Research report

Left parietal alpha enhancement during working memory-intensive sentence processing

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ABSTRACT

Both functional magnetic resonance imaging (fMRI) and event-related brain potential (ERP) studies have shown that verbal working memory plays an important role during sentence processing. There is growing evidence from outside of sentence processing that human alpha oscillations (7–13 Hz) play a critical role in working memory. This study aims to link this to the sentence processing domain. Time-frequency analyses and source localization were performed on electroencephalography (EEG) data that were recorded during the processing of auditorily presented sentences involving either a short or a long distance between an argument (subject or object) and the respective sentence-final verb. We reasoned that oscillatory activity in the alpha band should increase during sentences with longer argument-verb distances, since decreased temporal proximity should result in increased memory demands. When verbal working memory-intensive long-dependency sentences were compared to short-dependency sentences, a sustained oscillatory enhancement at 10 Hz was found during storage prior to the sentence-final verb, turning into a transient power increase in the beta band (13–20 Hz) at the sentence-final verb. The sources of the alpha oscillations were localized to bilaterally occipital and left parietal cortices. Only the source activity in the left parietal cortex was negatively correlated with verbal working memory abilities. These findings indicate that the parsimonious role of alpha oscillations in domain-general working memory can be extended to language, that is, sentence processing. We suggest that the function of left parietal cortex underlying verbal working memory storage during sentence processing is to inhibit the premature release of verbal information that will subsequently be integrated.

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1. Introduction

Traditionally, it had been assumed that the human alpha rhythm (7–13 Hz) represents an idle cortical state (Berger, 1929), based mainly on the observation that alpha oscillations increase as a preface to sleep, during eye closure, or motor relaxation (for a review, see Klimesch et al., 2007). More recently it has been proposed that the idea of alpha oscillations as an idling rhythm of the cortex may not reflect the full picture, in particular in the auditory domain (for a review, see Weisz et al., 2011). Following Lehtelä et al.'s (1997) report of a 10 Hz rhythm in primary auditory cortex which is sensitive to

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changes in auditory input, a number of recent articles have pointed out the significance of alpha oscillations for verbal working memory. For example, a magnetoencephalography (MEG) study by Jensen et al. (2002) used a modified version of Sternberg's (1966) letter-based working memory paradigm, finding increased alpha power over posterior electrodes with increased verbal working memory load. Along these lines, Leiberg et al. (2006) reported increased alpha activity under conditions of increased verbal working memory storage demands. Finally, Van Dijk et al. (2010) reported increased alpha amplitude during storage of task-relevant pitch information. In sum, there is good evidence that enhanced alpha oscillations are a robust neural correlate of verbal working memory.

Given this role of alpha oscillations in item or pitch retention, we hypothesized that also higher-level cognitive processes in the auditory domain that exhibit increased verbal working memory demands—such as sentence processing—will increase alpha activity as well. Verbal working memory is commonly agreed on to play an important role in sentence processing (Just and Carpenter, 1992; Rogalsky and Hickok, 2010; Waters and Caplan, 1996; Wingfield and Butterworth, 1984). Baddeley and Hitch's (1974) initial work found that concurrent memory load decreases reading comprehension performance, inducing that reading comprehension is sub-served by a capacity-constrained verbal working memory. More specific work showed that working memory capacity determines the ability to store and retrieve the arguments (both subject and object) until they can be syntactically linked to the main verb of the sentence and the sentence meaning can be inferred (King and Just, 1991)—which is of particular relevance in languages with sentence constructions requiring the verb to be in sentence-final position such as German and Japanese.

While there is support for an involvement of verbal working memory resources during argument-verb dependency processing (i.e., domain-specific functions), this support is hard to map onto the literature on alpha oscillations during verbal working memory storage outside of the sentence processing domain. Previous event-related brain potential (ERP) studies on verbal working memory from the sentence processing domain rather focused on word ordering processes during sentence processing, mostly triggered by research questions derived from theoretical linguistics. Such studies isolated sustained negative ERP effects for object-first as compared to subject-first sentences (Felser et al., 2003; Fiebach et al., 2001, 2002; Kluender and Kutas, 1993; Phillips et al., 2005; Ueno and Kluender, 2003). However, more general work on working memory, in particular on visual working memory, suggests that the retention of order information may be distinct from mere (that is, order-indifferent) storage: Hsieh et al. (2011) had their participants to focus on either the presence or absence of an item or the order of items in a delayed-response paradigm, obtaining enhanced posterior alpha for storage only, independent of the order of items. Given that behavioral work suggests that argument retrieval in the vicinity of verbs is a mechanism common to both subject- and object-first sentences (Nicol and Swinney, 1989), we hypothesize common oscillatory dynamics of argument storage, independent of the relative order of arguments—as opposed to distinct sustained ERP indices which are sensitive to the relative order of arguments.

The current study on sentence processing was designed to investigate verbal working memory storage processes independent of a particular sentence structure: these are required for the processing of any argument-verb dependency, regardless of the argument order. If alpha oscillations during sentence processing are independent from the processing of order information, such a result may help in disentangling verbal working memory and ordering processes during sentence processing.

