# Rearranging the world: Neural networks supporting the processing of temporal connectives 

Zheng Ye ${ }^{\mathrm{a}, \mathrm{b}}$, Marta Kutas ${ }^{\text {c }}$, Marie St. George ${ }^{\mathrm{d}}$, Marty Sereno ${ }^{\mathrm{e}}$, and Thomas F. Münte ${ }^{\text {b,f }}$<br>${ }^{\text {a Department of Psychology, Peking University, Beijing, China }}$<br>${ }^{\text {b }}$ Department of Neuropsychology, University of Magdeburg, Magdeburg, Germany<br>cDepartment of Cognitive Science, University of California at San Diego, San Diego, USA<br>${ }^{\text {d}}$ Department of Psychology, San Diego City College, San Diego, USA<br>${ }^{\text {es }}$ School of Psychology, Birkbeck College London, London, UK<br>${ }^{\text {f }}$ Center for Behavioral Brain Sciences, Magdeburg, Germany

## Summary

Temporal conjunctions 'before' and 'after' give us freedom to describe a series of events in different orders. Previous studies suggested 'before' sentences in which events were expresses in an order inconsistent with their actual order of occurrence need additional computations, i.e. reversing the order of event mention to reach the actual order of event occurrence. This study found the additional computations may be supported by a neural network connecting the caudate nucleus with the medial prefrontal cortex, middle frontal gyrus (MFG), precuneus and occipital cortex. The connectivity in this network was strongly enhanced for 'before' than 'after' sentences. Meanwhile, another network was observed to support the memory retrieval, connecting the hippocampus with the MFG via the orbital inferior frontal gyrus and temporal pole. The connectivity pattern of this network was not different between conditions. With the common node MFG, these two networks may communicate in working memory to work together.

## Keywords

temporal conjunction; caudate nucleus; prefrontal cortex; precuneus; fMRI; functional connectivity

## Introduction

Temporal connective words such as 'before' and 'after' give us linguistic freedom to describe a series of events in different orders. The order of event mention can be consistent (e.g., After the scientist submitted the paper, the journal changed its policy) or inconsistent with (e.g., Before the journal changed its policy, the scientist submitted the paper) the actual order of events in real time. 'Before' sentences that present events out of chronological order

[^0]have been shown to be more difficult to understand, in particular for young children (Natsopoulos and Abadzi, 1986; Trosberg 1982), patients with Parkinson disease (Natsopoulos et al., 1991) or aphasics (Sasanuma and Kamio, 1976) ${ }^{1}$.


#### Abstract

Although healthy adults understand 'before' sentences as perfectly as they understood 'after' sentences (Natsopoulos et al., 1991), the former probably recruit additional discourse-level computations. In an event-related potential (ERP) study, Münte and colleagues (1998) found brain responses to 'before' and 'after' sentences diverged within 300 ms after the presentation of the word-initial temporal connective word. A sustained negativity showed up for 'before' vs. 'after' sentences over the left frontal scalp. The size of this effect was correlated with individual working-memory spans, with individuals with higher spans showing larger negative effects. Münte et al. suggested that the left anterior negativity reflects the differential involvement of working memory during the processing of 'before' and 'after' sentences.


Readers use both real-world knowledge and linguistic knowledge to create coherent representations during sentence/discourse comprehension (Hagoort et al., 2004; Hagoort and van Berkum, 2007). In the case of 'before/after' sentences, world knowledge leads us to expect that the order of event mention is similar to the order of event occurrence (the order of event mention strategy in Natsopoulos et al., 1991), because time unfolds sequentially in the real world and current events sometime cause future events. On the other hand, linguistic knowledge tells us that different temporal conjunctions indicate different mention order, with 'after' signaling events will be expressed in their actual order of occurrence and 'before' signaling events will be expressed in the reversed order. For 'before' sentences, consequently, additional computations are required to rearrange the representations structured by real-world knowledge of temporal sequence. The process of rearrangement is assumed to be implemented in working memory (Münte et al., 2007). If the process of rearrangement is defective, overapplication of the world-knowledge-driven heuristic strategy may lead to the misinterpretation of 'before' sentences, as has been shown in Parkinson's disease patients (Natsopoulos et al., 1991).

