TR, 4.77-ms TE, 1100-ms TI, and 7° flip angle. The structural image consisted of 192 slices, with 1-mm thickness, and 1 mm × 1 mm in-plane resolution.

Data analysis

Data were analyzed with SPM8 (http://www.fil.ion.ucl.ac.uk/spm) and visualized with MRIcron (http://www.cabiatl.com/mricro). The first four volumes were discarded owing to longitudinal magnetization equilibration effects. Functional images were first time-shifted with reference to the middle slice in time to correct differences in slice acquisition time. They were then realigned with a least squares approach and a rigid body spatial transformation to remove movement artifacts. Realigned images were normalized to the EPI-derived MNI template (ICBM 152, Montreal Neurological Institute), smoothed with a Gaussian kernel of 8-mm full-width half-maximum (FWHM), and finally filtered with a high-pass filter of 128 s. We carried out two statistical analyses, i.e. a regular univariate analysis and an independent component analysis (ICA).

Regular univariate analysis

The regular univariate analysis was performed to examine brain regions differentially activated in the processing of 'before' vs. 'after' sentences. This analysis was implemented on the basis of a general linear model (GLM) by using one covariate to model hemodynamic responses of all sentences of a condition. Three conditions were specified in the design matrix and time-locked to their onsets: the 'before' sentence, the 'after' sentence, and the 'and' sentence. Estimated movement parameters (six parameters per image: x, y, z, pitch, roll, and yaw) were included in the model as nuisance regressors of no interest to minimize signal-corrected motion effects. Classical parameter estimation was applied with a one-lag autoregressive model to whiten temporal noise in the fMRI time-courses of each participant to reduce the number of false-positive voxels. Contrast maps were calculated for 'before' > 'after' for each participant and entered into a one-sample t test on the group level (random effect). The resulting map was first considered at $p < 0.05$ (family-wise error-corrected). However, no voxel survived at the conservative threshold. Therefore, we used a relatively lenient threshold $p < 0.005$ (uncorrected) but masked the current result with the result of an independent set of fMRI data ($p < 0.05$ corrected) which were collected with the same paradigm from a group of older subjects (7 women and 9 men, mean age 64 years; for details, see Supplementary text and Supplemental Fig. S1) in order to examine the activity pattern replicated across studies.

Independent component analysis

The ICA was performed to examine functional brain networks dynamically modulated during the processing of 'before' vs. 'after' sentences. This analysis was implemented with the GIFT toolbox (http://mialab.mrn.org/software) using the infomax algorithm (Bell and Sejnowski, 1995). The fMRI data were split into a set of spatially independent functional networks (components). Each component was presented as a spatial map along with an associated time-course. The optimal number of independent components was estimated by using a modified minimum description length algorithm (Li et al., 2007) and found to be 40. To avoid the problem of matching components across participants, the ICA was performed on all participants at once (group ICA). It has been shown that the group ICA does not significantly detract or alter the result in comparison to an ICA performed on each participant separately (Calhoun et al., 2007, 2008, 2009). On the other hand, the group ICA computes components which are comparable across participants (e.g., Component 1 of Subject 1 is the same as Component 1 of Subject 2). The label of each component (e.g. Component 1, Component 2) has no particular meaning. To find out the independent component