While ERP findings from the sentence processing domain are hard to link to the underlying neuroanatomy, a number of functional imaging studies provide information about the neural underpinning of verbal working memory during sentence processing. As an example, Novais-Santos et al. (2007) reported left inferior parietal cortex to increase its activation with the retention interval for disambiguating information in ambiguous sentences, that is, verbal working memory load. In addition, Grossman et al. (2002) found an age-related decrease of brain activation related to increased argument-verb distance in the left parietal cortex, alongside sentence processing difficulties in seniors. The notion of left parietal cortex as potential neural substrate of verbal working memory during sentence processing is in line with meta-analyses, imaging studies and clinical work from outside of sentence processing (Awh et al., 1996, 1995; D'Esposito et al., 1999; Jonides et al., 1998; Leff et al., 2009; Owen et al., 2005; Petrides et al., 1993; Smith and Jonides, 1999; Wager and Smith, 2003). However, other studies focusing on verbal working memory during sentence processing reported Brodmann Area (BA) 45 in the left prefrontal cortex to play a role, using paradigms comparing different syntactic dependencies (Fiebach et al., 2005; Makuuchi et al., 2009; Santi and Grodzinsky, 2007, 2010). Hence, the imaging results for verbal working memory during sentence processing and their relation to the ERP literature are unequivocal, and a temporally more fine-grained method may complement the discussion.

Due to the potential role of cortical alpha oscillations in higher-level cognitive tasks such as sentence processing, we investigated cortical oscillations during the processing of sentences that involve greater working memory load without additionally increasing ordering demands. We hypothesized that any argument—regardless of whether it is a subject or an object—is stored in verbal working memory until the verb position at which retrieval of the argument becomes necessary for sentence interpretation. Consequently, we reasoned that oscillatory activity in the alpha band should increase with verbal working memory demands (Leiberg et al., 2006; Van Dijk et al., 2010) regardless of argument order. Testing this assumption will help to bridge the gap between the emerging literature on alpha oscillations in verbal working memory and the supposed role of verbal working memory during argument-verb dependency processing. In a similar vein, we will link changes in oscillatory power during storage-intensive sentence processing to a classical working memory measure from the sentence processing domain, that is, reading span (Daneman and Carpenter, 1980). Finally, we investigate the neural generators of the observed responses using source localization to provide a tentative link to

neuroimaging studies of sentence processing and verbal working memory.

2. Methods

2.1. Participants

Thirty-six participants took part in the study (mean age 26.4 years, standard deviation (SD) 3 years; 18 males, all native speakers of German). All of them were right-handed as assessed by an abridged German version of the Edinburgh Inventory (Oldfield, 1971). They were matched for reading span (mean reading span 3.6, SD .8) according to an abridged version of the reading span test (Daneman and Carpenter, 1980). None of the participants reported neurological or hearing deficits, and all had normal or corrected to normal vision. All participants were naïve as to the purpose of the study. They were paid €17.50 for participating.

2.2. Materials

German sentences with argument-verb dependencies of varying length were used to allow a manipulation of verbal working memory demands. The stimulus set originally involved a 2 × 2 factorial design crossing the factors argument-verb distance (short vs long) and argument order (canonical vs non-canonical), as shown in Fig. 1. To keep the argument retrieval point constant across conditions, the absolute position of the main verb was kept to the sentence-final position across all conditions, which is the default in German syntax (Haider, 1993). As we were only interested in the oscillatory dynamics of verbal working memory storage, and as the argument-verb distance is identical for both short and long conditions, respectively, we discarded the argument order factor from this paradigm, although we checked for potential oscillatory effects of the second original factor (see Data analysis). In the first and second conditions, both arguments (subject noun phrase and object noun phrase) are in the immediate vicinity of the main verb, such that the

Fig. 1 — Overview of experimental sentence materials; the upper panel shows short distance conditions, the lower panel shows long distance conditions. All sentences translate *After a season in the German soccer league, the coach honored the striker*. For literal translation see figure.

argument-verb distance is short. In the third and fourth conditions, the subject or object noun phrase is the first phrase in the sentence. Our rationale was that this manipulation lengthens the retention interval for the argument and thus increases verbal working memory storage demands. Since it has been shown that the ease of sentence processing as measured by processing speed can significantly speed up (Ferreira and Henderson, 1993) or slow-down (Friedman et al., 1975) toward the end of a sentence due to cumulative propositional load, a conjunct clause (i.e., a short, second sentence) was added (not shown in Fig. 1), which was identical for all four conditions of a set. Furthermore, to avoid any influence of frequency and sentence-level semantic coherence (Van Petten, 1993), for each structural position in the sentence a lemma frequency and syllable count matching using the CELEX database (Baayen et al., 1995) were performed and supplemented by positional word form frequency, lemma frequency and syllable count analyses using the Projekt Deutscher Wortschatz database (Biemann et al., 2004). Sentence-level semantic coherence was balanced by a sentential neighborhood analysis using the same corpus. Specifically, both arguments of each verb were matched in length and frequency to avoid confounding of the verbal working memory storage demands. Using these criteria, 48 sets of sentences in the four conditions were created, resulting in a set of 192 stimuli.

All sentences were recorded in a sound-proof chamber by a trained female German speaker with a Sennheiser® MKH 40 condenser microphone and a Roland® CD-2 digital sound recorder. The recordings were cut and normalized in Praat (Boersma and Weenink, 2001) according to the root mean square amplitude of all files. To avoid onset and offset artifacts, a cosine fade in and out sequence of 5 msec was attached. For each subject, an individual pseudo-randomized list of all 192 stimuli was generated using MATLAB® (The MathWorks, Inc., Natick, MA, USA) scripts. As a task to maintain participants' attention and to get a behavioral performance measure, a quarter of trials was followed by a yes/no comprehension question (e.g., *Hat der Trainer den Stürmer geehrt?/Did the coach honor the center forward?*), whereby the proportion of yes — correct and no — incorrect questions was balanced.

