



Alignment of alpha-band desynchronization with syntactic structure predicts successful sentence comprehension

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ABSTRACT

Sentence comprehension requires the encoding of phrases and their relationships into working memory. To date, despite the importance of neural oscillations in language comprehension, the neural-oscillatory dynamics of sentence encoding are only sparsely understood. Although oscillations in a wide range of frequency bands have been reported both for the encoding of unstructured word lists and for working-memory intensive sentences, it is unclear to what extent these frequency bands subserve processes specific to the working-memory component of sentence comprehension or to general verbal working memory. In our auditory electroencephalography study, we isolated the working-memory component of sentence comprehension by adapting a subsequent memory paradigm to sentence comprehension and assessing oscillatory power changes during successful sentence encoding. Time–frequency analyses and source reconstruction revealed alpha-power desynchronization in left-hemispheric language-relevant regions during successful sentence encoding. We further showed that sentence encoding was more successful when source-level alpha-band desynchronization aligned with computational measures of syntactic—compared to lexical-semantic—difficulty. Our results are a preliminary indication of a domain-general mechanism of cortical disinhibition via alpha-band desynchronization superimposed onto the language-relevant cortex, which is beneficial for encoding sentences into working memory.

Introduction

Successful sentence comprehension critically relies on verbal working memory for the encoding and maintenance of syntactic and semantic representations (Caplan, 2016; Caplan and Waters, 2013; Gibson, 1998, 2000; Lewis et al., 2006; McElree et al., 2003; Fedorenko et al., 2004; Just and Carpenter, 1992; Rogalsky and Hickok, 2011). Working-memory capacity can predict sentence comprehension abilities (Daneman and Carpenter, 1980; Daneman and Merikle, 1996), in particular when comprehension increases working-memory demands due to syntactic ambiguity (MacDonald et al., 1992) or due to long dependencies between words that do not occur in succession (King and Just, 1991; Meyer et al., 2012, 2015) and when increasing working-memory load limits reading comprehension (Baddeley and Hitch, 1974).

While the functional neuroanatomy of the working memory underlying sentence comprehension likely involves a dorsal left-hemispheric network of inferior frontal, inferior parietal, and superior temporal cortices (Cooke et al., 2002; Friederici et al., 2006; Grodzinsky and Friederici, 2006; Grossman et al., 2002; Meyer et al., 2012; Novais-Santos

et al., 2007), the spatiotemporal dynamics inside this network are still poorly understood. From a neurophysiological viewpoint, neural communication within such large-scale (inter-regional) networks can be indexed through the analysis of brain rhythms in various frequency bands (Buzsáki, 2006), as processes of network (de)synchronization and integration underlying cognitive functioning are reflected in neural oscillatory-power patterns (Varela et al., 2001) that can be decomposed from electroencephalographic (EEG) recordings. Therefore, to gain insight into the spatiotemporal dynamics of this network, we looked at neural oscillations related to sentence-level working memory.

In recent years, the role of neural oscillations in high-level language processing, such as sentence processing, has been emphasized (e.g., Bastiaansen and Hagoort, 2015; Ding et al., 2016; Friederici and Singer, 2015; Lewis et al., 2015; Mellem et al., 2013; Meyer et al., 2016; Röhm et al., 2001; Rommers et al., 2017; Weiss and Mueller, 2003, 2012; Weiss et al., 2005), apart from their established role in low-level speech perception (Giraud and Poeppel, 2012; Peelle and Davis, 2012). Previous studies particularly linking neural oscillations to working-memory processes supporting sentence processing have resulted in a diverse picture: Bonhage et al. (2017) reported delta-band power increase during

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sentence encoding; Bastiaansen et al. (2010) reported theta-band power increases for the processing of grammatically correct sentences; Meyer et al. (2013) found alpha-band power increases during processing of working-memory intensive sentences; Bonhage et al. (2017) showed that beta-band oscillations are sensitive to sentence-encoding demands. In the broad alpha/beta band, desynchronization was observed during sentence maintenance (i.e., delay period) in working memory (Meltzer et al., 2017), while synchronization was observed for syntactic binding in two-word sentences (Segaert et al., 2018). At the same time, theta-, alpha-, and beta-band activity has also been associated with verbal working memory outside of the sentence-comprehension domain. Successful encoding of unstructured word lists is accompanied by theta-band power increases (Hanslmayr et al., 2011; Klimesch et al., 1996a, 1997; Lega et al., 2012; Staudigl and Hanslmayr, 2013; Weiss et al., 2000), as well as alpha- and beta-band power decreases (Fell et al., 2008; Fellner et al., 2013; Hanslmayr et al., 2009; Klimesch et al., 1996b; Sederberg et al., 2007), the latter being interpreted as reflecting (word-level) semantic memory processes (Hanslmayr and Staudigl, 2014; Hanslmayr et al., 2012; Klimesch et al., 1997).

Given this diversity, it is unclear whether the observed oscillatory activity during sentence comprehension in delta, theta, alpha, and beta bands subserves functions specific to the working-memory component of sentence comprehension, specific to other sentence-level linguistic processes (e.g., syntactic complexity), or general to verbal processing (i.e., similar for the processing of word lists and sentences). To directly study the encoding of sentences into working memory without tapping into other sources of processing complexity, our present EEG study employed a subsequent memory paradigm (Friedman and Johnson, 2000; Paller and Wagner, 2002; Rugg and Alan, 2000), which was based on the post-hoc binning of experimental trials into successfully encoded (SE) and later forgotten (LF) sentences. By contrasting oscillatory power spectra during successful encoding for SE and failed encoding for LF, we thus assessed those oscillatory power changes that were critical for the encoding of sentences into verbal working memory—the so-called *subsequent memory effect* (SME). Stimuli to be encoded into working memory were long sentences consisting of two clauses each, which cannot, in principle, be encoded without forming a syntactic structure amongst the to-be-encoded words. In a subsequent retrieval task, parts of the encoded sentences were to be recalled via a naturalistic, implicit retrieval process. A following comprehension question assessed retrieval success—and indirectly, encoding success. Given prior findings, we initially hypothesized that the successful encoding of sentences may be reflected in power increases in the delta and/or theta band(s), and/or power decreases in the alpha and/or beta band(s). In addition, as the memorization of words inside sentences is facilitated by relational information amongst the words, we post-hoc hypothesized that the pattern of any emerging frequency-dedicated oscillatory changes may selectively track the pattern of sentences' syntactic or lexical-semantic processing difficulty. We examined these hypotheses by performing scalp-level time–frequency analysis, source reconstruction, and computational modeling of sentence-processing difficulty. Our findings confirm the hypothesis of an alpha-band desynchronization underlying a mechanism that enables the language-relevant cortex to successfully encode sentences into working memory via tracking the sentences' syntactic structure.