How are the additional discourse-level computations engaged by 'before' sentences implemented in the brain. Previous functional magnetic resonance imaging (fMRI) studies revealed a distributed set of brain areas to be involved in discourse-level processing comprising the medial prefrontal cortex (mPFC), middle frontal gyrus (MFG), inferior frontal gyrus (IFG), temporal pole (TP) and basal ganglia (caudate nucleus and putamen) (Caplan and Dapretto, 2001; Ferstl et al., 2005, 2008; St George et al., 1999; Xu et al., 2005).

In the present investigation we specifically tested which brain areas support the rearrangement processes engaged by before sentences using functional MRI. Standard

[^1]univariate analysis, showing regions more activated for 'before' than 'after' sentences, was followed by functional connectivity analysis to identify functionally related brain networks specific for each condition. The connectivity approach is based on the "beta series correlation" method proposed by Rissman et al. (2004) which has been successfully applied in studies of different cognitive domains (e.g., Camara et al., 2008, 2009; Fiebach et al., 2006; Rissman et al., 2008). This method is implemented on the basis of a general linear model (GLM), using separate covariates to model hemodynamic responses of a particular stage in each single trial and giving rise to series of parameter estimates (beta values) for the stage. If two regions are functionally connected within a network, their beta series should be strongly correlated. A neural network would be considered to support the process of rearrangement, if the connectivity in this network was stronger for 'before' than 'after' sentences.

## Results and Discussion

## Recognition test

In two functional runs, participants read sentences for comprehension. To test whether they read sentences attentively, a recognition task was carried out after scanning. One half of testing sentences were from the first run, while the other half were from the second run. Participants were asked to judge whether they read a particular sentence in the first or the second run. Their recognition accuracies were $75 \%$ ( $\mathrm{SE}=3 \%$ ) for 'before' sentences and $69 \%(4 \%)$ for 'after' sentences. There was no difference between conditions ( $\mathrm{F}(1,17)=$ $1.90, p=0.19)$ indicating that participants paid attention equally to the two types of sentences.

## fMRI results

To investigate the processing of temporal connective words, we performed two statistical analyses, i.e. the standard univariate analysis and the functional connectivity analysis. The standard univariate analysis was implemented on the basis of a GLM using one covariate to model hemodynamic responses of all sentences of a condition. For each participant, a contrast map was calculated by comparing the 'before' condition with the 'after' condition. Contrast maps were entered into a one sample $t$ test on the group level. The resulting map was considered at $p<0.005$ (uncorrected) with a minimum cluster size of 20 voxels. The standard analysis revealed several regions more activated for 'before' than 'after' sentences (see Figure 1 and Table 1), including the medial superior frontal gyrus (mSFG), left MFG, right IFG, bilateral temporal gyrus, basal ganglia (caudate nucleus and putamen), hippocampus and right cerebellum. To investigate interactions among these regions using connectivity analysis, we selected three seed regions, i.e. the caudate nucleus, MFG and hippocampus. Each seed was defined as a sphere with $6-\mathrm{mm}$ radius centered at the activation peak obtained in the standard analysis (caudate nucleus: $6,10,0$; MFG: $-38,6,58$, hippocampus: -28-14-20).