2.3. Procedure

Participants were seated in a dimly lit, magnetically shielded and sound-proof room. Stimuli were presented using the Presentation® software package (Neurobehavioral Systems, Inc., Albany, CA, USA). Auditory stimuli were presented using a pair of Infinity® Reference I MkII stereo speakers (Harman International Industries, Inc., Stamford, CT, USA), approximately 100 cm to the left and right front of the participants. In a quarter of trials, comprehension questions were presented visually, using a proportional, sans-serif font, black characters on a light gray background—a Sony Trinitron® Multiscan G220 CRT VGA monitor with a refresh rate of 75 Hz (Sony Corporation, Tokyo, Japan) was used, approximately 70 cm in front of the participants. A trial started with a green fixation cross of a random length between 2000 and 3500 msec. After this, the fixation cross turned red, and an auditory stimulus was
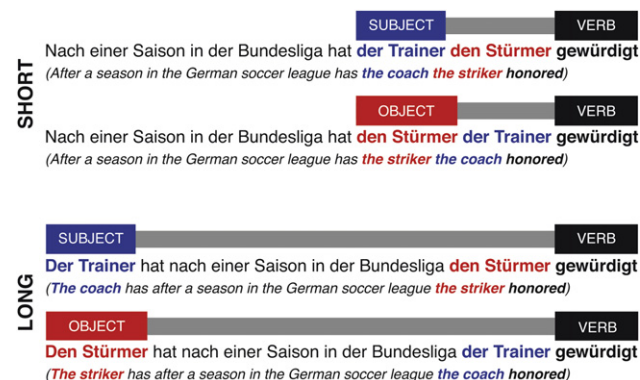
presented—participants were instructed to blink only when the fixation cross showed up green, ensuring a low amount of blink-artifacts in the data.

A sequence was either followed by the next trial or—in one-fourth of the stimuli—by the yes—no comprehension question. Participants had to answer these questions by pressing one of the two buttons of a two-button response box. Response button assignment was counterbalanced across participants. Prior to comprehension questions, a green fixation cross of a random length was presented to avoid task-preparation effects during the processing of the acoustic input. Comprehension questions were present on the screen until a button press occurred; this ensured participants were comfortable and avoided task-artifacts (Hagoort et al., 1993). Following a comprehension question, visual feedback was given for 800 msec in the form of a happy green or sad red emotion. An experimental run, consisting of 192 trials, lasted for approximately 35 min. Including preparation, the experiment lasted approximately 1.5 h. The electroencephalogram (EEG) was recorded with a pair of Brainvision BrainAmp DC amplifiers (Brain Products GmbH, Munich, Germany) from 64 tin scalp electrodes, attached to an elastic cap (Electro-Cap International, Inc., Eaton, OH, USA). The electrodes were placed at the standard positions based on the extended international 10—20 system. Each of the electrodes was referenced to the left mastoid, and the setup grounded to the sternum. The vertical electro-oculogram (EOG) was recorded from electrodes located above and below the left eye. The horizontal EOG was recorded from electrodes positioned at the outer canthus of each eye. The resistance of the electrodes was kept below 3 kΩ. The EEG and EOG were recorded continuously with a band-pass filter from DC to 250 Hz with a sampling rate of 500 Hz. Electrode positions were tracked using a Polhemus FASTRAK® electromagnetic motion tracker (Polhemus, Colchester, VT, USA). In five participants, tracking failed and mean positions of all other participants were used.

2.4. Data analysis

All analyses were carried out using the Fieldtrip toolbox for EEG/MEG analysis (Oostenveld et al., 2011). An epoch of 3.5 sec length was defined for analysis because we were interested in sentential oscillatory effects prior to the main verb, whose mean onset latency was 2933 msec (SD 276 msec). To resolve slow electrode drifts, the data were high-pass filtered at .03 Hz with a Hamming-windowed sixth-order two-pass Finite Impulse Response filter (Edgar et al., 2005). The experimental trials, including a 1-sec pre-stimulus baseline, were then extracted from the data. For artifact rejection, EEG epochs were off-line re-referenced to linked mastoid electrodes, and automatic EOG and muscle artifact rejection were performed on a trial-by-channel basis. Cutoffs for the EOG and muscle artifact rejection were set at $z = 3$ and $z = 7$ and performed inside frequency bands of 1—14 Hz and 110—140 Hz, respectively. The rejection procedure followed a distribution-based artifact identification approach (as implemented in Fieldtrip), that is, z-scores for rejection result from the amplitude distribution across trials and channels, resulting in rejection rate of 34.40% of trials, with no significant differences in rejection rates between conditions as verified by an Analysis of Variance (ANOVA). After preprocessing, time-frequency analysis was carried out using Morlet wavelets (Lachaux et al., 1999) in 50 frequency windows of 2 Hz each between 2 Hz and 100 Hz and in adjacent time windows of 50 msec length each. A fixed time-frequency resolution m of seven cycles was chosen. For statistical analyses, a massed cluster permutation test (Maris and Oostenveld, 2007) was carried out on the resulting (baseline-corrected) power change estimates inside the time-frequency subspace from 5 Hz to 20 Hz. As outlined above, we tested our main hypothesis (higher oscillatory power during sentences with long distances) in this massed permutation test framework using a paired t-test on data that were collapsed across the two levels of the factor deemed irrelevant to this analysis (i.e., argument order). To ensure that collapsing across the levels of the original argument order factor would yield a statistically reliable result, we also ran the identical analysis for this factor. A Monte—Carlo simulation with 1000 repetitions was used to identify significant clusters in time-frequency space, while controlling for false positives. We set the algorithm to first identify time-frequency bins that showed a significant effect at $p < .025$ and then searched for time-frequency-electrode clusters that behaved similarly, considering a minimum of three neighboring (i.e., inter-electrode distance <6.5 cm) electrodes as a cluster.