Materials and methods

Participants

Thirty-two native speakers of German participated (16 females, mean age = 25.25 years, standard deviation [SD] = 2.0 years) in this study. All participants were right-handed (Oldfield, 1971; mean lateralization quotient = 88.63, SD = 14.23) adults. Due to low quality of individual EEG datasets, unclear individual alpha frequency in the resting-state EEG frequency spectra, and/or behavioral outliers (see Data analysis), 8 participants were excluded from further analyses and 24 participants (10

females; mean age = 22.96 years, SD = 1.85 years) remained in the final group. Participants had no history of neurological or hearing deficits and had normal or corrected-to-normal vision. Experimental procedures were approved by the Institutional Review Board of the University of Leipzig, Germany, in accordance with the Declaration of Helsinki, and written informed consent was obtained from all participants. Monetary compensation of € 7,00 was given per hour of participation.

Stimuli

To study the contrast between sentences that were successfully encoded (SE) into working memory and sentences that were later forgotten (LF), we adapted a subsequent memory paradigm with immediate cued recall to auditory sentence comprehension (used also in Beese et al., 2017).

Encoding sentences (Fig. 1A) contained two clauses linked by *und* (and; coordinating conjunction). Each clause consisted of a subject noun phrase (NP; *der Komponist / the male composer*) and two object NPs (one male, one female; *den Solisten und die Bassistin / the male soloist and the female bassist*). The two clause subjects were the male and the female forms of the same noun (*der Komponist / the male composer* and *die Komponistin / the female composer*). Grammatical gender of all nouns was marked by suffixes (e.g., male: *-er, -ant*; female: *-erin, -antin*) rather than natural gender (Comrie, 1999; Lieber, 2010). The extended duration of the encoding sentences (mean duration = 6.82 s, SD = 0.45 s) enabled us to retrieve reliable estimation of low-frequency spectral power along the sentence (Basar et al., 1999; Samar et al., 1999; see Data analysis).

Retrieval sentences (Fig. 1B) were designed to unambiguously cue retrieval of one specific NP out of the six possible NPs in the encoding sentence via two retrieval cues (*die Angewiesene / the female instructed* and *von ihm / by him*, specifically referring to the female object instructed by the male subject, that is, *die Bassistin / the female bassist*). For comprehension of a retrieval sentence, subjects had to link an adjective (*vorlaut / impertinent*) to the to-be-retrieved NP. Two types of retrieval sentences were used to avoid the encoding of the preceding sentence as simple word list (i.e., without encoding relational grammatical information); thus, subject and object retrieval (*die ihn Anweisende / the female instructing the male* and *die von ihm Angewiesene / the female instructed by the male*, respectively) was counterbalanced. Crossing 2 retrieval cues \times 2 grammatical genders resulted in 4 variants per retrieval sentence.

The comprehension of the retrieval sentence, and thus indirectly, the encoding of the NPs in the encoding sentences, was assessed by a subsequent comprehension question (Fig. 1C). A correct answer to the comprehension question implied that the participant had linked the adjective in the retrieval sentence to the correctly-retrieved, and thus correctly-encoded, NP from the encoding sentence; likewise, an incorrect answer implied failed retrieval, and thus failed encoding. In half of the stimuli, the correct answer to the question was yes; in the other half, it was no: either the question would wrongly query the subject instead of the object or vice versa (subject/object lure), or the question would query the object with the opposite gender from the same clause (gender lure). Lure types were counterbalanced.

We designed an initial stimulus pool of 128 encoding items. All nouns were unique across the pool. Across items, each object noun could appear in only one grammatical gender; subject noun gender was counterbalanced within item. Word length (mean syllable count = 3.60, SD = 0.49, range = 3–4 syllables) and lemma frequency (mean frequency class across items = 14.21, SD = 2.16, range = 9–19; mean difference of frequency classes within item = 1.89, SD = 0.31; *Projekt Deutscher Wortschatz*; Biemann et al., 2007; Quasthoff et al., 2006) were matched within item, within sentential position, and across items to avoid confounding encoding demands (Diana and Reder, 2006; Halgren et al., 2002; Leiberg et al., 2006). To avoid noun gender \times noun position confounds, we permuted both objects and clauses, resulting in 8 variants of each initial stimulus item (i.e., 1024 stimuli in total). Stimuli were recorded by a professional male speaker in a soundproof booth. Using Praat (Boersma

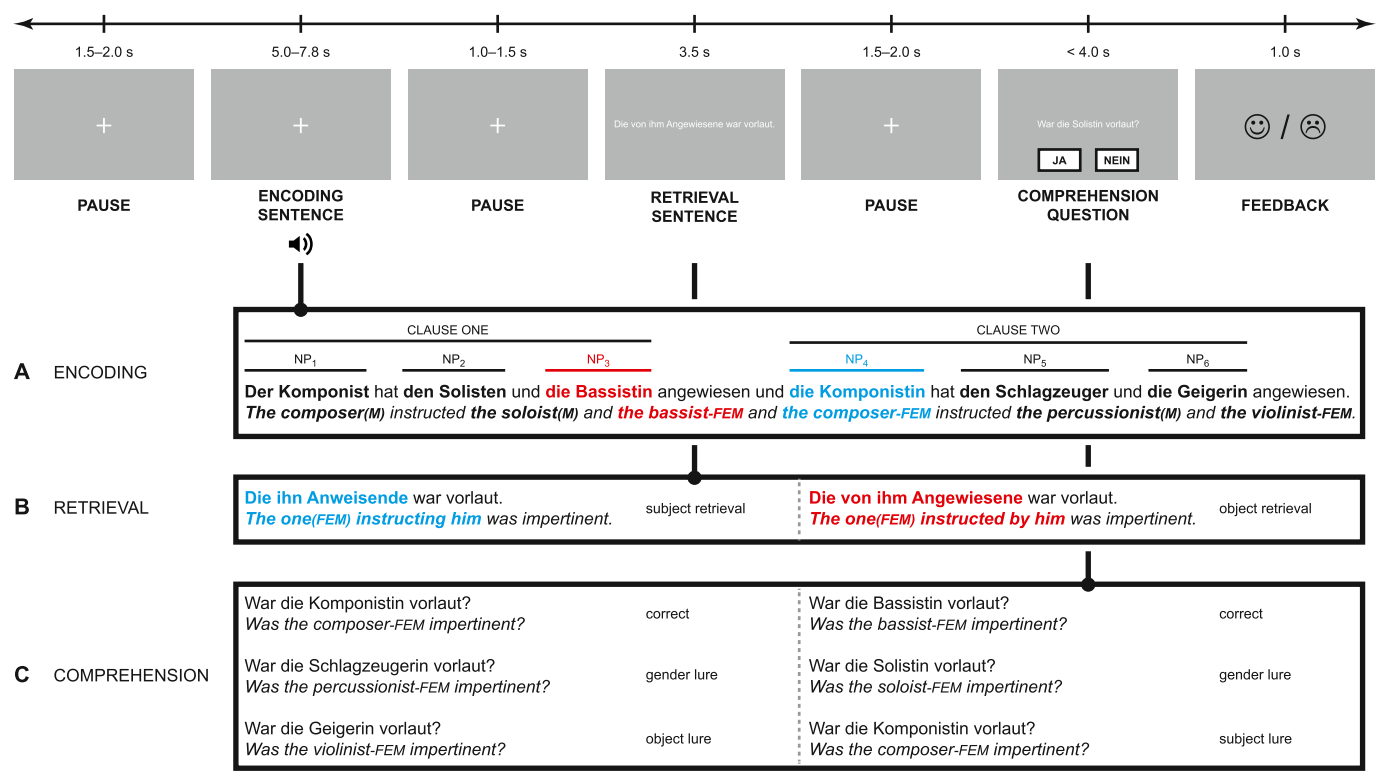


Fig. 1. Overview of the experimental materials and procedure: The encoding sentence consisted of two clauses; each clause contained a subject NP and two object NPs (indicated in bold strings); in the retrieval sentence, retrieval of one of the NPs (either a subject or an object; i.e., subject retrieval and object retrieval, respectively) was cued through the combination of two retrieval cues marked for grammatical gender (male [M] or female [FEM]); word strings in blue and red in the encoding sentence indicate the NPs cued by the respective retrieval sentences; the comprehension question assessed retrieval success, and thus, indirectly encoding success (correct, gender lure, and object lure or subject lure).