The functional connectivity analysis was implemented on the basis of another GLM using separate covariates to model hemodynamic responses of each single sentence in each condition. For each condition, beta values of all sentences were extracted to form a set of
beta series. Beta series of each seed were averaged across voxels within the critical region and correlated with beta series of every other voxel in the whole brain. For each participant, maps of correlation coefficients were calculated separately for 'before' and 'after' sentences. Correlation maps were normalized by using an arc-hyperbolic tangent transform and then entered into one sample $t$ tests on the group level. Resulting maps were considered at $p<$ 0.005 (family-wise error correction, FWE-correction) with a minimum cluster size of 100 voxels. The resulting map showed regions which were correlated with a particular seed in beta series and were inferred to be functionally connected with the seed. Figure 2 and Table 2-4 showed the connectivity results. The caudate nucleus interacted with the mSFG, MFG, precuneus and inferior occipital gyrus (IOG), but not with the hippocampus. These connections were stronger for 'before' than 'after' sentences (Figure 2a). Although the MFG and the hippocampus were not directly connected, they were linked via the left orbital IFG (IFGorb) and TP. The interaction between the left MFG and the left IFGorb, and the interaction between the left hippocampus and the left TP appeared to be subtly modulated by 'before' vs. 'after' sentences (Figure 2b and 2c).

The results of whole brain analysis were confirmed by further regions-of-interest (ROI) analysis. ROIs were defined with WFU PickAtlas (http://www.fmri.wfubmc.edu/cms/ software) according to Anatomical Automatic Labeling (AAL) for the mSFG, MFG, precuneus, IOG, IFGorb and TP. For each ROI, we calculated the percentage of voxels significantly ( $p<0.05$ on the subject level) positively correlated with a particular seed in each condition. We then conducted paired-sample $t$ tests for 'before' vs. 'after' sentences. Figure 3 show the ROI results for regions interacting with the caudate nucleus. In the mSFG, there were $15 \%$ more voxels significantly positively correlated with the caudate nucleus for 'before' than 'after' sentences in the right $(\mathrm{t}(1,17)=2.18, p<0.05)$, but not in the left hemisphere $(\mathrm{t}(1,17)=0.98, p=0.34)$. In the MFG, there were $11 \%$ more caudatecorrelated voxels for 'before' than 'after' sentences in the left hemisphere $(\mathrm{t}(1,17)=1.97, p$ $=0.07)$, and $12 \%$ more in the right hemispheres $(\mathrm{t}(1,17)=2.37, p<0.05$; with two hemispheres combined: $12 \%, \mathrm{t}(1,17)=2.28, p<0.04)$. In the precuneus, caudatecorrelated voxels increased $10 \%$ from 'after' to 'before' sentences in both the left (left: $\mathrm{t}(1$, $17)=2.24, p<0.05$ ) and the right hemispheres (right: $\mathrm{t}(1,17)=1.85, p=0.08$; with two hemispheres combined: $10 \%, \mathrm{t}(1,17)=2.08, p=0.05)$. In the IOG, caudate-correlated voxels increased $18 \%$ in the right hemisphere $(\mathrm{t}(1,17)=2.49, p<0.05)$, but not in the left hemisphere $(\mathrm{t}(1,17)=1.54, p=0.14$; but with two hemispheres combined: $15 \%, \mathrm{t}(1,17)=$ $2.17, p<0.05)$. For the IFGorb interacting with the MFG, or the TP interacting with the hippocampus, we did not obtain significant increase in the percentage of correlated voxels in either hemisphere, $p \mathrm{~s}>0.10$. In other words, the connections between the caudate nucleus and related regions were enhanced for 'before' vs. 'after' sentences, while the connections from the hippocampus to the MFG were not.

To summarize, we observed a set of cortical and sub-cortical areas involved in the processing of temporal connective words, including the mSFG, MFG, IFG, temporal gyrus, basal ganglia and hippocampus. More importantly, we found these brain areas worked together in two different networks, which shared a common node, i.e. the MFG (see Figure 4). One network connected the caudate nucleus with the mSFG, MFG, precuneus and IOG.

