



Electrophysiological signatures of conceptual and lexical retrieval from semantic memory

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ABSTRACT

Retrieval from semantic memory of conceptual and lexical information is essential for producing speech. It is unclear whether there are differences in the neural mechanisms of conceptual and lexical retrieval when spreading activation through semantic memory is initiated by verbal or nonverbal settings. The same twenty participants took part in two EEG experiments. The first experiment examined conceptual and lexical retrieval following nonverbal settings, whereas the second experiment was a replication of previous studies examining conceptual and lexical retrieval following verbal settings. Target pictures were presented after constraining and nonconstraining contexts. In the nonverbal settings, contexts were provided as two priming pictures (e.g., constraining: nest, feather; nonconstraining: anchor, lipstick; target picture: BIRD). In the verbal settings, contexts were provided as sentences (e.g., constraining: “The farmer milked a ...”; nonconstraining: “The child drew a ...”; target picture: COW). Target pictures were named faster following constraining contexts in both experiments, indicating that conceptual preparation starts before target picture onset in constraining conditions. In the verbal experiment, we replicated the alpha-beta power decreases in constraining relative to nonconstraining conditions before target picture onset. No such power decreases were found in the nonverbal experiment. Power decreases in constraining relative to nonconstraining conditions were significantly different between experiments. Our findings suggest that participants engage in conceptual preparation following verbal and nonverbal settings, albeit differently. The retrieval of a target word, initiated by verbal settings, is associated with alpha-beta power decreases. By contrast, broad conceptual preparation alone, prompted by nonverbal settings, does not seem enough to elicit alpha-beta power decreases. These findings have implications for theories of oscillations and semantic memory.

1. Introduction

Semantic memory is the encyclopedia of our brain that contains all of the factual information necessary for many everyday activities, including speaking. Speaking relies on a series of mental operations partly dependent on semantic memory. Before articulating a word, speakers activate concepts associated with the intended message, retrieve lexical information about these concepts, as well as corresponding sound properties of the target word from semantic memory (e.g., Dell, 1986; Garrett, 1988; Levelt et al., 1999); these stages are commonly referred to as word planning. The neuronal signatures of encoding and retrieving from episodic memory have been well studied

(e.g., Düzel et al., 2003; Hanslmayr et al., 2016; Lega et al., 2012). However, retrieval from semantic memory, as required for speaking, is less understood. The current study investigated how the semantic setting leads to spreading activation in semantic memory, enabling conceptual and lexical retrieval as a speaker plans his or her utterance. This question has implications for understanding the neuronal signatures of semantic-memory processes.

The excellent temporal resolution of the electroencephalogram (EEG) and its fairly direct relation to neuronal activity makes electrophysiological signatures an ideal method to investigate covert and rapid processes, such as those involved in word planning. We were primarily interested in brain oscillations. Oscillations, as measured over the scalp,

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are thought to result from synchronized firing of thousands of neurons at the same frequency (Buzsáki et al., 2012), which control diverse cognitive processes. The amplitude of the oscillations at different frequency bands (e.g., theta, alpha, beta) is argued to serve as a proxy for the amount of synchronization in the underlying neuronal populations.

Previous research has indicated that semantic-based episodic or recognition memory is reflected in alpha-band as well as beta-band desynchronization (Fellner and Hanslmayr, 2017; Hanslmayr et al., 2009; Klimesch et al., 1997a,b). Retrieval from semantic memory that precedes language production has also been associated with alpha-beta band desynchronization in studies examining word planning embedded in different semantic contexts (e.g., Piai et al., 2017; Piai et al., 2015; Piai et al., 2018; Piai et al., 2014b). These studies utilized a verbal-context picture-naming task where the goal is to name target pictures that complete sentences with constraining and nonconstraining contexts. By providing participants with mini-contexts, we can better capture spreading activation as it would more naturally occur in real-life conversation (Bögels, 2020). Constraining sentences have a strong bias toward one completion (“The farmer milked a ...”, target picture: COW), while the nonconstraining sentences do not (“The child drew a ...”, target picture: COW). Conceptual and lexical retrieval can start prior to the target picture onset in the constraining condition as a function of spreading activation in the semantic network, which has been associated with left lateralized desynchronization in the alpha and beta bands (Piai et al., 2015; Roos and Piai, 2020). Thus, retrieval from semantic memory

for planning a word seems to be associated with desynchronization in the alpha-beta bands in a similar manner as semantic processing without the intent to speak as observed in semantic-based episodic memory tasks.

Studies utilizing event related potentials (ERP) in addition to oscillations have found that the two measures reveal complementary information on time course and involved brain regions (for language studies, e.g., Davidson and Indefrey, 2007; Laaksonen et al., 2012; Piai et al., 2014a,b). Conceptual and lexical retrieval from semantic memory is known to affect the amplitudes of several ERP components (Strijkers et al., 2012). Strijkers and colleagues have shown that lexical access affects amplitudes of the P200 (an early sensory component) or the N400 (a component generally modulated by conceptual and lexical information). If participants are instructed to name pictures, lexical access already modulates the P200 amplitude, but if participants only engage in semantic categorization, modulations are only seen in the N400 amplitude.