which represents the functional network dynamically modulated for 'before' vs. 'after' sentences, spatially and temporal sorting were applied to all 40 components (for a similar approach of component selection, see Kim et al., 2009a, 2009b). The spatial sorting was implemented by correlating the spatial map of each component (averaged across participants) with prior probabilistic maps of gray matter, white matter and cerebral spinal fluid (MNI templates provided in SPM). If the spatial correlation for white matter was greater than $R^2 = 0.02$ or greater than $R^2 = 0.05$ for cerebral spinal fluid, the component was considered to represent artifacts and therefore should be discarded. The component was also excluded if the spatial correlation for gray matter was smaller than that for white matter or cerebral spinal fluid. The temporal sorting was implemented by regressing the time-course of each component with the design matrix at subject level. For each participant, the regression resulted in one beta weight for each component in each condition. The beta weight indicates the degree to which a particular component was modulated by a particular experimental condition. Higher beta weights suggest larger condition-specific modulation (analogous to the univariate GLM). The beta weights of each component were entered into paired-sample t tests on the group level. p values were adjusted for multiple comparisons with permutation test. The permutation test is conducted by computing all possible t values (reference distribution) and the possibility of obtaining the real t value from the reference distribution (Blair and Karniski, 1993). For the selected component, its spatial map was averaged across sessions, entered into a one-sample t test and thresholded at $p < 0.05$ (familywise-error-corrected). The resulting map reflected the contribution of a particular region to the associated component time-course. Higher t values suggest greater contributions.

Results

Recognition test

Recognition accuracy was 75% (SE = 3%) for 'before' sentences and 69% (4%) for 'after' sentences (t (17) = 1.38, $p = 0.19$, 2-tailed) indicating that participants did indeed pay attention to the sentences, and did so for both sentence types.

fMRI results

Fig. 1A and Table 1 show that the bilateral caudate nucleus and left middle frontal/precentral gyrus were more activated for 'before' than 'after' sentences. No region showed more activation for 'after' than 'before' sentences.

Among all 40 independent components, ten were identified as artifacts because their spatial correlations with white matter were greater than $R^2 = 0.02$, or $R^2 = 0.05$ with cerebral spinal fluid. Five components were further excluded because their spatial correlations for gray matter were smaller than their correlations for cerebral spinal fluid. Among the rest, Component 40 was the only component sensitive to the experimental conditions, showing larger beta weight (larger modulation) for 'before' than 'after' sentences (paired-sample t test, two-tail: t (17) = −3.01, permutation 5000 times, estimated familywise alpha level: $p < 0.01$). This component revealed a functional network of the bilateral caudate nucleus, right middle frontal gyrus, left precentral gyrus, bilateral parietal lobule and inferior temporal gyrus (also see Table 2). The spatial map of Component 40 overlapped with the activity map identified in the univariate analysis in the caudate nucleus, but not in the left middle frontal gyrus/precentral gyrus over the current threshold (familywise-error-corrected $p < 0.05$). When thresholded with the false-discovery-rate-corrected $p < 0.05$, Component 40 overlapped with the activity map in both the caudate nucleus and the left precentral gyrus/middle frontal gyrus.
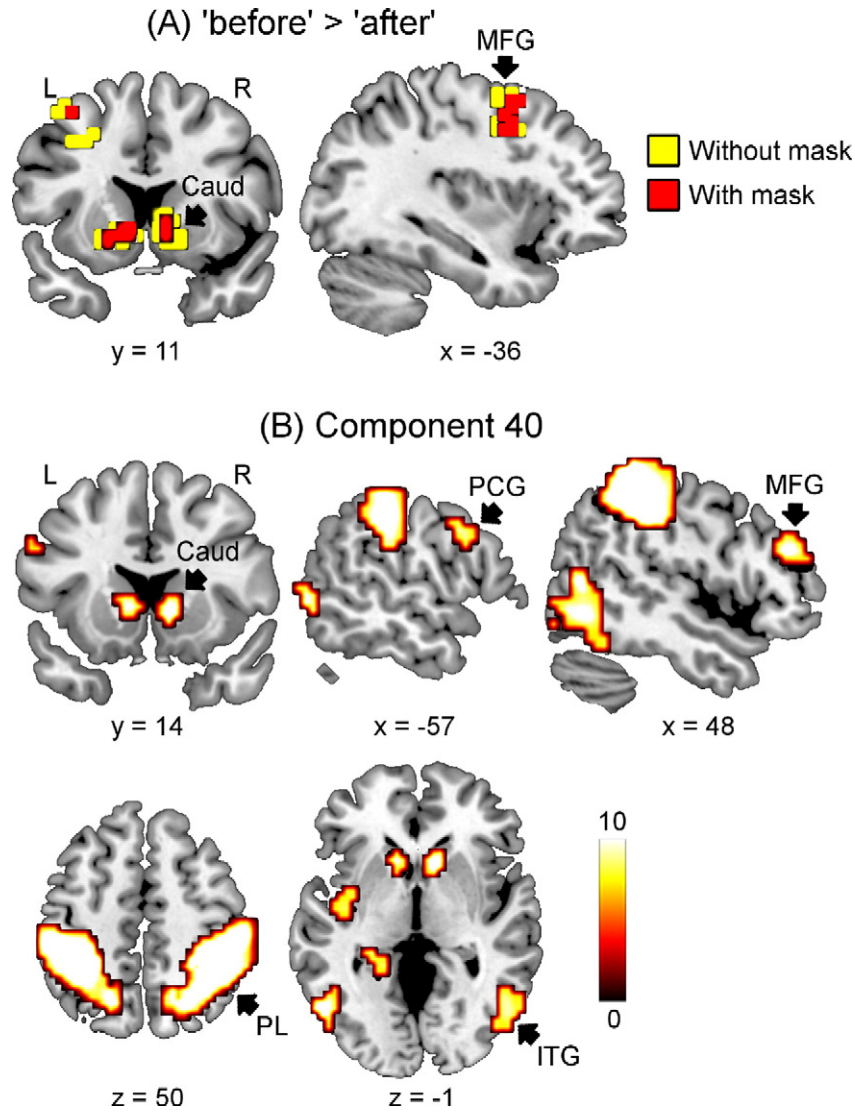
(A) 'before' > 'after'