and van Heuven, 2001), we cut the stimuli and normalized their intensity to 65 dB. To avoid acoustic flank artifacts, we attached cosine-shaped 50-ms onset and offset ramps. The duration of the pause between the two clauses was matched across stimuli (200 ms) to achieve better clause alignment across experimental trials. From the 8 variants of the encoding sentence of each experimental item, we recorded only 4 variants; the remaining variants were cross-spliced. Taking into account the clause and object permutations of the encoding sentence and the gender permutations of the retrieval sentence, we ended up with a full set of 32 variants per experimental item. According to a Latin square, we distributed the final item pool across 32 individual lists, each containing 128 experimental items. Retrieval type (subject versus object retrieval), answer type (correct or incorrect), and type of incorrect response (subject/object lure versus gender lure) were counterbalanced within lists. Each list also contained additionally 64 fillers to prevent habituation effects and strategy build-up. Fillers were object-relative sentences adapted from a previous study (Meyer et al., 2015). Each final individual list contained 192 stimuli and was pseudo-randomized.

Procedure

Participants were seated in a dimly lit, electrically shielded, sound-proof booth. Prior to the experiment, resting-state EEG data were recorded with closed eyes (EC) and open eyes (EO), each for 5 min. In the experiment, stimuli were presented using the Presentation® software package (Version 17.0, Neurobehavioral Systems, Inc., Berkeley, CA, USA). Auditory stimuli were played through a pair of Sony stereo MDR-XD100 headphones (Sony Corporation, Tokyo, Japan). Visual stimuli were displayed in white Arial font (font size = 30 points) on a gray background through a Sony Trinitron Multiscan E220 CRT 17" monitor (Sony Corporation), which was placed within 1-m distance from the participant.

Trials consisted of an encoding sentence, a retrieval sentence, and a comprehension question (Fig. 1). Each trial began with a fixation cross (random duration between 1500 and 2000 ms) that remained on screen during stimulus playback. Presentation of the auditory encoding sentence followed. After another interval (random duration between 1000 and 1500 ms), a visual retrieval sentence was shown on screen (3500 ms), followed by another interval (random duration between 1500 and 2000 ms). Subsequently, the visual comprehension question was presented. The two answering options (i.e., yes or no / no or yes) were displayed underneath. Participants were given a fixed response-time window (4000 ms). The experiment began with 24 practice items, common to all participants and different from the items used in the main experiment. To avoid fatigue, the main experiment's trials were presented in six blocks of 32 trials each, with short breaks (1–4 min) between blocks. The experiment lasted for approximately 1 h, plus 1 h for preparation.

Data acquisition

The EEG, electrooculogram (EOG), and surface electromyogram (sEMG) were continuously recorded with a bandwidth from DC to 270 at a sample rate of 1 kHz through a 72-channel Refa8 amplifier (TMS International BV, Oldenzaal, The Netherlands) from 63 Ag/AgCl unipolar scalp electrodes mounted in an elastic cap (WaveGuard™ original, eemagine GmbH, Berlin, Germany) according to the extended international 10–20 system. Vertical and horizontal EOGs were recorded from 2 sets of bipolar electrodes positioned at the outer canthi of both eyes and above and below the right eye, respectively. For accurate response assessment (see Data analysis), sEMG was recorded from the extensor digitorum communis muscle using 1 set of bipolar electrodes on each forearm (~15 mm centre-to-centre inter-electrode spacing). The setup was online referenced to the left mastoid and grounded to the sternum. Electrode impedances were kept below 5 kΩ. Behavioral responses to the

comprehension question (i.e., yes or no) were recorded through 2 single button boxes.

Data analysis

Data analysis was carried out in MATLAB® (The MathWorks®, Inc., Natick, MA, USA). Based on behavioral responses, trials were classified as SE (i.e., hits and correct rejections) or LF (i.e., misses and false positives). We quantified participants' response accuracy with d' -scores, accounting for the individual sensitivity to the experimental manipulations (Macmillan and Creelman, 2005). To optimize the ratio between SE and LF trials, we excluded participants with d' -scores below or above 1.96 SD from the group mean. For reaction time assessment, we transformed the reaction times to logarithms to normalize the distribution's typical skewness (Ratcliff, 1993) and compared the mean reaction times for SE and LF trials using paired-samples t -test. Because previously reported decision conflict in two-alternative forced-choice tasks may give rise to contaminated neural responses (Allain et al., 2009; Cohen, 2014; Cohen and van Gaal, 2014), we removed partial errors (Coles et al., 1995). To this end, the sEMG between the question onset and the button press of both arms was low-pass filtered at 250 Hz, baseline-corrected (0.5 s), and z -transformed; partial errors were SE trials with muscle activity in the incorrect-response arm that exceeded 2 SD in the time window of interest and had a peak two times larger than baseline (Cohen and van Gaal, 2014). On average, 7.00% (SD = 6.94%) of trials were excluded from further analysis.

Electrophysiological data were analyzed using the Fieldtrip toolbox (Oostenveld et al., 2011). For time–frequency decomposition, we used individually adjusted frequency bands based on each participant's individual alpha frequency (IAF; Grandy et al., 2013; Klimesch, 1999; Klimesch et al., 1996a; Moretti et al., 2012; Smit et al., 2006). To this end, we first segmented the EC and EO resting-state EEG into 150 continuous 2-s epochs each. We then re-referenced the data to the average of all EEG channels excluding the EOG and applied a 6th-order finite-impulse-response 0.1-Hz high-pass Butterworth filter. We used a distribution-based identification method ($z = 5$) to detect muscle artifacts; artifacts were rejected after visual inspection of waveform morphology. On average, 13.68% (SD = 10.19%) of EC data and 17.58% (SD = 9.72%) of EO data were rejected (no differences in rejection rates; paired-samples t -test; $t(26) = -1.74$, $p > 0.05$). Blinks, eye movements, and heartbeat artifacts were corrected using independent component (IC) analysis (Makeig et al., 1996); to-be-rejected components were identified visually, based on component topography and waveform morphology (mean IC rejection rate = 14.71, SD = 3.33). We then conducted power-spectral analysis (Welch's method, Hanning window, no phase shift) from 1 to 20 Hz with a frequency resolution of 0.1 Hz. We then averaged the power values over 17 posterior channels (i.e., Pz, P1/2, P3/4, P5/6, P7/8, POz, PO3/4, PO7/8, Oz, O1/2; Grandy et al., 2013) separately for the EC and the EO spectra. The IAF was defined as the peak of the difference spectrum within the alpha frequency range (7–14 Hz; mean IAF = 10.38 Hz, SD = 0.83 Hz); frequency bands were then defined accordingly (Doppelmayr et al., 1998; Klimesch, 1999): delta ([IAF – 8 Hz]–[IAF – 6 Hz]; mean frequency = 2.38–4.38 Hz), theta ([IAF – 6 Hz]–[IAF – 4 Hz]; mean frequency = 4.38–6.38 Hz), and alpha ([IAF – 4 Hz]–[IAF + 2 Hz]; mean frequency = 6.38–12.38 Hz) comprising three sub-bands of 2-Hz bandwidth each (i.e., lower alpha 1, lower alpha 2, and upper alpha).