All of the aforementioned studies that investigated semantic processing in relation to word planning and language production have used verbal contexts to trigger spreading activation. Thus, semantic processing of nonverbal information leading to conceptual and lexical activation remains underinvestigated. Semantic information is argued to be “stored” within distinct neural encodings depending on the modality of this information (see Neural Hybrid model; Hart et al., 2007). Previous studies have shown that stimulus modality affects the underlying

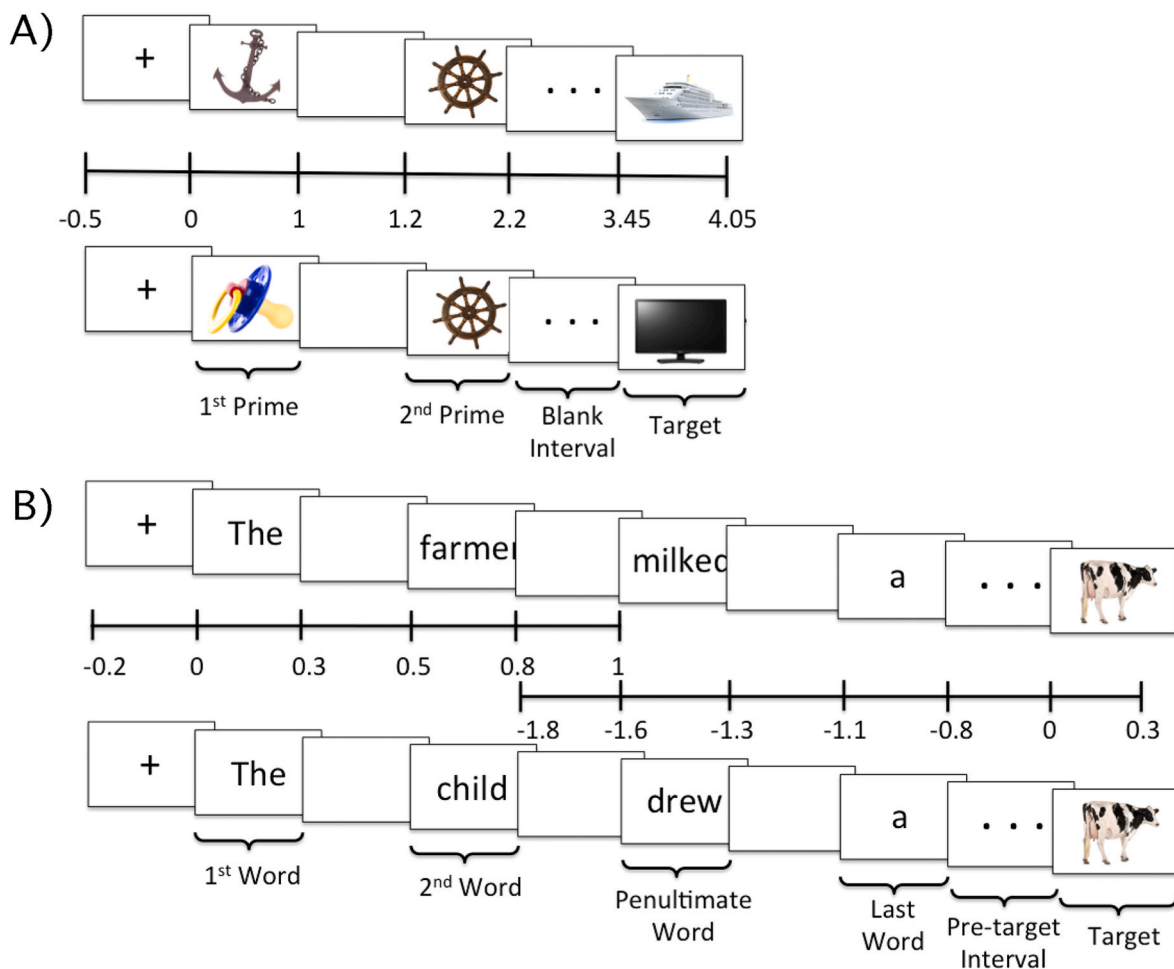


Fig. 1. Task schematics for A) Experiment 1 utilizing the nonverbal-context picture-naming task and B) Experiment 2 utilizing the verbal-context picture-naming task. Both schematics include an example of constraining (top) and nonconstraining (bottom) trials. The numbers indicate the time scale locked to the first word/picture onset (in both A and B) or the target picture onset (in B) (in seconds). Participants name the target picture at target onset. Sentences were presented in Dutch and all verbal responses were also delivered in Dutch.

mechanism of semantic processing as measured in the EEG through ERPs (e.g., Kutas and Van Petten, 1990; Kutas and van Petten, 1994) and alpha oscillations (Chiang et al., 2016). Thus, studying semantic processing exclusively following verbal material may lead to a skewed view about the timing as well as the nature of spreading activation, given that the modality prompting semantic processing could affect how it is carried out (and potentially the type of representations it activates).

The present study investigated how nonverbal, i.e. picture-based, semantic contexts lead to spreading activation associated with conceptual and lexical retrieval from semantic memory. In Experiment 1, henceforth referred to as the nonverbal experiment, we developed a novel nonverbal-context picture-naming task to investigate nonverbal semantic processing. In this task, three pictures appear consecutively on the screen (Fig. 1A). The first two priming pictures provide either a constraining context (e.g., nest, feather, which leads to the target picture “bird”) or a nonconstraining context (e.g., anchor, lipstick, which leads to the target picture “bird”). The participants’ task is to name the third target picture. In the nonconstraining conditions, semantic priming of the target by the context is weak or absent; therefore, participants have to wait for the target to appear to plan its name. Conversely, in the constraining conditions, the context enables spreading activation toward one target picture. Hence, looking at the time interval prior to the appearance of the target in the constraining conditions allows us to investigate conceptual and lexical retrieval from semantic memory resulting from spreading activation (Piai et al., 2015). By contrasting the constraining and nonconstraining conditions, we can tap into conceptual and lexical retrieval during word planning independently of other cognitive processes (e.g., processing of visual information), as these remain constant across both conditions.