Within the caudate network, regions such as the mSFG , MFG and caudate nucleus were more activated and interregional interactions were much stronger for 'before' than 'after' sentences. The other network connected the hippocampus with the left MFG, the left orbital IFG and TP. The connectivity pattern of the hippocampus network did not differ between conditions. These two networks may support different functions during the processing of 'before/after' sentences. Different from an 'after' sentence, a 'before' sentence needs additional discourse-level computations to reverse the order of the two constituent clauses, in order to establish a correct temporal relation between events. The additional computations may be supported by the caudate network, as a stronger connectivity in this network showed up for 'before' as compared with 'after' sentences. Similar to an 'after' sentence, a 'before' sentence needs the retrieval of real-world knowledge and linguistic knowledge stored in long-term memory for sentential integration. This retrieval process may be mediated by the hippocampus network, as the connectivity pattern of this network was not significantly modulated by 'before/after' sentences. The involvement of the MFG as the common node is in line with the interpretation of our previous ERP study (Münte et al., 1998), because the MFG has been associated to working memory (McCarthy et al., 1994, 1996; Tsukiura et al., 2001). Thus, the MFG may serve as a common work space in which information from the caudate and hippocampus networks is integrated.

The caudate nucleus receives cortical input and projects back to cortical regions, forming parallel (Middleton and Strick, 2000, 2002) and integrative circuits (Bar-Gad and Bergman, 2001; Haber, 2003) in support of motor, cognitive and emotional processes. The function of each loop is associated with the cortical region to which the caudate nucleus projects. In the current study, the caudate nucleus was functionally connected with the dorsal mSFG, which is assumed to maintain task goals and to monitor and adjust cognitive processes in sensory, memory and motor systems (Botvinick et al., 2001; Carter et al., 1998; Dosenbach et al., 2007). Another crucial area is the precuneus, which has afferent and/or efferent connections with the mid-dorsolateral prefrontal cortex (BA8, 9 and 46), the parieto-occipital visual area, and the dorsolateral caudate nucleus (Goldman-Rakic, 1988; Leichnetz, 2001). The activation of bilateral precuneus was observed in cognitive tasks requiring mental imagery, such as the mental simulation of increasing 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; for a review, see Cavanna and Trimble, 2006). In these tasks, the precuneus was co-activated with the left MFG and the bilateral middle/ inferior occipital gyrus (Kucian et al., 2007; Malouin et al., 2003; Suchan et al., 2002). A combination of these functions fits well with our analysis of the computational requirements posited by 'before' sentences. The caudate network may re-arrange events along the time axis by reversing the linguistic order of clauses with the help of mental imagery.

Within the other network, the hippocampus was more activated for 'before' than 'after' sentences. The activation of hippocampus was observed during the comprehension of short stories (Schmithorst et al., 2006). The left IFGorb is assumed to support controlled access to stored conceptual and episodic representations (Badre and Wagner, 2007; Badre et al., 2005). It is anatomically connected with the anterior temporal lobe (including the temporal pole), which is further linked with the occipital lobe via the inferior longitudinal fascicle (Anwander et al., 2007). The left IFGorb has shown to be functionally coupled with the
hippocampus during memory encoding (Grady et al., 2003) and retrieval (Daglish et al., 2003). The absence of left IFGorb activation for 'before' vs. 'after' sentences and the similar connectivity pattern of this network in the two conditions suggested that 'before' and 'after' sentences engaged memory processes to a similar extent.

In conclusion, we found two neural networks during the processing of temporal connective words. The caudate network may support the re-arrangement process necessary for 'before' sentences, reversing the mention order of events with the help of mental imagery to establish the actual temporal relation between events. The hippocampus network may mediate the retrieval of real-world knowledge and linguistic knowledge necessary for both 'before' and 'after' in sentential integration. With the common node MFG, these two networks may communicate in working memory to work together.

## Experimental Procedures

All procedures had been cleared by the ethical review board of the University of Magdeburg.