2.5. Source localization

Source localization of the significant time-frequency cluster in the alpha band (see Results) first involved warping participants' individual electrode positions to the cortical mesh of a standard Boundary Element Model (BEM) head model as derived from a standard structural magnetic resonance image, using a rigid-body transform (Besl and McKay, 1992). For each point along a 1-cm-spaced grid in this volume conductor, a forward model was estimated.

The source localization followed the workflow proposed by various previous studies using an adaptive beamformer in the frequency domain (the "dynamic imaging of coherent sources" beamformer, Gross et al., 2001; for applications see e.g., Haegens et al., 2010; Jensen and Mazaheri, 2010; Medendorp et al., 2007; Obleser and Weisz, 2011): To attain a good spatial filter for all conditions, an additional time-frequency analysis on the data segments of interest (see Results) and their respective baselines was carried out, centered at 10 Hz (±2 Hz spectral smoothing) and 2500 msec (±250 msec relative to sentence onset, see Results; plus respective estimates from −500 to 0 msec baseline intervals), using a multitaper approach (Mitra and Pesaran, 1999). From this, the cross-spectral density matrix was gathered for subsequent localization. In this way, a spatial filter for each grid point in the volume conductor was generated. Subject- and condition-specific source activity estimates were derived by applying this spatial filter to the condition-specific sensor data. The resulting source activity volumes were corrected for activity during the baseline period, collapsed across short and long conditions (see above), and passed into a paired t-test. This procedure resulted in a source-level t statistic of alpha power change for each voxel in the volume grid, which could then be mapped back onto a standard structural magnetic resonance image. Resulting peak coordinates in MNI space were

converted into the space of Talairach and Tournoux' (1988) atlas using a non-linear transformation (Lacadie et al., 2008) for anatomical labeling.

2.6. Correlation analyses

Because the behavioral performance as determined by d'-scores was positively correlated with reading span test scores (see Results), we also sought to further elucidate the relation between participants' verbal working memory abilities and alpha power. To this end, we first computed individual differences between the individual averaged source activity volumes for the long and short conditions (see Results). We masked these volumes for all voxels that had shown a significant difference in source activity between the two conditions of at least $t(35) > 2.5$ at the group level. All voxels inside these volumes underwent a linear regression analysis between the increase in source activity for the long as compared to the short argument-verb conditions and individual reading span scores (see Results).

3. Results

3.1. Behavioral data for sentence processing

We calculated d'-scores in order to avoid participants response bias (i.e., the individual tendency to respond either yes — correct or no — incorrect) from obscuring the behavioral result. Mean d'-scores for the yes—no sentence comprehension were 3.80 (SD = .97) for the short and 3.96 (SD = 1.00) for the long argument-verb dependencies. Mean percentage correct scores for the short and long conditions were 89.01% (SD 7.89%) and 92.06% (SD 9.18%), respectively. For comparison to d'-scores, we cleaned these mean percentage correct scores for the mean response bias of $c = -.24$ (short condition) and $c = -.13$ (long condition) according to the procedure suggested by Macmillan and Creelman (2005). Bias-free percentage-correct estimates of 81.82 (short condition) and 82.56 (long condition) resulted. A dependent-samples t-test on the d'-scores found no significant difference between the two conditions. Also, mean d'-scores were positively correlated with reading span test scores across participants ($r = .38$, $p < .05$).

3.2. Time-frequency data during sentence processing

The statistical comparison between the time-frequency patterns of the short and long argument-verb distances yielded a single, sustained difference ($p < .025$), lasting from 2.25 sec to 3.20 sec in the 7—13 Hz (alpha band) range. It was most pronounced at 10 Hz, ranging from 2.25 to 2.75 sec. From 2.75 sec onwards (i.e., adjacent to the sentence-final verb, which began at 2.9 sec on average) this cluster broadened in frequency and ranged up to the 20-Hz limit (beta band) of our analysis window. For the second factor in the original design (argument order), no effect was obtained. Fig. 2 summarizes the results: While baseline-corrected spectral power in the 4—20 Hz range is shown in the upper panel, the experimental manipulation elicits a significant increase of alpha

activity for long as compared to short argument-verb dependencies (lower panel; shown are t-values from the statistical comparison).

3.3. Source localization of alpha activity during sentence processing

Source localization on the cluster segment of interest from 2.25 to 2.75 sec which showed a sustained effect at 10 Hz yielded maxima in bilateral occipital cortices (left: $x = -31$, $y = -88$, $z = 22$; right: $x = 7$, $y = -94$, $z = -20$; all coordinates in MNI space) as well as in left parietal cortex ($x = -60$, $y = -14$, $z = 44$). The peaks correspond to the left superior occipital gyrus, right lingual gyrus and the transition between the left supramarginal gyrus and left precentral gyrus, respectively. Statistical maps of these results are given in Fig. 3.