To be able to interpret the novel nonverbal experiment in light of previous studies investigating conceptual and lexical retrieval following verbal settings, we simultaneously performed Experiment 2, henceforth referred to as the verbal experiment. In the verbal experiment, we tried to replicate how verbal contexts lead to spreading activation associated with conceptual and lexical retrieval, by utilizing the previously described verbal-context picture-naming task (Fig. 1B; Piai et al., 2017, 2015, 2018; Piai et al., 2014b). Even though the two experiments differed in the manner in which the context was provided, we expected that conceptual and lexical retrieval would occur in a similar manner following nonverbal and verbal settings. Importantly, both experiments were conducted in the same participants within the same session, enabling us to interpret the nonverbal experiment in consideration of the verbal experiment while controlling for the variability across individuals.

We expected qualitatively similar results for the verbal and nonverbal experiments. In particular, we expected to replicate that naming would be faster following the constraining than nonconstraining contexts in the verbal experiment. We also expected to find a faster naming for constraining than for nonconstraining conditions in the nonverbal experiment. With regards to the oscillations, we expected to replicate the alpha-beta desynchronization associated with word planning following verbal semantic processing (Piai et al., 2015, 2017, 2018, 2015; Piai et al., 2014b) originating from the left temporal and inferior parietal cortices (Klaus et al., 2020; Piai et al., 2015; Roos and Piai, 2020). Most crucially, we predicted that alpha-beta desynchronization would be associated with conceptual and lexical retrieval following nonverbal semantic processing as well. However, we expected a potentially distinct spatial and temporal profile of the alpha-beta desynchronization following nonverbal as compared to verbal semantic processing, as words can modulate the EEG signal differently from pictures (cf. Kutas and Van Petten, 1990; Kutas and van Petten, 1994). We also expected to find differences in ERPs between constraining and nonconstraining conditions in each experiment. However, we did not have predictions with regards to individual components, especially for the nonverbal experiment, given the paucity in the literature of studies we could rely on to make specific predictions.

2. Method

Behavioral and EEG data, experimental scripts, and analysis scripts are available via the Donders repository (tinyurl.com/7ap58xz8). The present study was in line with the declaration of Helsinki (World Medical Association, 1964, 2008) and was approved by the Ethics Committee of the Faculty of Social Sciences of Radboud University.

2.1. Overall structure

The present study consisted of two experiments: the nonverbal experiment utilizing the nonverbal-context picture-naming task and the verbal experiment utilizing the verbal-context picture-naming task. All participants first took part in the nonverbal experiment and then in the verbal experiment. We conducted the two experiments with the same group of participants to improve interpretability across the two experiments. The verbal experiment has been previously used and is known to replicate well (Klaus et al., 2020; Piai et al., 2020; Piai et al., 2015, 2017, 2018, 2015; Piai et al., 2014b; Roos and Piai, 2020), so we knew what effects to expect for the oscillations. By having this fixed order, the verbal experiment would not influence the effects of interest in the novel nonverbal experiment.

2.1.1. Participants

The same 20, right-handed, native Dutch speakers participated in both experiments for financial compensation. Data of two participants was excluded from the analyses: one because of technical issues and the other because of excessive movement artifacts (<70 % of the trials remaining). The mean age of the remaining 18 participants (seven males) was 22.66 (range: 18–33).

2.1.2. EEG acquisition

EEG was recorded from 64-scalp electrodes using the Acticap system with the left mastoid electrode as online reference. The signal was amplified by BrainAmps DC amplifier using 500 Hz sampling rate and a 0.016–125 Hz band-pass filter. Additionally, we used seven passive electrodes to monitor eye movements and mouth movements. We placed the electrodes above and below the left eye, on the left and right temples, and at the top and bottom of the right side of the orbicularis oris muscle and they were referenced to an electrode positioned on the left earlobe. The impedances of all electrodes were adjusted to below 20 kΩ.

At the beginning of each session, a 3D scan of the participants’ head with an EEG cap was taken with a Structure Sensor (Homölle and Oostenfeld, 2019) to determine precise electrode positions for each participant.

2.2. Experiment 1: nonverbal-context picture-naming task

2.2.1. Materials and design

To create the constraining condition, we collected 60 item sets, each composed of three pictures, retrieved from BOSS photograph database (Brodeur et al., 2014) or from the internet. The first two priming pictures, or primes, provided a strongly constraining context to what the third target picture was going to be (e.g., nest, feather, which leads to the target picture “bird”). The pictures from all item sets were subsequently reshuffled to create nonconstraining contexts. This was done in such a way that the two primes were semantically and phonologically unrelated to each other and to the target picture (e.g., anchor, lipstick, with the target picture “bird”; see Fig. 1A). The target pictures that the participants had to name were identical in the constraining and the nonconstraining condition and were named in Dutch.