For time–frequency analysis of the task-related EEG, we segmented 7.9-s trials time-locked to the onset of the first NP of the sentence, including a 0.5-s pre-stimulus baseline, 5-s time window of interest, plus 1.2-s buffer on each flank to allow edge artifacts to subside for decomposition of frequencies below 2 Hz. Artifact detection and rejection were analogous to the resting-state data (mean overall rejection rate = 29.23%, SD = 10.31%; no significant difference in rejection rates between correct and incorrect; mean rejection rate SE = 28.70%, SD = 10.69%; mean rejection rate LF = 31.50%, SD = 10.84%; paired-

samples t -test; $t(23) = -1.72$, $p > 0.05$). From the experimental epochs, we then segmented the data corresponding to the six NPs (mean length = 0.83 s, SD = 0.17 s). To each segment, we then applied Multi-taper analysis (Hanning window, 1 Hz spectral smoothing, 1 Hz spectral resolution) for the individually-adjusted delta, theta, and alpha bands, as well as for the fixed beta band (15–28 Hz), which cannot be adjusted individually, to the best of our knowledge. Power was averaged across trials per condition and participant and then quantified in terms of its change relative to baseline, power spectra for each NP were concatenated per condition, and power was averaged across NPs. To identify significant clusters of power change, we compared SE to LF trials using a paired-samples t -test and corrected for Type I error probability ($\alpha = 0.05$) using cluster-based Monte-Carlo non-parametric permutation statistics (10,000 permutations; Maris and Oostenveld, 2007), with a conservative threshold for the definition of significant clusters at each permutation (i.e., precluster threshold; $\alpha = 0.01$). Note that this method for multiple-testing correction controls for spatial autocorrelation in the EEG data, as it defines the probability of an observed cluster of independently suprathreshold electrodes to be significantly large based on a distribution of cluster sizes that is generated by randomly shuffling the observed data (Cohen, 2014; Maris, 2012). For each electrode, we defined neighboring electrodes using triangulation (mean number of neighboring electrodes = 6.62, SD = 1.63), based on template electrode positions. A minimum of 2 neighboring electrodes was considered a cluster.

We localized the sources of the sensor-level effect (see Results) by employing template electrode positions in combination with a standard boundary-element model (BEM; Fuchs et al., 2002) provided with the Fieldtrip toolbox, as well as a matching lead field matrix for a 10-mm-spaced 3-D volume-conductor source grid. For each participant, we then performed a dipole beamformer analysis on the broadband of the sensor-level effect using the Dynamic Imaging of Coherent-Sources (DICS; Gross et al., 2001) method. To this end, we generated a spatial filter common to both experimental conditions for each grid point (1% regularization), first for the experimental epoch, then for the baseline interval. In time–frequency analysis we calculated the cross-spectral density matrices for the baseline and each of the 6 time windows for the NPs for both conditions. The matrices were concatenated within condition along the time dimension and the spatial filter was applied. We then calculated the relative change of source power from the baseline and obtained the t -contrast map of the average source power of SE and LF using a paired-samples t -test. To identify significant clusters of source power change, we used a Monte-Carlo simulation as implemented in the Analysis-of-Functional-Neuroimages (AFNI) toolbox (3dClustSim; 10,000 iterations, $15 \times 18 \times 15$ volume-conductor resolution, 10 mm³ grid-point size, no volume mask; spatial autocorrelation parameters estimated by 3dFWHMx on the actual t -contrast in $15 \times 18 \times 15$ volume-conductor with 10 mm³ grid-point size; NIMH Scientific and Statistical Computing Core, Bethesda, MD, USA), which suggested that a cluster extent of at least 148 volume-conductor grid points at uncorrected $p < 0.05$ (i.e., $-2.07 > t > 2.07$) would ensure whole-volume Type I error probability $\alpha < 0.05$ (e.g., Meyer et al., 2015; Obleser et al., 2011). For anatomical description of the resulting clusters, we used the Automated-Anatomical-Labeling (AAL) brain atlas (Tzourio-Mazoyer et al., 2002) provided with the Fieldtrip toolbox.

Results

On average, participants remembered successfully 72.97% (SD = 9.37%, range = 48.41–85.94%) of the trials (mean d' -score = 1.31, SD = 0.60). Group performance exceeded chance level (one-sample t -tests; accuracy: $t(23) = 12.01$, $p < 0.001$; d' -score: $t(23) = 10.75$, $p < 0.001$). Two participants were excluded as they scored below -1.96 SD from the group mean. A high LF rate (mean percentage = 27.03%, SD = 9.37%, range = 14.06–51.59%) is required for SME analysis (i.e., the contrast between SE and LF sentences), as it ensures statistically reliable comparison with SE trials without reflecting chance-level

performance (i.e., an SE/LF ratio approximating 50%/50%). Optimal SE/LF ratios lie typically within the range of 60–75%/25–40% (e.g., Gruber et al., 2004; Hanslmayr et al., 2011; Meeuwissen et al., 2011; Osipova et al., 2006; Staudigl and Hanslmayr, 2013). Reaction times were lower for SE trials (mean log reaction time = 7.11, SD = 0.27) as compared to LF trials (mean log reaction time = 7.28, SD = 0.24; $t(23) = -10.74$, $p < 0.001$).

Sensor-level time–frequency analysis revealed a significant and robust negative SME in the alpha band, that is, a significant power decrease for SE as compared to LF trials averaged across time over central midline and right posterior electrodes (cluster's maximum: $t(23) = -3.87$, $p = 0.01$; Fig. 2). No significant SMEs were observed in delta-, theta-, and beta-band power.

Source localization of the significant sensor-level alpha-band cluster (Fig. 3A; Table 1) suggested a cluster of 174 volume-conductor grid points (i.e., total volume of $\sim 174,000 \text{ mm}^3$), which extended in both hemispheres and most prominently (i.e., in a total of 47.86%) encompassed the middle and inferior frontal gyri, the inferior parietal gyrus, and the supramarginal gyrus of the left hemisphere. As the size of this cluster exceeded the Monte-Carlo-simulation-derived cluster size of 148 volume-conductor grid points (see Data analysis), we considered the whole cluster as the potential cortical generators of alpha-band power.