## 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 sentences for comprehension during scanning and completed a recognition test after scanning. Each sentence consisted of two clauses, with each clause describing a distinct event which was neither logically nor causally related to the other. These clauses were connected by temporal ('after/before') or coordinating conjunctions ('and'). The 'and' sentence was used as a neutral condition in which two events were not linked in time. The behavioral and fMRI results of the 'and' condition are shown in the supplemental materials. We created 120 sets of sentences and split them into three lists so that the 'after' version, the 'before' version and the 'and' version of a pair of clauses would not appear in the same list. One participant read only one list, which contained 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 functional runs, each lasting 20 min .

## Data acquisition

Data were collected on a 3-T Siemens Trio system. Functional images were acquired using a T2*-weighted echo planar imaging (EPI) sequence, with 2000-ms time repetition (TR), 30ms time echo (TE), and $80^{\circ}$ flip angle. Each functional image consisted of 32 axial slices, with $64 * 64$ matrix, $224 \mathrm{~mm} * 224 \mathrm{~mm}$ field of view, 4-mm thickness, no gap, and 3.5 $\mathrm{mm} * 3.5 \mathrm{~mm}$ in-plane resolution. Structural images were acquired using a T1-weighted magnetization-prepared rapid-acquired gradient echo (MPRAGE) sequence, with 2500-ms

TR, 4.77-ms TE, $1100-\mathrm{ms} \mathrm{TI}$, and $7^{\circ}$ flip angle. The structural image consisted of 192 slices, with 1-mm thickness, no gap, and $1 \mathrm{~mm} * 1 \mathrm{~mm}$ in-plane resolution.

## Data preprocessing

Data were analyzed with SPM5 (http://www.fil.ion.ucl.ac.uk/spm). The first four volumes were discarded owing to equilibration effects. Functional images were first phase-shifted with reference to the middle slice to correct differences in slice acquisition time. They were then realigned with a least squares approach and a rigid body spatial transformation to remove artifacts. Realigned images were normalized to the EPI-derived MNI template (ICBM 152, Montreal Neurological Institute) and resampled to $2 * 2 * 2 \mathrm{~mm}^{3}$ voxel. Normalized images were finally smoothed with a Gaussian kernel of 8-mm full-width halfmaximum (FWHM). Estimated movement parameters obtained in the realignment step were involved in GLMs to minimize signal-correlated motion effects.

## Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Figure 1.
Activations for 'before' vs. 'after' sentences over the medial superior frontal gyrus (mSFG), left middle frontal gyrus (MFG), bilateral hippocampus and right caudate nucleus. White arrows point to related regions. Color scale indicates $t$ values. Coordinates are given in the MNI space. $p<0.005$ (uncorrected); minimum of 20 voxels extent; L, left; R, right.


Figure 2.
Regions functionally connected with the (a) caudate nucleus, (b) MFG, and (c) hippocampus (HC) for 'before' and 'after' sentences. Sections are selected to show seeds' interactions with mSFG, precuneus, MFG, inferior occipital gyrus (IOG), HC, inferior frontal gyrus (orbital, IFGorb), and temporal pole (TP). White arrows point to related regions. Color scale indicates $t$ values. Coordinates are given in the MNI space. $p<0.005$ (FWE-corrected); minimum of 100 voxels extent; L. left; R, right.


Figure 3.
Percentage of voxels significantly positively correlated with the caudate nucleus in the right mSFG, MFG (with two hemispheres combined), precuneus (with two hemispheres combined), and right IOG. Error bars indicate standard errors. *, $p<0.05$; L. left; R, right.


Figure 4.
Neural networks in support of the processing of temporal connective words.