We administered an online pretest to 20 participants. They were presented with the two priming pictures each flashing on the screen for 1 s. They were asked to report two possible associations that were related to both of the previously presented priming pictures. An answer was considered correct if it matched the target picture and was

mentioned as either the first or the second association. The pre-test confirmed that the context affects the degree of expectancy for the target word (i.e., cloze probability; Taylor, 1953). The cloze probability (or the proportion of participants who used the target picture name in their completion) was significantly higher for the constraining ($M = 0.79$, $SD = 0.20$, range: 0.3–1) than for the nonconstraining condition ($M = 0$, $SD = 0$, range: 0–0, $t(59) = 31.52$, $p < 0.001$, $d = 4.10$).

We pseudorandomized the trials with MIX (Van Casteren and Davis, 2006). This resulted in a unique trial list for each participant. There were no more than four instances of the same condition on subsequent trials. Repetition of the same target pictures had a minimum distance of 10 trials, and repetition of the same primes had a minimum distance of four trials.

2.2.2. Procedure

Stimuli were displayed using Presentation Software (Neurobehavioral Systems). Before the experiment began, participants were familiarized with the target picture names in a slide presentation, to insure minimal loss of data due to misnaming targets. Each trial began with a fixation cross (500 ms), followed by the two primes (each presented for 1000 ms) with an interleaving blank screen (200 ms). Subsequently, a pre-target interval with three dots was presented (1250 ms). Participants were asked to name the target pictures right after they appeared. When a response was registered, target pictures disappeared from the screen, and a blinking interval was presented after 300 ms. The blinking interval was presented with duration jittered between 1200 and 1500 ms.

2.2.3. Behavioral analysis

We evaluated the responses of each participant in real time. They were coded as (1) correct answer, (2) synonym of a correct answer, or (3) incorrect answer, omission, or hesitation. Trials in the last category were subsequently excluded from all behavioral and EEG analyses. Response times (RTs) were determined manually using Praat (Boersma and Weenink, 2013) blind to conditions.

We performed paired sample *t*-tests to examine the RT differences between the constraining and nonconstraining contexts. Additionally, we examined the RT distribution by Vincentizing (Ratcliff, 1979). For this analysis, the responses from each condition were ordered from the fastest to slowest for every participant and separated into five bins of response latencies. The response latencies in all bins were subsequently averaged per condition and participant. This allowed us to check whether the responses were shorter in the constraining condition throughout the response latency distribution.

2.2.4. EEG preprocessing

We analyzed all EEG data using FieldTrip (Oostenveld et al., 2011) in Matlab (R2019b). The data was segmented around first picture onset, starting from –500 ms to 4050 ms, corresponding to the entire trial, including 600 ms post target onset. Subsequently, we removed the nonfunctioning channels or channels with high noise. On average, 1.64 % of channels were excluded. The data was then rereferenced to a common average reference and filtered with a band-pass filter with a cutoff of 60 Hz (low-pass) and 0.1 Hz (high-pass). We visually inspected the data and removed the segments containing nonphysiological artifacts, resulting from other devices or electrical phenomena. Independent component analysis (ICA) was performed to correct for EOG artifacts if participants blinked on more than 10 trials. Alternatively, the trials with EOG artifacts were rejected during last visual inspection, where we excluded all remaining artifacts. After all the rounds of artifact rejection, there was a minimum of 50 trials per condition for each participant. The individual EEG channels that were initially removed were interpolated by a weighted average of the data from neighboring channels of the same participant. For the ERP analysis, the trials were baseline corrected, using the baseline of –500 ms–0 ms timelocked to the first picture onset, and further low-pass filtered at 30 Hz.

2.2.5. Scalp-level analysis

We performed four analyses on the segments of interest: time-frequency representations (TFR), ERPs, correlations between observed EEG effects and picture naming RTs, and correlations between observed EEG effects and cloze probability. The TFRs were computed for frequencies starting from 5 to 40 Hz. For all segments, we specified 3 cycles per time window sliding in steps of 50 ms in the time dimension and 1 Hz in the frequency dimension. Each time point was tapered with a Hanning window, followed by the Fourier transform of the tapered signal. Subsequently, for each participant, we computed averages per condition. Note that for the correlations, single-trial data was used.

2.2.6. Statistical testing

We performed non-parametric cluster-based permutation tests for the TFR and ERP (main analyses), and correlation analyses, see 2.4 (Maris and Oostenveld, 2007). All analyses were two-tailed and an alpha level of 0.05 was employed for the main analyses. Here we provide a brief overview of the method. We created a three-dimensional space of all time points, frequency steps, and channels for all TFR analyses, and a similar two-dimensional space of all time points and channels for all ERP analyses. Dependent samples *t*-tests (between constraining and nonconstraining conditions) were computed for all points in the three- and two-dimensional spaces. If two or more neighboring points reached the significance threshold ($p < 0.05$), they formed a cluster. Subsequently, a sum of all the *t*-values of each cluster was calculated. To control for the family-wise error rate at the nominal alpha level of 0.05, the constraining and nonconstraining conditions were combined and subsequently randomly separated into two artificial groups 500 times. The summed *t*-values of all of the randomly generated clusters were computed in the same way as described above. Subsequently, a distribution of these summed *t*-values was generated. Comparing the summed *t*-values computed based on the original clusters to this distribution resulted in Monte-Carlo significance probabilities, which were considered significant if smaller than 0.05.