Post-hoc analysis: computational modeling

Four arguments motivated our post-hoc hypothesis: First, the working memory underlying sentence comprehension is supposed to involve different levels of linguistic representation, such as syntactic (McElree, 2000) and lexical-semantic (Martin, 2005; Shivde and Anderson, 2011), with distinct neural correlates (Bornkessel-Schlesewsky and Schlewsky, 2013; Friederici, 2011; Hickok and Poeppel, 2004). Second, the encoding of sentences is facilitated by syntactic structure (Baddeley et al., 2009; Bastiaansen et al., 2010; Bonhage et al., 2014; Jefferies et al., 2004; Lombardi and Potter, 1992; Marks and Miller, 1964; Potter and Lombardi, 1998; Wingfield and Butterworth, 1984), which allows the generation of syntactic chunks in working memory (Bor and Owen, 2007; Gobet et al., 2001; Mathy and Feldman, 2012) and leads to better

memorization of words inside sentences than in unstructured word lists (*sentence superiority effect*; Brener, 1940; Epstein, 1961; Miller, 1956). Third, working-memory-related modulations of alpha-band power in the sentence-comprehension domain have been previously observed (Bastiaansen et al., 2002; Bonhage et al., 2017; Meyer et al., 2013). Fourth, the time series of alpha-band source power along the sentence in our data (Fig. 3B) was characterized by a plunge at the boundary between the two clauses and a pattern of within-clause increase, which pointed towards possible sensitivity of alpha-band power to the sentences' syntactic structure.

Therefore, we tested whether the observed SME in alpha-band power might reflect the encoding of sentences' syntactic properties. First, we estimated alpha-band power for each NP after applying the spatial filter to the single-trial cross-spectral density matrices, calculating the power change relative to baseline, and averaging source power across the 174 grid points of the significant cluster (e.g., Meyer et al., 2015; Meyer et al., 2013; Piai et al., 2015, Fig. 3B). Second, we estimated syntactic and lexical-semantic processing difficulty for each NP with a left-corner top-down parser using a context-free lexicalized grammar (Roark, 2001; Roark et al., 2009) that had been trained on the TIGER treebank before (Brants et al., 2004). Syntactic and lexical processing difficulty were quantified by syntactic (SynS) and lexical surprisal (LexS) respectively, capturing the probability of a syntactic category or word form, respectively, not to occur given the preceding words (Hale, 2001; Levy, 2008; Roark et al., 2009).

To test whether alpha-band power reflected genuine syntactic processing, we calculated partial correlations between power estimates and SynS/LexS across the six NPs, controlling for the NPs' sentence position and for the random factor of trial, on a single-trial basis, separately for SE and LF trials, and then Fisher-transformed them. We then compared the group means of correlation coefficients across participants. We ran a two-way repeated-measures analysis of variance (Response [SE versus LF] \times Surprisal [SynS versus LexS]), which showed only a main effect of Surprisal ($F(1,23) = 139.4$, $p < 0.001$): SynS was correlated significantly stronger with alpha-band power ($M = -0.19$, standard error of the mean [SEM] = 0.02) than was LexS ($M = 0.03$, SEM = 0.02; Fig. 3C) over the course of the sentence; no further main effects or interactions were

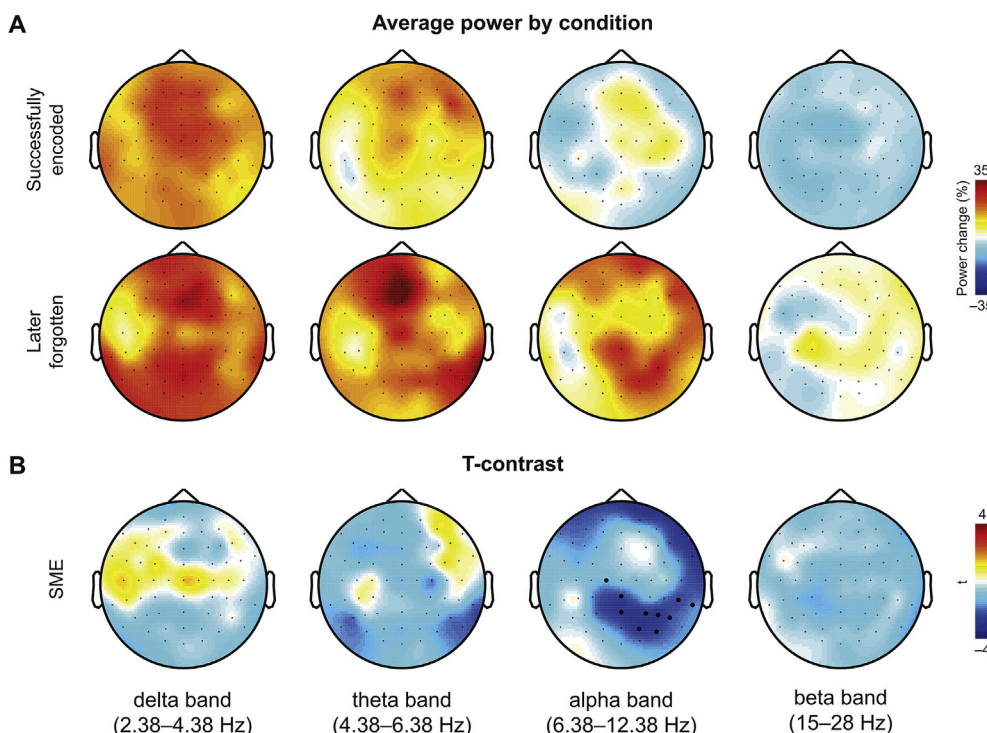


Fig. 2. Sensor level results: (A) Topographies of power representations relative to baseline for SE (upper panel) and LF (lower panel) trials in delta (2.38–4.38 Hz), theta (4.38–6.38 Hz), alpha (6.38–12.38 Hz), and beta (15–28 Hz), averaged across the six NPs of the encoding sentence; (B) t-maps of the statistical comparison of sensor power between the two conditions (SE versus LF trials); significant power changes ($-2.07 > t > 2.07$, $p < 0.05$, corrected) are obtained only in the alpha band (cluster's maximum $t(23) = -3.87$, $p < 0.01$); significant clusters are marked in solid-black sensors.