3.4. Correlation analysis between alpha activity during sentence processing and reading span

As can be seen in the right panel of Fig. 4, a voxel-wise correlation analysis of individuals' source-level alpha power change and reading span yielded a strong negative peak in the left parietal cortex (peak at $x = -51$, $y = -16$, $z = 49$; $r = -.42$, $p < .01$), while no significant correlation was obtained for neither the entire cluster level (right panel) nor the peak voxel level (left panel) in the occipital area (peak at $x = 12$, $y = -79$, $z = -4$; $r = .26$, $p > .1$). The left panel of Fig. 4 illustrates the correlations between source-level alpha power change and reading span at the respective cluster peaks. The parietal peak corresponded to the left postcentral gyrus.

4. Discussion

This study sets out to elucidate the potential role of alpha oscillations during the processing of sentences that place high storage demands on verbal working memory, whereby verbal working memory storage was scrutinized by systematically varying the distance of an argument-verb dependency.

The results of this study show that long argument-verb distances in sentence processing elicit stronger sustained oscillations at 10 Hz (alpha band) during the storage phase than short argument-verb distances. This difference starts about 2 sec after argument presentation with a maximum immediately prior to memory retrieval at the main verb in sentence-final position. This effect turns into a transient beta band effect (13—20 Hz) immediately at the main verb. As the time-frequency representations in the upper panel of Fig. 2 illustrate, the processing of all sentence types used in our paradigm elicits an alpha enhancement that builds up throughout the sentence. The lower panel of Fig. 2 illustrates that this increase in alpha activity is significantly stronger for long as compared to short argument-verb dependencies.

The sources of this alpha power increase were localized to bilateral occipital and left parietal cortices. Only in parietal cortex did source activity correlate significantly and negatively with reading span, a classic behavioral measure of verbal working memory ability from the sentence processing domain. Because reading span was also predictive of
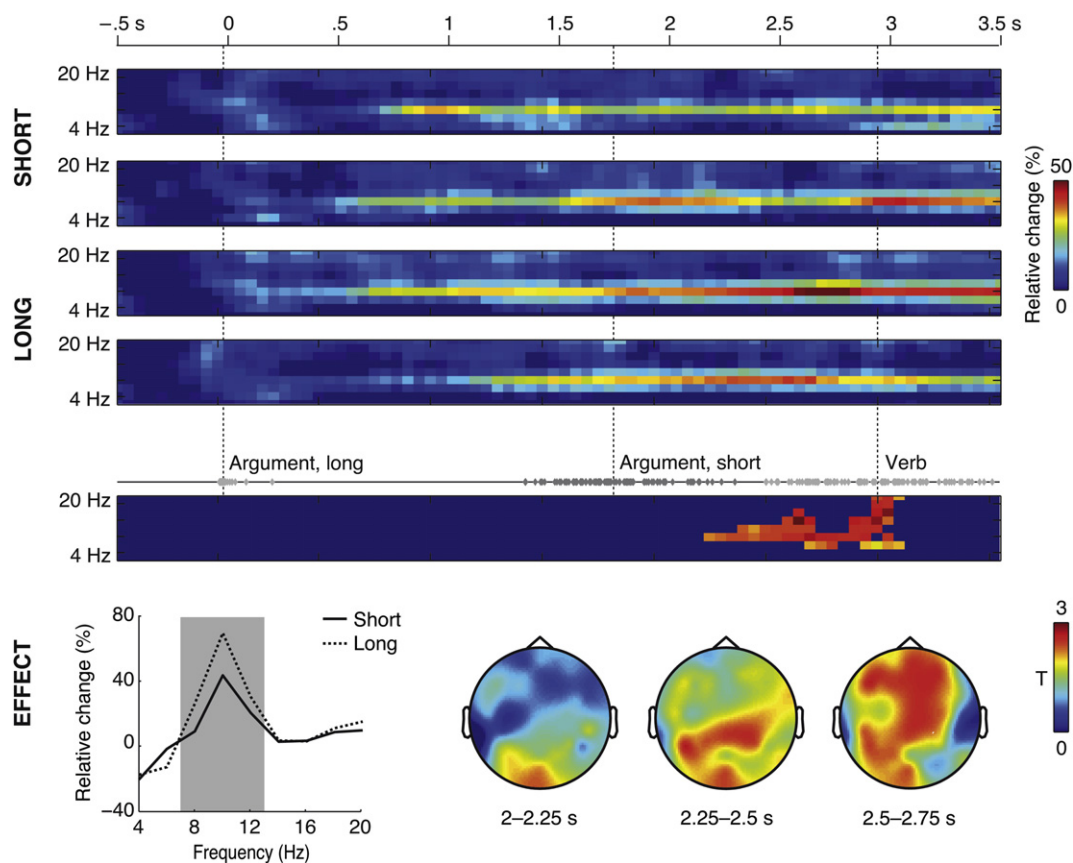
Fig. 2 — Time-frequency results during sentence processing with respect to the cumulative and average latency of the arguments and the sentence-final verb. The upper panel shows the raw grand average sustained alpha activity (10 Hz) for the four conditions: subject-first short, object-first short, subject-first long and object-first long displayed in the top four rows, respectively. The lower panel displays the t-values from the paired-samples t-test on the long and short conditions, averaged across significant time-frequency bins. The alpha cluster starts approximately .75 sec prior to and ends with the main verb onset. The bottom left panel shows the average frequency spectrum, the bottom right panel shows the scalp distribution in the 10-Hz band in steps of .5 sec, starting at 2 sec. Effects are thresholded at $p < .025$ and cluster-size corrected.

participants' behavioral performance on the experimental task, we specifically suggest that left parietal cortex may be an important neural substrate for verbal working memory during sentence processing. We interpret these results as evidence that the role of alpha oscillations previously shown in verbal working memory tasks from outside the sentence processing domain also applies to sentence processing. We will now discuss our time-frequency findings from a functional, psycholinguistic, and neuroanatomical perspective.