We ran the non-parametric cluster-based permutation tests for the TFRs for frequencies ranging from 5 to 40 Hz. The TFR analysis was run starting at the second picture onset (1.2 s in Fig. 1A) until 300 ms after target picture onset (3.75s in Fig. 1A) and the ERP analysis until 600 ms after the target picture onset (4.05s in Fig. 1A). The larger time window for the ERPs was chosen to have a clearer picture of the possible ERPs after the display of the target picture.

2.3. Experiment 2: verbal-context picture-naming task

All analyses of the verbal experiment were kept as similar to the nonverbal experiment as possible given the design and procedure.

2.3.1. Materials and design

We selected 60 constraining and 60 matching nonconstraining Dutch sentences from previous studies (see Klaus et al., 2020; Piai et al., 2014b; Piai et al., 2015; Roos and Piai, 2020). In the constraining sentences, the context primed the target picture strongly (e.g., “The farmer milked a”, which leads to the target picture “cow”), whereas in the nonconstraining sentences the context was neutral (e.g., “The child drew a”, which leads to the target picture “cow”; see Fig. 1B). Previously conducted pre-tests (see for previous study Piai et al., 2014b) confirmed that the context affects the cloze probability. It was significantly higher for the constraining ($M = 0.93$, $SD = 0.06$, range: 0.8–1) than for the nonconstraining condition ($M = 0.04$, $SD = 0.09$, range: 0–0.39, $t(59) = 67.64$, $p < 0.001$, $d = 8.81$). The target pictures that the participants had to name were identical in the constraining and the nonconstraining condition and were named in Dutch.

The same pseudorandomization procedure was followed as in the nonverbal experiment, with no more than four instances of the same condition on subsequent trials and with at least 10 trials between the same target pictures.

2.3.2. Procedure

Stimuli were also displayed using Presentation Software (Neurobehavioral Systems) and participants were familiarized with the target picture names before the start of the experiment. Each trial began with a fixation cross (200 ms). This was followed by the individual words of the sentence (each presented for 300 ms), interleaved with a blank screen (200 ms). The number of words per sentence varied from four to six. Subsequently, a pre-target interval was presented during which three dots appeared on the screen (800 ms). This was followed by the target picture that had to be named. When a response was registered, target pictures were replaced by a blank screen for 300 ms, after which a blinking interval was presented and remained on the screen for 2000 ms.

2.3.3. EEG preprocessing

All the preprocessing steps were kept identical to the nonverbal experiment, apart from the segmentations, which was adjusted to the specific timing of the verbal experiment. We first segmented the data into two long epochs to allow for better pre-processing of the data and to capture the different length of sentences. The first segment was time-locked to the first word onset and the second was time-locked to the target picture onset. Both segments started 1800 ms prior and ended 1000 ms post word/picture onset. After the ICA, the preprocessed data was resegmented into the periods of interest: a beginning segment included the start of the sentence and was time-locked to the first word onset (from -200 ms to 1000 ms); an end segment included the end of the sentence and was time-locked to the target picture onset (from -1800 ms to 300 ms). Note that only 300 ms interval post-target could be analyzed because only this interval was free of speech artifacts due to short naming latencies. For the ERP analysis, the trials were baseline corrected using the baseline period of -200 ms to 0 ms time-locked to the first word onset.

2.3.4. Behavioral, scalp-level, and statistical analysis

Behavioral and scalp-level analyses were identical to the nonverbal experiment (see sections 2.2.3 and 2.2.5). The statistical analyses for the TFRs and ERPs were again identical between the experiments, but with different time windows selected. For the verbal experiment, the TFR analysis was run over both the beginning and the end segments, and the ERP analysis only over the end segments.

2.3.5. Source-level analysis

To compare our verbal-experiment results to previous studies, which found that the alpha-beta desynchronization originated from left temporal and parietal regions (Klaus et al., 2020; Piai et al., 2015; Roos and Piai, 2020), we performed source localization for the alpha-beta desynchronization effect, which was only found in the verbal experiment (see 3. Results). The source localization was performed for the duration of the pre-target interval (-800 to 0 ms), and interpolated channels were not included. We created the volume conduction model from a standard MRI template ("Colin 27"; Holmes et al., 1998) using the Boundary Element Method (BEM). For each participant, the exact coordinates of all electrodes were determined from the 3D scans (see 2.4), which were subsequently manually aligned to the BEM model utilizing fiducials. We then represented the brain volume as a regular grid with 1 cm resolution. We applied a frequency domain beamforming technique (DICS) to estimate the activity at the source level (Gross et al., 2001). The leadfield matrix was calculated for each grid point. The cross-spectral density matrix for both conditions combined was computed at 14 Hz. Spectral smoothing of 6 Hz yielded a cross-spectral density matrix between 8 and 20 Hz. These were then used to compute common spatial filters for both conditions combined. These filters were then used to compute the source-level spectral power estimates for each grid point obtained separately for constraining and nonconstraining conditions.