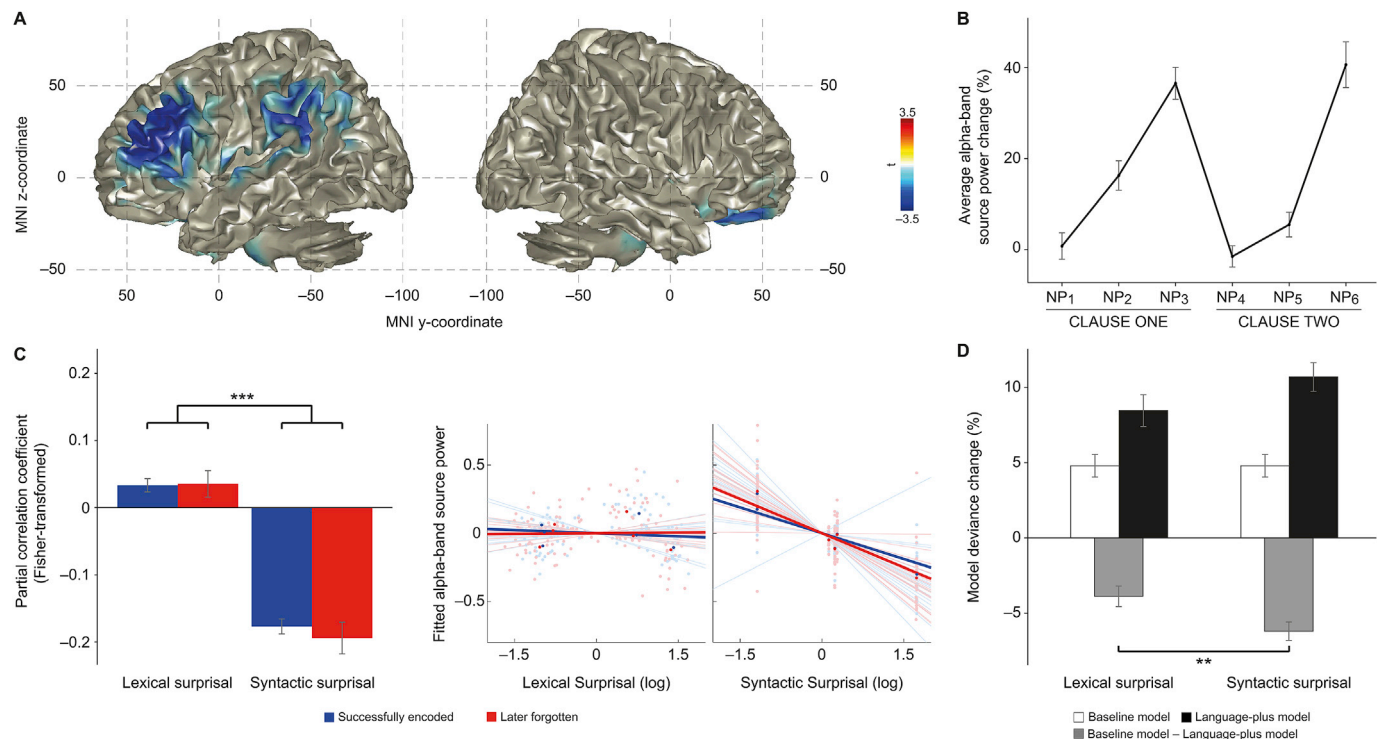


Fig. 3. Source level and post-hoc analysis results: (A) t-map ($-2.07 > t > 2.07$; $p < 0.05$, uncorrected) of the statistical comparison of alpha-band source power between the two conditions (i.e., SE versus LF trials) projected onto a standard Montreal-Neurological-Institute (MNI) brain template; dashed gray lines mark MNI coordinates; only the significant cluster of 174 volume-conductor grid points (i.e., exceeding 148 grid points; $\alpha = 0.05$) is plotted (see also Table 1); (B) Grand-averaged time course of alpha-band source power along the six NPs of the encoding sentence, averaged within and across participants, across all volume-conductor grid points of the significant cluster; error bars indicate standard error of the mean; note the within-clause incremental power increase and the plunge at the boundary between clause one and clause two; (C, left panel) Bar plot of the across-participant mean partial correlation coefficients computed between alpha-band power and SynS/LexS for SE (blue bars) and LF (red bars) trials, controlling for trial and NP's sentence position; error bars indicate standard error of the across-participant mean; a main effect of Surprisal shows that the time course of alpha-band power is more strongly correlated with the time course of SynS compared to the time course of LexS; (C, right panel) Individual (transparent-colored) and group-level mean (opaque-colored) scatter plots and regression lines of partial correlation between alpha-band power and LexS/SynS (controlling for the NP's sentence position) for SE (blue markers–lines) and LF (red markers–lines) trials; (D) Bar plot of the group-level mean normalized model deviances (i.e., difference between null and residual deviances divided by null deviance) for the baseline model (white bar) and the language-plus model (black bar) for LexS and SynS; gray bars show the mean difference between the baseline and the language-plus model for each surprisal; error bars indicate standard error of the mean; the amount of explained variance in encoding success is significantly greater when both alpha-band power and SynS are model regressors than when alpha-band power and LexS are.

Table 1

Source reconstruction results: Significant source activity in the t-map of the volume-conductor grid ($-2.07 > t > 2.07$; $p < 0.05$, uncorrected) at a cluster size of at least 148 grid points ($\sim 148,000 \text{ mm}^3$; $\alpha = 0.05$) is reported; only one cluster exceeded the cluster-size threshold (total volume = $174,000 \text{ mm}^3$). Only anatomical labels with more than 5% cluster share are listed; unlabeled regions are discarded from map share; anatomical labels were taken from the Automated-Anatomical-Labeling brain atlas. All reported regions are located in the left hemisphere. Peak coordinates for each area are given in Montreal-Neurological-Institute (MNI) space with reference to the volume-conductor grid.

Region	Max. t-value	Cluster share (%)	MNI coordinates (mm)		
			x	y	z
Middle frontal gyrus	−2.94	20.45	−50	30	30
Inferior frontal gyrus	−2.79	14.89	−40	30	20
Inferior parietal gyrus	−3.02	6.85	−60	−40	40
Supramarginal gyrus	−3.19	5.67	−60	−40	30

observed. Moreover, the negative correlation of alpha-band power with SynS indicated that the lower the alpha-band power, the higher the SynS, implying that the strength of alpha-band desynchronization varies with the NP's syntactic-processing difficulty.

As the correlation between alpha-band power and SynS across the whole encoding sentence was not different between SE and LF sentences,

we next tested whether encoding success of a sentence was predicted by the degree of alpha-band power–SynS alignment at the to-be-retrieved (critical) NP. We used alpha-band source power, SynS, and LexS of each trial's critical NP and fitted single-trial binary logistic regression models (e.g., Cohen and Cavanagh, 2011; Field et al., 2012) in RStudio® (RStudio, Inc., Boston, MA, USA). For each participant, one baseline model predicted encoding success as a function of alpha-band power only, and two language-plus models predicted encoding success as a function of alpha-band power, surprisal (SynS versus LexS), and all interactions. In all models, we controlled for the critical NP's sentence position and all resulting interactions.