The functional significance of alpha oscillations for verbal working memory revealed in the present study is in line with data from various earlier working memory studies conducted on pitch (Van Dijk et al., 2010), letter (Krause et al., 1996), syllable (Leiberg et al., 2006; Luo et al., 2005) and digit retention (Schack et al., 2005) in the auditory, non-sentential domain. In particular, the present result from a sentence comprehension task converges on a seminal study on letter retention by Jensen et al. (2002), who report alpha power over posterior EEG sensors to increase with higher demands in the letter retention task. Jensen et al.'s (2002) effect was most pronounced during the

late storage phase, immediately prior to memory retrieval. In particular, this detail matches our data, since the observed alpha cluster in our data occurred in temporal proximity to the verb, where working memory retrieval is most likely to take place, and was less pronounced during the early storage phase. Along these lines, Maltseva et al. (2000) observed increased alpha phase locking prior to omitted stimuli when participants were given a series of identical auditory stimuli. Crucially, this increased alpha phase locking was observed prior to the anticipated retrieval of a stimulus, that is, during trials where no actual retrieval took place. Given this finding, we suggest that the increased alpha power in our results for the long argument-verb dependency reflects increased inhibition demands for the argument immediately prior to argument retrieval at the sentence-final verb. Since an increased likelihood for the sentence-final verb to occur entails a potential for argument retrieval, increased alpha activity in temporal proximity to the verb ("honored" in the example sentences displayed in Fig. 1) may index the inhibition of a premature argument release ("the coach", "the striker").
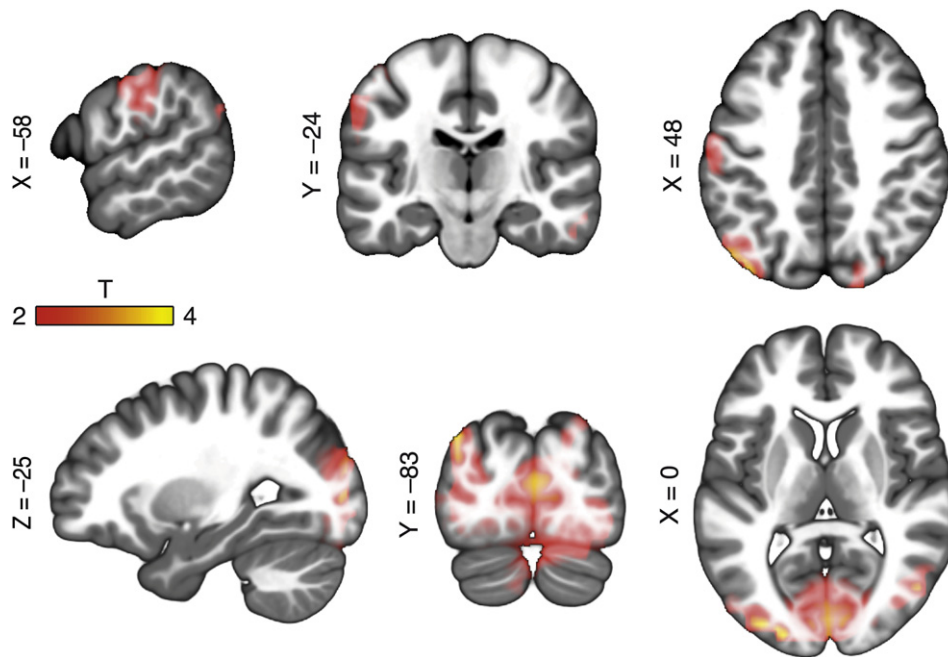
Fig. 3 — Statistical maps of the comparison between alpha activity during the short and long conditions in source space. The upper panel shows sagittal, coronal and axial slices at local source maxima in the left parietal cortex. The lower row shows slices for the local source maxima in the bilateral occipital cortices. Maps are thresholded at t(35) = 2, approximating the uncorrected threshold from the statistical analysis in source space.

This view converges surprisingly well on a classical psycholinguistic theory of argument-verb dependency processing, the active filler hypothesis (Clifton and Frazier, 1988) according to which a stored argument will be released from verbal working memory as soon as the verb which the argument will be linked to is likely to occur. In the light of our data, this view nicely goes together with a major theoretical approach of oscillatory brain activity that puts forward the idea of alpha oscillations as a domain-general mechanism for the functional inhibition of neural activity (Jensen and Mazaheri, 2010; Klimesch et al., 2007). For the domain of working memory processes, Klimesch et al. (2007) propose that alpha activity increases with inhibition demands to avoid premature information release. Under this view, our finding of parietal alpha activity being negatively correlated with reading span might index that participants with higher reading spans need to tax their functional inhibition system less to achieve good sentence comprehension performance, reflected in relatively less alpha power in high-span as compared to low-span participants in spite of an overall alpha power increase on the group level. This interpretation is supported by the fact that behavioral performance in our study was positively correlated with reading span scores, and it is in line with Klimesch et al. (2007), who find alpha power during task performance to be negatively correlated with cognitive abilities.