2.4. Correlation analyses of EEG effects with RTs and with cloze probability

For the correlations with RTs, we examined whether there was a relationship between oscillatory power and RTs, as well as ERP amplitudes and RTs in each experiment separately. We controlled for multiple comparisons by using an alpha level of 0.006 (0.05/8 comparisons in total). The correlation analyses were conducted for the pre-target picture interval for both conditions in each experiment. However, retrieval in the pre-target picture interval can only occur consistently across trials in the constraining conditions. Therefore, we only expected significant correlations following constraining contexts (see also Roos and Piai, 2020). For every participant, Pearson's correlation coefficients were computed between frequency in the alpha-beta range (8–30 Hz) and RTs, and between ERP amplitude and RTs, at the single-trial level following the same clustering procedure described above. This resulted in a correlation-coefficient matrix (channel, time, and frequency when relevant) per participant summarizing the strength and direction of the relationship between EEG effects and RTs. Then these participant-level matrices were entered into a group-level cluster-based permutation procedure as described above. If alpha-beta power and ERP amplitude consistently correlated with RTs at the single-trial level over participants, this would result in group-level clusters indicating the direction of this correlation. Correlation between RTs and EEG signatures pre-target picture would indicate that the EEG modulations relate to how spreading activation in semantic memory facilitates retrieval.

For the correlations with cloze probabilities, we examined whether cloze probability influences oscillatory power and ERP amplitudes on a single-trial level. The correlation analyses were conducted for the pre-target picture interval. In the verbal experiment, they were performed for both constraining and nonconstraining conditions, and in the nonverbal experiment, only for the constraining condition as the cloze probability in each trial of the nonconstraining condition was zero. These correlations were performed using the same procedure and parameters as for the correlations with RTs, using an alpha level of 0.008 (0.05/6 comparisons).

2.5. Between experiments comparison

To statistically evaluate the different outcomes of the verbal and nonverbal experiments (see 3. Results), we compared RTs and alpha-beta power between experiments with post hoc analyses.

2.5.1. Reaction time comparison

We computed a linear mixed effects model with RTs as dependent variable and condition (i.e. constraining, nonconstraining), experiment (i.e. verbal, nonverbal), and their interaction as fixed effects. The model included by-subject random intercepts. The model was computed in R (version 3.4.2) and fitted with the lmerTest package (version 3.4; including the lme4 package, Bates et al., 2015).

2.5.2. Alpha-beta power comparison

To compare the power differences between experiments in the alpha-beta range (see 3. Results), the timing differences between the two experiments had to be taken into account. A common time interval for both experiments was chosen that did not include any evoked responses of word offsets, i.e., the time interval of 0.8 s ending at the target onset for both experiments, as the presence of evoked responses in one but not in the other experiment could bias the power estimates. We then computed power at the single-trial level between 8 and 25 Hz with 1 Hz resolution, using a Hanning taper, for each experiment and condition, and subsequently averaged the power spectra for each participant over trials. For each participant, normalized power spectra of the context effect were computed for each experiment separately (constraining minus nonconstraining conditions divided by their mean). Finally, using the normalized spectra, we tested for an interaction between condition and

experiment using non-parametric cluster-based permutation tests (using the same procedure as described in 2.2.6).

We further compared the TFR effects between the two experiments by means of effect sizes. We utilized Cohen's d to estimate effect sizes for the alpha-beta power decreases in constraining relative to non-constraining conditions. Based on previous studies (e.g., Piai et al., 2020, 2017; 2018; Piai et al., 2014), the effect sizes were estimated from the averaged power over 8–25 Hz in left central and parietal electrodes over the interval of 0.8 s ending at the target onset for both experiments (i.e., the same intervals used for the interaction analyses explained above). Note that these dimensions were not selected based on the present results, but rather based on previous studies.

3. Results

For brevity and clarity, the results of the nonverbal and verbal experiments are reported together.

3.1. Sentence and picture context facilitate naming

In the nonverbal experiment, participants were significantly faster in naming the target pictures in the constraining ($M = 660$ ms, $SD = 147$) as compared to the nonconstraining condition ($M = 782$ ms, $SD = 91.7$), $t(17) = -6.02$, $p < 0.001$, $d = 1.42$. Examination of the cumulative relative frequencies showed that the RTs are shorter in the constraining than in the nonconstraining condition for the entire RT distribution, i.e., regardless of how fast or slow pictures were named (Fig. 2, green lines). In the verbal experiment, participants were significantly faster in naming the target pictures in the constraining ($M = 456$ ms, $SD = 112$) as compared to the nonconstraining condition ($M = 660$ ms, $SD = 64.8$), $t(17) = -10.53$, $p < 0.001$, $d = 2.48$. Also for the verbal experiment, the constraining condition had shorter RTs throughout the entire distribution (Fig. 2, orange lines). From Fig. 2, it is clear that participants were faster to name the target pictures in the verbal as compared to the nonverbal experiment (see also 3.3 below). In fact, the slowest non-constraining verbal responses (orange dashed lines in Fig. 2) are still faster than the slowest constraining nonverbal responses (green solid lines in Fig. 2).