Baseline model: $y_i = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \beta_3 x_{1i} x_{2i} + \varepsilon_i$

Language-plus model: $y_i = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} + \beta_3 x_{3i} + \beta_4 x_{1i} x_{2i} + \beta_5 x_{1i} x_{3i} + \beta_6 x_{1i} x_{2i} x_{3i} + \varepsilon_i$

Terms: y , behavioral response (i.e., SE versus LF); β_0 , fixed intercept; β_{1-6} , regression coefficients for fixed effects and interactions; x_1 , source power; x_2 , regressor for NP's sentence position; x_3 , SynS/LexS; ε , error term. Prior to model fitting, we log-transformed SynS and LexS to correct for non-normal distribution (Shapiro-Wilk normality test; SynS: $W = 0.62$, $p < 0.001$; LexS: $W = 0.84$, $p < 0.001$; Zeltermann, 2015), z-transformed all continuous variables (e.g., Vittinghoff et al., 2011), and set LF as baseline of the behavioral variable (i.e., the model predicts the

change from LF to SE; Field et al., 2012). Then, we calculated magnitudes of gain in the behavioral variance explained by the SynS- and the LexS-model. To this end, we calculated the difference in residual deviances between baseline and language-plus model using a χ^2 statistic; we then normalized the difference by dividing it by the baseline model's residual deviance (RD; i.e., (RD baseline – RD language-plus)/RD baseline). Group-level model-deviance differences were compared using a paired-samples t-test: alpha-band power explained significantly greater behavioral variance when it interacted with SynS ($M = -6.20\%$, $SEM = 0.62\%$) than when it did with LexS ($M = -3.88\%$, $SEM = 0.68\%$; $t(23) = 2.90$, $p < 0.01$; Fig. 3D). To confirm this finding, we ran a subsequent single linear mixed-effects logistic regression model predicting single-trial behavioral response from the fixed effects of alpha-band power, SynS, LexS, NP's sentence position, and the fixed interactions of alpha-band power with the other regressors, with participant as a random effect. Significant predictors of behavioral response were SynS ($\beta = 0.27$, $z = 3.65$, $p < 0.001$), NP's sentence position ($\beta = 0.09$, $z = 1.97$, $p < 0.05$), the two-way interaction of alpha-band power and SynS ($\beta = -0.33$, $z = -2.77$, $p < 0.01$), and the three-way interaction of alpha-band power, SynS and NP's sentence position ($\beta = 0.10$, $z = 2.72$, $p < 0.01$). No other significant main effects or interactions involving LexS were observed (all absolute $z < 1.20$, all $p > 0.20$). Together, these two analyses suggest that the interaction between alpha-band power and SynS is more relevant for the prediction of the behavioral outcome.

Discussion

Our study sought to clarify the oscillatory underpinnings of sentence encoding, given prior evidence for a range of frequency bands being involved in sentence-level working memory processes. However, in contrast to prior experimental designs that assessed the working-memory component of sentence comprehension somewhat indirectly, our experimental paradigm directly tapped into the encoding of sentences into working memory. Previous studies have implied delta-, theta-, alpha-, and beta-band oscillatory activity in working-memory processes during sentence comprehension; however, as they mostly crossed working-memory demands with other aspects of sentence processing, such as syntactic complexity, some of the prior effects cannot be unequivocally interpreted as modulations by genuine working-memory processes, such as encoding. Therefore, to ultimately isolate the genuine working-memory component of sentence comprehension and study its oscillatory underpinnings, we employed a subsequent memory paradigm, contrasting SE and LF sentences as classified based on participants' subsequent retrieval success, and we hypothesized that delta-, theta-, alpha-, and/or beta-band power changes may reflect neural activity that is beneficial for the successful encoding of sentences into working memory.

Our results showed that alpha-band desynchronization, most likely generated in left-hemispheric language-relevant cortical areas, is beneficial for the successful encoding of sentences into working memory, whereas delta-, theta-, and beta-band activity failed to qualify as such. Alpha-band power fluctuations more strongly mirror a computational metric of syntactic processing as compared to a metric of lexical-semantic processing along a sentence. Finally, successful sentence encoding seems to occur together with an alignment of alpha-band desynchronization to SynS. Our result may indicate an alpha-band-moderated mechanism, through which left-hemispheric language-relevant brain areas functionally subserve the formation of a syntactic representation amongst a sentence's NPs, allowing successful sentence encoding. In the remainder of the Discussion we will elaborate on our main findings.

Preference of alpha-band oscillations for syntax-related aspects of sentence encoding

The striking finding that the temporal structure of alpha-band

desynchronization along a to-be-encoded sentence mirrors a pattern of the sentence's structure adds to a line of evidence of accumulation of neural activity during sentence processing, supporting prior evidence on the neurophysiological reality of sentence structure. Pallier et al. (2011) first showed parametric increase of neural activity with increasing size of syntactic constituents, arguing that this may reflect the online construction–encoding of linguistic structures. Fedorenko et al. (2016) reported monotonic gamma-power increases for the processing of sentences as compared to non-word lists, which may indicate the formation of sentence structure. Nelson et al. (2017) extended this evidence beyond the gross level of sentences, showing that high-gamma power increased with each successive word that was added to a multiword syntactic phrase, dropping sharply on phrase termination. Our data provide a similar progression of alpha-band power, with a power increase within clause, followed by a power drop on clause ending.

Going beyond these prior reports on a potential association of syntactic structure formation and oscillatory power changes, our study dissociates such power changes from non-syntactic processes—suggesting a functional preference of the temporal pattern of alpha-band source power to align more strongly with SynS as compared to LexS along the encoding sentence. Similarly, previous studies have associated activity in the broad alpha/beta band with syntactic operations: Desynchronization was shown to be induced by syntactic but not semantic violations (Davidson and Indefrey, 2007) and by detailed post-hoc syntactic parsing of semantically reversible sentences, that is, when semantic cues for assigning “who did what to whom” are absent (Meltzer and Braun, 2011; cf., Kiehl et al., 2014; Kiehl et al., 2015), whereas synchronization was induced by syntactic binding in two-word sentences (Segaert et al., 2018). Our finding resonates with the well-established idea that, as sentence comprehension requires the integration of multilevel information (e.g., phonological, syntactic, and semantic; Jackendoff, 2007), the working memory underlying sentence comprehension is supposed to involve different levels of linguistic representation, such as syntactic (McElree, 2000) and lexical-semantic (Martin, 2005; Shivde and Anderson, 2011). Psycholinguistic and neuroimaging evidence suggests that syntactic and semantic representations are temporally dissociated in working memory, such that semantic representations emerge after the formation of syntactic representations (Sachs, 1967), and also that the two types of representations have distinct neural correlates (Bornkessel-Schlesewsky and Schlewsky, 2013; Friederici, 2011, 2012; Friederici et al., 2000; Friederici et al., 2003; Hickok and Poeppel, 2004; Humphries et al., 2006; cf. Glaser et al., 2013). This dissociation is also corroborated by clinical findings from the semantic variant of primary progressive aphasia, in which patients present with lexical-semantic deficits due to degenerated anterior temporal lobe, while syntactic functioning is intact due to preserved functioning of the left inferior frontal, posterior temporal, and inferior parietal cortex (Agosta et al., 2010; Galantucci et al., 2011; Mesulam, 2016; Wilson et al., 2014), regions that are found to function abnormally in primary-progressive-aphasia patients with impaired syntactic abilities (Wilson et al., 2016); also, aphasic patients with selective disruption of the semantic short-term memory and intact syntactic abilities fail in comprehension of sentences requiring the simultaneous retention of multiple word meanings (Martin and He, 2004; Martin and Romani, 1994).