From a psycholinguistic point of view, the characterization of alpha power as an index of functional inhibition is in line with our finding that the present alpha-cluster offset closely matches the verb onset, rising into the beta band at this point (see Fig. 2). Evidence for the view that arguments are retrieved in the vicinity of verbs comes from a number of behavioral cross-modal priming studies (McElree, 2000; McElree et al., 2003; Nicol et al., 1994; Nicol and Swinney, 1989; Tanenhaus et al., 1985). These studies showed that arguments which are encountered early in a sentence prime lexically or phonologically related target words at immediately pre- or post-verbal positions, pointing to argument reactivation in verbal working memory. Importantly, such behavioral priming effects were present independently of whether a subject or an object was reactivated.

The psycholinguistic evidence that arguments are retrieved in the vicinity of verbs may also explain why we also obtained more transient significant beta-band oscillations immediately at the sentence-final main verb, in addition to the prior alpha effect. This is in line with a recent report on the significance of beta oscillations for processes related to structural aspects of sentence processing (Bastiaansen et al., 2010). Enhanced oscillatory power in the beta band was found during the processing of syntactically correct sentences as compared to word lists and violated sentence structures: Beta oscillations were visible in the violation condition until the violation could be detected, and increased during the ongoing sentence in the correct sentence condition. The authors suggested that this effect is linked to the integration of incoming information into the ongoing syntactic representation of the sentence. The beta effect in the current study is in line with this proposal in that it occurs at a point where a link between the incoming verb and the stored argument is established, that is, during argument retrieval from verbal working memory (McElree, 2000; McElree et al., 2003; Nicol et al., 1994; Nicol and Swinney, 1989; Tanenhaus et al., 1985).
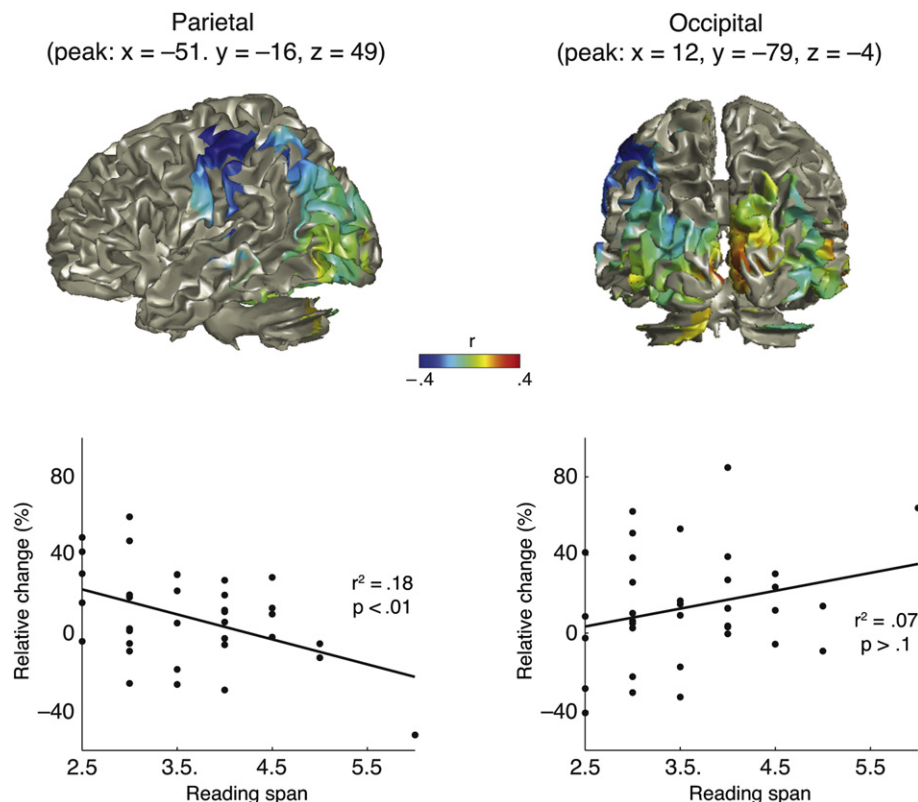
Fig. 4 – Statistical maps of the whole-brain correlation analysis between alpha power change during sentence processing and reading span. The left panels illustrate the cortical distribution of the correlation across the left hemisphere, with the scatterplot showing the negative correlation between source activity at the peak correlating voxel in the parietal cortex. The right panels show the correlation across bilateral occipital cortices, with the scatterplot showing the non-significant correlation at the peak in the occipital region.

Evidence for this interpretation is further provided by data from Weiss et al. (2005), who report increasing beta coherence between anterior and posterior sensors at a sentence position where a subject argument needed to be linked to a sentence-final verb. Although not discussed in depth by Weiss et al. (2005), their data also show sustained increased alpha coherence toward the end of the argument retention interval, prior to the beta coherence increase, similar to our own effect.