3.2. Only the verbal context modulates pre-picture alpha-beta power

The non-parametric cluster-based permutation tests of the nonverbal experiment revealed no significant power differences as a function of context ($p = 0.204$). The TFR, averaged over the same channels as the ones used for the verbal experiment (Fig. 3A), clearly indicates no alpha-

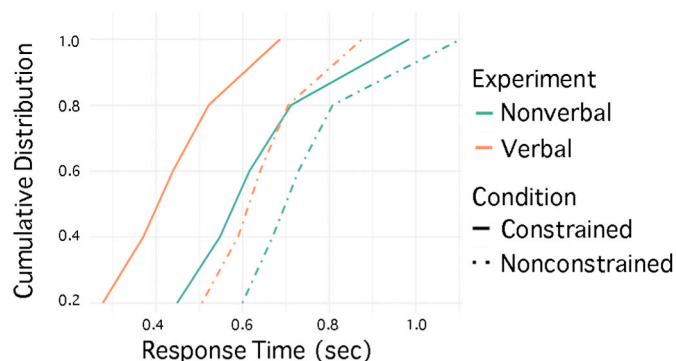


Fig. 2. Cumulative Relative Frequencies. Vincentized cumulative response time distribution curves are depicted separately for the nonverbal (green lines) and verbal (orange lines) experiments, as well as for the constraining (solid lines) and nonconstraining (dashed lines) conditions. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

beta modulation following nonverbal settings (Fig. 3B).

By contrast, as expected, for the beginning segments of the verbal experiment, there were no significant power differences as a function of context ($p = 1$). The oscillatory differences for constraining relative to nonconstraining condition started to be apparent in the end segments, when the context had time to impact the word planning process ($p = 0.004$). Power started decreasing for the constraining relative to the nonconstraining contexts approximately 1300 ms before target picture onset and was prominent in the 7–30 Hz, alpha-beta frequency range, most strongly over the left posterior electrodes (Fig. 3B). Source-localization revealed that the alpha-beta desynchronization found in the verbal experiment originated from the left hemisphere. Alpha-beta power was decreased for constraining relative to nonconstraining contexts ($p = 0.018$). The effect was most prominent around inferior temporal gyrus, temporo-parietal junction extending dorsally, and premotor cortex (Fig. 4).

To determine whether the differences in cloze probability between the verbal and nonverbal experiment could explain the differences between the TFR findings, we analyzed oscillatory power for a subset of verbal and nonverbal trials with comparable cloze probabilities. This was done by selecting 30 items from the nonverbal experiment with the highest cloze probabilities ($M = 0.87$, $SD = 0.09$, range: 0.7–0.95) and 30 items from the verbal experiment with the lowest cloze probabilities ($M = 0.88$, $SD = 0.04$, range: 0.8–1). The power between constraining and nonconstraining conditions (all nonconstraining items were used) was compared for the 8–30 Hz spectrum for the pre-target interval. In the verbal experiment, there was a significant, around 6 % power decrease between 8 and 30 Hz range in the constraining relative to the nonconstraining condition ($p = 0.024$), replicating the TFR findings. By contrast, in the nonverbal experiment, descriptively there was around 4 % power decrease between 8 and 16 Hz range in the constraining relative to the nonconstraining condition, but this effect was not significant ($p = 0.192$), again replicating the TFR findings (see Supplement).

3.3. RTs and alpha-beta power differ between experiments

In addition to the within-experiment context effects we observed (see 3.1), a mixed-effect analysis of the RTs showed that subjects were overall faster to name following constraining ($M = 558$ ms) compared to nonconstraining contexts ($M = 721$ ms, $\beta = 204.07$, $S.E. = 8.63$, $t = 23.64$, $p < 0.001$), and overall faster in the verbal ($M = 558$ ms) compared to the nonverbal experiment ($M = 721$ ms, $\beta = 204.03$, $S.E. = 8.66$, $t = 23.55$, $p < 0.001$). There was also a significant interaction between experiment and condition ($\beta = -82.22$, $S.E. = 12.24$, $t = -6.72$, $p < 0.001$). The effect sizes provide converging evidence to this interaction, as the effect size was considerably larger for the difference between constraining and nonconstraining conditions in the verbal experiment ($d = 2.48$) than in the nonverbal experiment ($d = 1.42$).

The non-parametric cluster-based permutation test examining alpha-beta power between experiments showed one significant cluster ($p < 0.024$), indicating that relative power differences between context conditions were significantly larger for the verbal experiment relative to the nonverbal experiment. The effect sizes provided converging evidence for this interaction as well: The effect size was larger for the difference between constraining and nonconstraining conditions in the verbal experiment ($d = 0.62$) than in the nonverbal experiment ($d = 0.28$). We note that these effect size estimates were not based on the significant cluster found for the verbal experiment (i.e., we did not analyze the whole time interval for which we found a significant difference in the verbal task) in order to keep the estimates comparable between the two experiments. Thus, the effect size for the verbal experiment may be an underestimate in this particular case.