Therefore, we here argue that alpha-band oscillations underlie syntactic—rather than lexical-semantic—representations in working memory during sentence encoding. This view accounts for three major observations in the prior literature: First, alpha-band oscillations have been shown to be involved in sentence processing (Bastiaansen et al., 2002; Bonhage et al., 2017; Davidson and Indefrey, 2007; Meltzer and Braun, 2011; Meltzer et al., 2017; Meyer et al., 2013; Segaert et al., 2018). Second, the formation of a representation that encodes the relational syntactic information of the NPs inside a sentence is essential for the encoding of a sentence into working memory (Baddeley et al., 2009; Bonhage et al., 2014; Jefferies et al., 2004; Lombardi and Potter, 1992;

Potter and Lombardi, 1998) and, thus, could be ascribed to the working-memory resources that are beneficial for successful encoding (i.e., the observed SME in the alpha band). Third, the spatial distribution of our alpha-band cortical generators indicated potential areas in the middle and inferior frontal gyri and the inferior parietal lobe that belong to the dorsal left-hemispheric language network, which is known to process syntax and sentence-level memory demands during sentence comprehension (Friederici, 2011; Meyer et al., 2012; Saur et al., 2010; Wilson et al., 2011).

Alpha-band activity: cortical (dis)inhibition superimposed on the language network?

The functional relevance of alpha-band oscillations for syntactic representations in working memory during the encoding of sentences may indirectly reflect a domain-general mechanism of functional disinhibition superimposed, potentially, on the left-hemispheric language-relevant cortex. As stronger neural desynchronization in the alpha band correlated with higher SynS, that is, with higher syntactic-processing difficulty, and as successful encoding of a specific NP within a sentence was more likely when the level of alpha-band desynchronization matched the level of its syntactic difficulty, it is possible that alpha-band oscillations play a disinhibitory role by actively enabling the language-specialized cortex to process more difficult stimuli and to encode less expected relational syntactic representations amongst the NPs. Although this interpretation must be taken with a grain of salt in the first place, the conception of the alpha-band brain rhythm as a functional switch between inhibition and disinhibition of the cortex (Jensen and Mazaheri, 2010; Klimesch, 2012; Klimesch et al., 2007) has by now overtaken the traditional role of alpha band as a modulator of active versus idling states of the cortex (Adrian and Matthews, 1934; Berger, 1929) and has been implicated in other cognitive domains as well (e.g., in primary sensory systems such as auditory and visual perception; Foxe and Snyder, 2011; Rihs et al., 2007; Strauß et al., 2014; Weisz et al., 2011). According to this view, the cortex is functionally disinhibited through alpha-band desynchronization, enabling information to be transferred from and to specific areas for processing (e.g., during encoding into working memory), whereas the cortex is functionally inhibited through alpha-band synchronization, forcing information to be withheld in the working-memory storage (e.g., during the retention interval). The stronger the alpha-band desynchronization, the stronger the disinhibition of the cortex, and the more capable the cortex is to process syntactically more difficult sentential content, as the negative correlation between the time series of our alpha-band power and of SynS suggests.

Within this framework, previously reported alpha-band desynchronization during the encoding of unstructured word lists (Fell et al., 2008; Fellner et al., 2013; Hanslmayr et al., 2009; Klimesch et al., 1996b; Sederberg et al., 2007) constitute no conflicting finding, as the supposedly functional relevance of the here reported alpha-band desynchronization for syntactic representations is motivated by the picture of likely cortical sources, which are found in areas known to underlie syntactic processing (e.g., left inferior frontal gyrus and inferior parietal lobe, *inter alia*; see *The locus of (dis)inhibition: an emerging neural network for sentence encoding?*). By contrast, Sederberg et al. (2007) reported alpha-band desynchronization for successful encoding of unstructured word lists generated in the left and right temporal lobes, known to be involved in semantic processing (e.g., Binder and Desai, 2011; Binder et al., 2009; Martin et al., 1990). Relatedly, alpha-band desynchronization in the left temporal lobe has been shown to index ease of access to single-word meaning (Becker et al., 2013). Also, our interpretation challenges the general assumption that alpha-band desynchronization reflects semantic memory processes in language comprehension (Hanslmayr and Staudigl, 2014; Hanslmayr et al., 2012; Klimesch et al., 1997), as the latter stems from word-level studies only and cannot integrate the here reported sentence-level alpha-band desynchronization.

Moreover, a line of seemingly opposing findings of alpha-band

synchronization (i.e., alpha-band power increase) in various verbal-working-memory tasks (Jensen et al., 2002; Khader et al., 2010; Meeuwissen et al., 2011; Meyer et al., 2013; cf., Meltzer et al., 2017) fit our proposed domain-general functionality of alpha-band oscillations in verbal-working-memory processes. These studies analyzed merely the retention interval, that is, the time window between encoding and retrieval, in which typically no (task-relevant) stimulation was provided. For example, alpha-band power increased parametrically with increasing memory load during the retention interval in a modified Sternberg task (Jensen et al., 2002) and also increased for SE versus LF drawings and verbal material (i.e., letter strings and word sequences) during the retention interval in a subsequent memory paradigm (Khader et al., 2010; Meeuwissen et al., 2011). This is firm evidence that alpha-band power manifests itself differently along different working-memory processes: it desynchronizes during the encoding interval and synchronizes during the retention interval, thus echoing the hypothesis of a domain-general (dis)inhibitory function.

The locus of (dis)inhibition: an emerging neural network for sentence encoding?

Our strong and robust sensor-level alpha-band desynchronization seemed to have been generated in areas of the left-hemispheric language-relevant network, which in turn was likely enabled to encode syntactic representations amongst the NPs of a sentence through alpha-band desynchronization. As shown in Fig. 3A (see also Table 1), the potential cortical sources were distributed predominantly (i.e., in a total of 47.86% of the significant group-level cluster) in the inferior and middle frontal gyri, the inferior parietal lobe, and the supramarginal gyrus, which constitute part of the left dorsal fronto-parietal system well-known to be implemented in syntactic processing during sentence comprehension (Friederici, 2011; Saur et al., 2010; Wilson et al., 2011, 2016) and in the processing of syntactically complex and memory intensive sentences (Fiebach et al., 2005; Meyer et al., 2012). In this context, Meyer et al. (2013) suggested that left parietal alpha-band oscillations subserve the retention of unintegrated information during the formation of syntactic dependencies for the comprehension of working-memory intensive sentences. Further research employing better-suited neuroimaging techniques is needed to pinpoint the anatomical underpinnings of this emerging neural network for sentence encoding.

Conclusion

Our study suggests a functional role of alpha-band oscillations for the encoding of sentences into verbal working memory. As long sentences are not encoded into working memory as simple word lists, but instead require relational syntactic information, the left-hemispheric language-relevant network appears to be functionally disinhibited through alpha-band desynchronization to track the syntactic structure of the sentential material, enabling the cortex to successfully encode sentences into working memory.

Conflicts of interest

None declared.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.neuroimage.2018.04.008>.

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