(B) Component 40

Fig. 1. (A) The bilateral caudate nucleus (Caud) and left middle frontal gyrus (MFG) showed larger activations for '*before*' than '*after*' sentences. L, left; R, right; coordinates in MNI. Yellow, $p<0.005$ uncorrected without mask; red, with mask ($p<0.05$ corrected). (B) Component 40 represented a functional network composed of the Caud, precentral gyrus (PCG), MFG, parietal lobule (PL) and inferior temporal gyrus (ITG). Color scale indicates t values. $p<0.05$ corrected.

Univariate and ICA results related to the processing of '*and*' sentences are presented in the supplementary text and Supplemental Fig. S2. In addition, we present the result of a similar fMRI experiment using a block design as supplemental materials.

Discussion

To summarize, we observed a set of cortical and sub-cortical areas during the processing of temporal connectives. To be specific, the

Table 1
Regions more activated for '*before*' than '*after*' sentences.

Region	BA	H	x	y	z	t	Size
Without mask							
Caudate nucleus/putamen		L	−15	11	−5	3.74	35
		R	6	11	−1	5.15	29
Middle frontal gyrus/precentral gyrus	6/9	L	−33	7	41	4.48	38
Medial superior frontal gyrus	8	R	13	39	45	3.82	38
With mask							
Caudate nucleus		L	−12	14	−5	3.56	7
		R	10	11	−5	4.76	3
Middle frontal gyrus	6/9	L	−36	7	52	3.45	12

BA, Brodmann Area; H, hemisphere; coordinates in MNI; t, statistic values; L, left; R, right; size, number of voxels; without mask, $p<0.005$ uncorrected; mask, $p<0.05$ corrected.

Table 2
Regions of Component 40.

Region	BA	H	x	y	z	t	Size
Caudate nucleus		L	10	18	−1	14.23	33
		R	12	18	−1	11.23	26
Middle frontal gyrus	46/45	R	48	35	24	12.98	44
Precentral gyrus	6	L	−36	−28	59	11.87	94
		R	31	−11	69	12.05	34
Parietal lobule	2/3/40	L	−26	−46	59	22.19	931
		R	41	−42	59	30.44	1009
Inferior temporal gyrus	37	L	−50	−70	−8	13.03	70
		R	52	−60	−7	14.32	159
Insula		L	−43	−7	−5	10.00	45
Hippocampus	37	L	−26	−35	−1	9.27	40

BA, Brodmann Area; H, hemisphere; coordinates in MNI; t, statistic values; L, left; R, right; size, number of voxels; $p<0.05$ corrected.

caudate nucleus and left MFG/precentral gyrus showed greater activations for 'before' than 'after' sentences. The activity pattern of the current study overlapped with that obtained from a different group of subjects. The bilateral caudate nucleus, right MFG, left precentral gyrus, bilateral parietal lobule and inferior temporal gyrus worked together as a functional network which was dynamically modulated in the processing of 'before' vs. 'after' sentences.