Finally, a recent non-sentential study by Hsieh et al. (2011) gives reason to assume that the alpha oscillations observed in the present study reflect a different underlying mechanism than that reflected in the sustained negativity observed in previous ERP studies from the sentence processing domain. While Hsieh et al. (2011) show that alpha oscillations during verbal working memory storage are independent of the order of memory items, the electrophysiological literature on argument-verb dependency processing revealed a sensitivity of the sustained negative ERP effect to the relative order of subject and object (Clahsen and Featherston, 1999; Felser et al., 2003; Fiebach et al., 2001; Kluender and Kutas, 1993; Nakano et al., 2002; Phillips et al., 2005; Ueno and Kluender, 2003). In contrast, and in line with Hsieh et al.'s (2011) findings, our sentence processing study did not show an oscillatory effect of argument order. Such an effect could have been expected since sustained negative ERP effects are

sensitive to argument order. In sum, the evidence so far suggests that alpha power changes can serve as an independent index of verbal working memory load during sentence comprehension.

Turning now to the current source localization results, the role of occipital and left parietal alpha sources for verbal working memory storage is partly corroborated by previous findings. We obtained both bilateral occipital and left parietal sources for the increased alpha activity, but only found left parietal source activity during argument storage and prior to argument release to correlate with a behavioral measure of verbal working memory performance: that is, reading span. These findings can be linked to the imaging literature from both sentence processing and outside the sentence processing domain, which also imply temporo-parietal brain regions as a neural substrate for verbal working memory storage (Awh et al., 1996, 1995; D'Esposito et al., 1999; Grossman et al., 2002; Jonides et al., 1998; Leff et al., 2009; Meyer et al., submitted for publication; Novais-Santos et al., 2007; Owen et al., 2005; Petrides et al., 1993; Smith and Jonides, 1999; Wager and Smith, 2003). For sentence processing, Grossman et al. (2002) found that brain activity in parietal cortex, related to increased argument-verb distance requiring increased verbal working memory storage resources, is decreased in seniors who show reduced sentence processing

performance. Additional support comes from a study on the processing of temporary ambiguous sentences (Novais-Santos et al., 2007) that reported increased left parietal activity with increased length of ambiguous sentence segments: that is, increased verbal working memory storage demands.

In contrast to these studies, other imaging work suggests that BA 45 in the inferior frontal gyrus, sometimes extending into the inferior frontal sulcus, subserves working memory during sentence processing (Fiebach et al., 2005; Makuuchi et al., 2009; Santi and Grodzinsky, 2007, 2010). However, these studies compared different kinds of syntactic dependencies across conditions. Particular syntactic dependencies in these studies may have engaged a syntactic working memory system, which has been suggested to be distinct from working memory used in other verbal tasks (Lewis et al., 2006; Van Dyke, 2007) and reported to activate BA 45 (Caplan et al., 2000). In contrast to the above studies, our paradigm kept the type of syntactic dependency constant across conditions. Furthermore, our experimental task was solvable using phonological strategies, which is also true for the reading span task used in our correlation analysis. In sum, we suggest that the above contrast between temporo-parietal and inferior frontal brain activations reflects the difference between phonological and syntactic working memory. An alternative hypothesis is that the frontal-posterior neural dichotomy rather mirrors a difference between domain-specific syntactic and domain-general attention-driven aspects of working memory processing: Buchsbaum and D'Esposito (2008) point out the possibility that brain activations in the middle and superior parietal lobe (regions above BA 40) may imply attentional mechanisms of working memory rather than storage *per se*. With respect to sentence processing, either suggestion must count as a hypothesis for future research.

With respect to parietal involvement in working memory during sentence processing, the connection between the current results, previous EEG findings and the functional magnetic resonance imaging (fMRI) literature also needs discussion: While Michels et al. (2010) reported a positive correlation between left parietal BOLD signal and left parietal alpha increase during a verbal working memory task in a combined fMRI and EEG study, Meltzer et al. (2007), report a negative correlation between bilateral parietal alpha and BOLD signal during a similar task. While our data cannot settle this argument, our localization agrees with the above studies in that it suggests a crucial role of left parietal cortex in verbal working memory. This supports the proposal of a functional relevance of this region in verbal working memory-related alpha oscillations during sentence processing.

While the data suggest a functional relevance of parietal alpha in higher-level cognitive processing, this is less straightforward for the occipital alpha sources. As occipital activity was not significantly correlated with reading span test scores, we suggest that occipital alpha activity does not reflect similar processes as the parietal alpha. This activity may rather reflect the inhibition of sensory bottom−up processes, potentially preventing incoming information from saturating the limited-capacity verbal working memory system (Jensen and Mazaheri, 2010; Just and Carpenter, 1992; King and Just, 1991; Thut et al., 2006). In the context of sentence processing, such a mechanism might serve to avoid new information

from interfering with arguments already stored in verbal working memory (Lewis, 1996; Van Dyke, 2007). While such a double role for alpha oscillations in the present study is speculative, a functional role of occipital cortices in verbal working memory is also unlikely given the fMRI data discussed above.

5. Conclusion

Our results show that in sentence processing, the storage of an argument (i.e., subject or object) over longer distances modulates and enhances alpha oscillations (10 Hz) in left parietal cortex. These oscillations are predictive of sentence processing performance as measured by a standardized sentence processing-specific verbal working memory test. Our results also support previous research that links argument-verb dependency establishment to beta oscillations. The time course and brain topography of the alpha effect suggests that alpha oscillations play a role in functionally inhibiting the premature release of verbal information that will subsequently be integrated. This is the first evidence that verbal working memory storage during sentence processing relies on oscillatory processes similar to those observed for domain-general working memory outside of sentence processing. Thus, oscillatory dynamics in the alpha range are a candidate neural surrogate that links listeners' language and sentence processing abilities to more domain-general neural and cognitive resources.

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