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

| Region | BA | $\mathbf{H}$ | $\mathbf{x}$ | $\mathbf{y}$ | $\mathbf{z}$ | $\boldsymbol{t}$ | Size |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Medial superior frontal gyrus | 8 | R | 6 | 40 | 52 | 3.50 | 47 |
| Middle frontal gyrus | 9 | L | -38 | 6 | 58 | 3.58 | 237 |
| Precentral cortex | 6 | L | -34 | 0 | 38 | 5.01 | SC |
| Inferior frontal gyrus | 45 | R | 58 | 32 | 18 | 4.20 | 35 |
| Middle temporal gyrus | $21 / 20$ | L | -62 | -6 | -22 | 4.27 | 26 |
| Caudate nucleus | R | 58 | -6 | -22 | 4.36 | 85 |  |
| Putamen |  | R | 6 | 10 | 0 | 4.27 | 206 |
|  |  | L | -18 | 10 | -4 | 3.36 | 31 |
| Hippocampus | L | -28 | -14 | -20 | 4.97 | 24 |  |
| Cerebellum | R | 28 | -10 | -24 | 3.43 | 66 |  |

BA, approximate Brodmann Area; H, hemisphere; coordinates in MNI; $t$, statistic values of peaks; L, left; R, right; $p<0.005$ (uncorrected); cluster size in voxel; SC , same cluster.

| Region | BA | H | 'After' |  |  |  | 'Before' |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | x | y | z | $t$ | x | y | z | $t$ |
| Medial superior frontal gyrus/supplementary motor area | 32/6 | L | -4 | 16 | 48 | 12.48 | -8 | 26 | 44 | 14.10 |
| Anterior cingulate cortex | 32 |  |  |  |  |  | 0 | 42 | 8 | 11.45 |
| Superior frontal gyrus | 9 | R | 22 | 36 | 48 | 13.96 |  |  |  |  |
| Middle frontal gyrus | 9/6 | L | -46 | 14 | 42 | 13.43 | -30 | 12 | 58 | 12.39 |
|  |  | R |  |  |  |  | 32 | 14 | 54 | 17.28 |
| Inferior frontal gyrus (pars triangularis) | 45 | L |  |  |  |  | -48 | 20 | 22 | 14.51 |
|  |  | R | 52 | 28 | 10 | 21.35 | 42 | 28 | 22 | 14.63 |
| Inferior frontal gyrus (pars orbitalis) | 47 | L |  |  |  |  | -42 | 48 | -14 | 16.17 |
| Superior temporal gyrus | 22/42 | R | 54 | -46 | 24 | 15.86 | 50 | -48 | 32 | 14.49 |
| Middle temporal gyrus | 21 | L | -62 | -22 | -10 | 10.72 | -62 | -32 | -14 | 13.55 |
|  |  | R | 62 | -22 | -8 | 12.30 | 62 | -24 | -12 | 12.60 |
| Inferior temporal gyrus | 20/37 | L |  |  |  |  | -50 | -54 | -16 | 15.90 |
|  |  | R |  |  |  |  | 52 | -62 | -14 | 16.92 |
| Fusiform gyrus | 37 | L | -30 | -38 | -16 | 12.47 | -44 | -48 | -22 | 14.28 |
|  |  |  |  |  |  |  | 46 | -48 | -22 | 14.62 |
| Inferior parietal lobule | 7 | L |  |  |  |  | -26 | -70 | 46 | 18.74 |
|  |  | R |  |  |  |  | 36 | -56 | 50 | 14.40 |
| Precuneus | 7 | L | -4 | -64 | 44 | 10.62 | -4 | -62 | 52 | 14.39 |
|  |  | R | 10 | -64 | 50 | 9.31 | 2 | -60 | 44 | 15.75 |
| Occipital gyrus | $19 / 7$ | L | -32 | -66 | 38 | 13.41 | -28 | -70 | 28 | 15.69 |
|  |  | R | 32 | -70 | 32 | 12.02 | 34 | -70 | 30 | 12.11 |
| Lingual gyrus | 18 | L | -22 | -74 | -6 | 12.47 | -12 | -56 | 0 | 15.56 |
|  |  | R |  |  |  |  | 16 | -54 | 2 | 12.56 |
| Calcarine | 17 | R |  |  |  |  | 2 | -90 | -4 | 14.76 |
| Caudate nucleus |  | L | -10 | 12 | -4 | 15.08 | -12 | 16 | 2 | 34.84 |
|  |  | R | 6 | 10 | 0 | 31.29 | 6 | 12 | 0 | 37.21 |