For 'after' sentences, it is good enough to rely on the order of event mention strategy driven by real-world knowledge of temporal sequence (Natsopoulos et al., 1991). Unlike 'after' sentences, 'before' sentences need additional computations to mentally reverse the order of two constituent clauses to establish a correct temporal relation between real world events. These additional computations seem to be supported by the caudate-prefrontal-parietal network. This proposal is consistent with previous fMRI evidence that the caudate nucleus is simultaneously active with the left MFG (Peigneux et al., 2000), precentral gyrus (Bahlmann et al., 2009) and parietal lobule (Lehéricy et al., 2006; Schubotz and von Cramon, 2004) in sequence learning and processing, additionally with the inferior temporal gyrus for language stimuli (Bahlmann et al., 2008).

The caudate nucleus receives cortical inputs and projects back to cortical regions via the global pallidus and thalamus, forming parallel (Middleton and Strick, 2002) and integrative circuits (Bar-Gad and Bergman, 2001) in support of motor, cognitive and emotional processes. The function of each loop appears to be associated with that of the cortical region to which that portion of the caudate nucleus projects. The observed involvement of the left MFG is in line with the interpretation of our previous ERP finding (Münte et al., 1998), given the link between the left MFG and the maintenance of temporal order in working memory (Wager and Smith, 2003). Although not observed in the univariate analysis, the parietal lobule was revealed by the ICA as another potential area of the network. This region has afferent and efferent connections with the mid-dorsolateral prefrontal cortex (BA 46, Goldman-Rakic, 1988) and the dorsolateral caudate nucleus (Leichnetz, 2001). The parietal activations have been observed in cognitive tasks requiring mental imagery, such as the mental simulation of increasingly complex locomotor tasks (e.g., 'walking with obstacles' vs. 'walking', see Malouin et al., 2003) and the mental rotation of 2D pictures (Kucian et al., 2007; Suchan et al., 2002). In these tasks, the parietal lobule was co-activated with the dorsolateral prefrontal cortex (BA9/46, see Kucian et al., 2007; Malouin et al., 2003). These results fit well with our proposal that differences between 'before' and 'after' sentences are driven by the computational requirements posited for the processing of 'before' sentences. The caudate network may re-arrange events along the time axis by reversing the linguistic order of clauses via mental imagery processes.

Although partially overlapping with the caudate-prefrontal-temporal network observed in recent neuroimaging studies (Fiebach et al., 2004; Snijders et al., 2010), the caudate–prefrontal–parietal network is unlikely to mediate the processing of ambiguous words or sentences in the current study. First, two crucial regions of the ambiguity-related network, namely the left inferior frontal gyrus and left middle temporal gyrus, did not show greater activation for 'before' than 'after' sentences. Second, the ambiguity of 'before' sentences (whether the subordinate clause is true or false) was diminished in our materials by using the past participle in both clauses. But the caudate–prefrontal–temporal network may also be impaired in Parkinson's disease patients who have difficulty in inhibiting simultaneously active lexical items (Copland et al., 2000, 2001; for a review, see Chenery et al., 2008).

In conclusion, we find that a caudate–prefrontal–parietal network is active during the processing of temporal connectives. We propose that this functional network supports the temporal re-ordering process necessary to align 'before' sentences with the timing of events in the real world, reversing the order of event mention perhaps via

mental imagery processes. The network observed in this study may support sequence learning and processing in a more general sense.

Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.neuroimage.2011.11.039.

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