Table 3

| Region | BA | H | 'After' |  |  |  | 'Before' |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | x | y | z | $t$ | x | y | z | $t$ |
| Medial superior frontal gyrus /supplementary motor area | $\begin{gathered} 32 / 8 / \\ 6 \end{gathered}$ | L | -6 | 36 | 40 | 20.78 | -8 | 24 | 54 | 15.39 |
|  |  | R | 10 | 26 | 60 | 15.84 | 2 | 34 | 42 | 11.82 |
| Superior frontal gyrus | 10 | R |  |  |  |  | 30 | 62 | 14 | 14.35 |
| Middle frontal gyrus | 6/8/9 | L | -36 | 6 | 58 | 40.55 | -38 | 4 | 58 | 34.51 |
|  |  | R | 40 | 4 | 56 | 13.47 | 40 | 6 | 58 | 15.19 |
| Inferior frontal gyrus (par triangularis) | 45 | L | -58 | 18 | 10 | 13.80 | -42 | 10 | 32 | 14.79 |
|  |  | R | 52 | 22 | 4 | 12.76 | 48 | 24 | 26 | 12.14 |
| Inferior frontal gyrus (pars orbitalis) | 47 | L | -44 | 30 | -14 | 10.69 | -32 | 28 | -14 | 16.15 |
|  |  | R | 42 | 30 | -12 | 12.76 | 36 | 28 | -8 | 17.39 |
| Middle temporal gyrus | 21 | L | -54 | -40 | -6 | 14.38 | -54 | -44 | -8 | 21.83 |
|  |  | R | 66 | -42 | -6 | 14.57 | 66 | -48 | -4 | 11.92 |
| Inferior temporal gyrus | 20 | L | -54 | -2 | -34 | 15.58 | -54 | -8 | -38 | 13.82 |
|  |  | R |  |  |  |  | 48 | -16 | -28 | 15.33 |
| Angular gyrus /inferior parietal gyrus | 39/40 | L | -42 | -62 | 32 | 14.89 | -50 | -56 | 30 | 13.90 |
|  |  | R | 56 | -52 | 40 | 14.42 | 44 | -72 | 36 | 13.08 |
| Rectus | 11 | L | -4 | 48 | -20 | 12.77 | -2 | 34 | -22 | 10.53 |
|  |  | R | 2 | 36 | -14 | 13.32 | 12 | 34 | -10 | 12.17 |
| Precuneus |  | L | -12 | -44 | 36 | 11.83 |  |  |  |  |
|  |  | R | 8 | -48 | 34 | 11.17 | 4 | -40 | 62 | 11.02 |
| Caudate nucleus |  | L | -10 | 10 | 10 | 11.99 | -12 | 14 | 2 | 14.27 |
|  |  | R | 12 | 16 | 8 | 11.70 | 10 | 4 | 0 | 13.13 |
| Cerebellum |  | R | 16 | -78 | -32 | 15.61 | 16 | -82 | -26 | 15.99 |

BA, approximate Brodmann Area; H, hemisphere; coordinates in MNI; $t$, statistic values of peaks; L, left; R, right; p < 0.005 (FWE-corrected); minimum of 100 voxels extent.

[^2]
[^0]:    Corresponding author: Thomas F. Münte Department of Neuropsychology University of Magdeburg 39106 Magdeburg, Germany Thomas.muente@med.uni-magdeburg.de.

[^1]:    ${ }^{1}$ 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, care was taken in selecting sentence materials that 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.

[^2]:    BA, approximate Brodmann Area; H, hemisphere; coordinates in MNI; $t$, statistic values of peaks; L, left; R, right; p < 0.005 (FWE-corrected); minimum of 100 voxels extent.