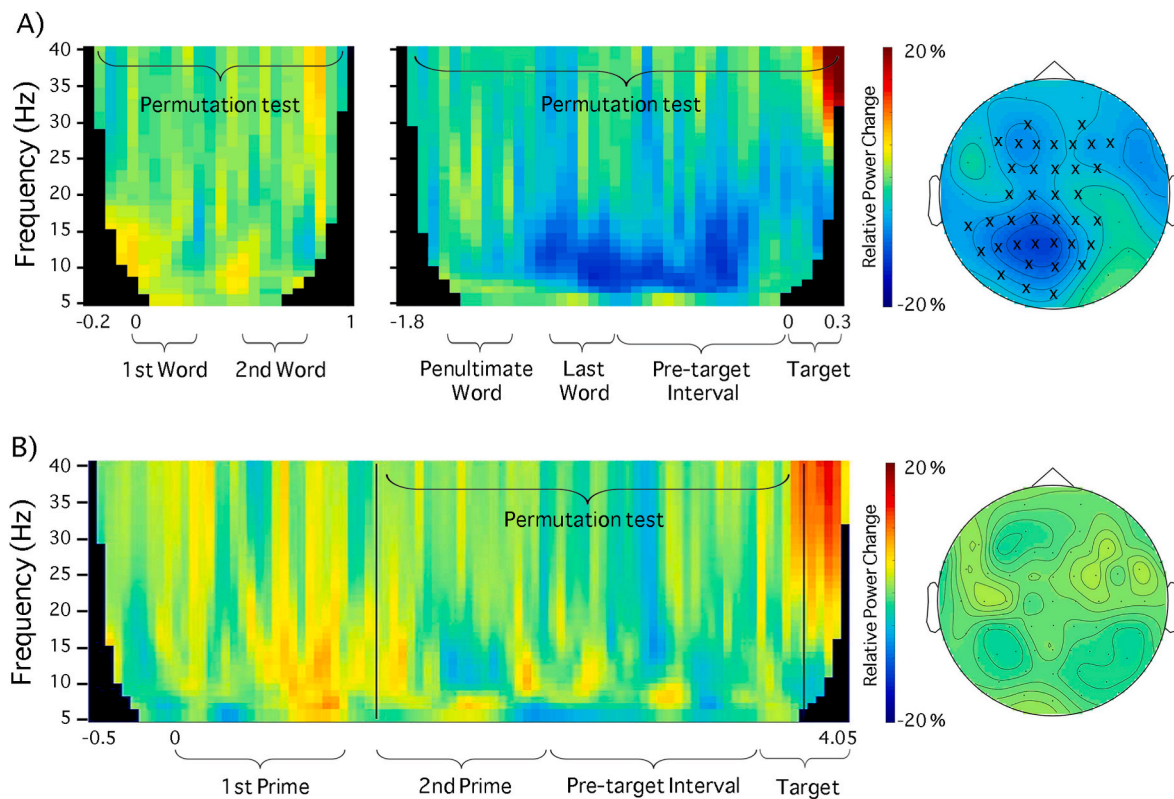


Fig. 3. Time-frequency representations (TFR) of the contextual constraint effect represented as relative power changes for the constraining relative to the nonconstraining condition normalized against their mean. TFRs are shown for the averaged channels highlighted on the right topographical plots for A) nonverbal experiment and for B) verbal experiment. For each experiment, the onset and duration of stimuli are visualized below the beginning and end segments of the respective experiment. The TFRs for all segments (nonverbal and verbal) are visualized over channels associated with the significant cluster in the end segments of the verbal experiment, which are highlighted in the topographical representations.

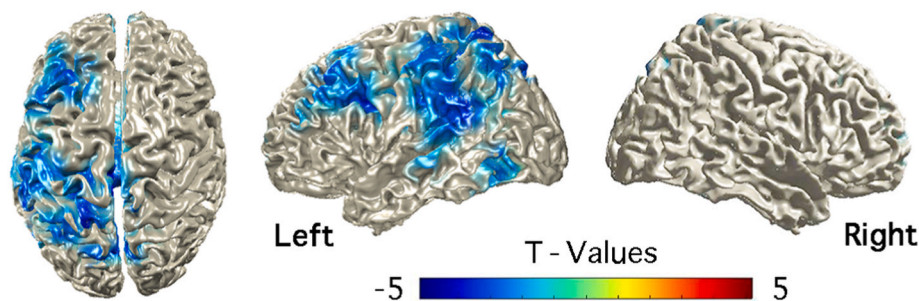


Fig. 4. Source localization of the power differences (constraining relative to the nonconstraining condition normalized against their mean) found in the verbal experiment between 8 and 20 Hz. The color bar shows t-values, masked by the statistically significant cluster. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.4. Both nonverbal and verbal context modulates ERP amplitudes

In the nonverbal experiment, there were three time windows where the ERP waveforms differed between the constraining and nonconstraining condition. Firstly, during the second prime presentation, ERP amplitude was more negative in the nonconstraining than in the constraining condition ($p = 0.002$). The difference was most prominent from 115 to 730 ms relative to second prime onset (i.e., around 1315 ms relative to first prime onset, see Fig. 1) over central-posterior regions (Fig. 5A). Secondly, during the whole pre-target interval, there was a late potential from 1170 to 2500 ms relative to second prime onset (i.e., 2370 ms relative to first prime onset). This component had a complex topography. More specifically, the constraining condition was more negative than the nonconstraining condition over the frontal channels ($p = 0.002$) and this difference was reversed over the posterior channels

($p = 0.003$, Fig. 5B). Thirdly, post target-picture onset, a positive potential was more pronounced in the constraining as compared to the nonconstraining condition ($p = 0.002$). It lasted from 240 until 450 ms relative to target picture onset and it was mostly pronounced over central electrodes (Fig. 5A).

In the verbal experiment, the ERP waveforms differed between the constraining and nonconstraining conditions in two different time windows (Fig. 5C). Firstly, there was a difference between the conditions starting even before the onset of the penultimate word, from -1800 to -445 ms relative to target picture onset. The constraining condition was more negative than the nonconstraining condition over the frontal channels (appearing as four separate clusters: $p = 0.024$; $p = 0.024$; $p = 0.002$; $p = 0.042$) and this difference was reversed over the posterior channels ($p = 0.002$). Secondly, the constraining condition had higher amplitude in the anterior channels starting from 85 to 300 ms

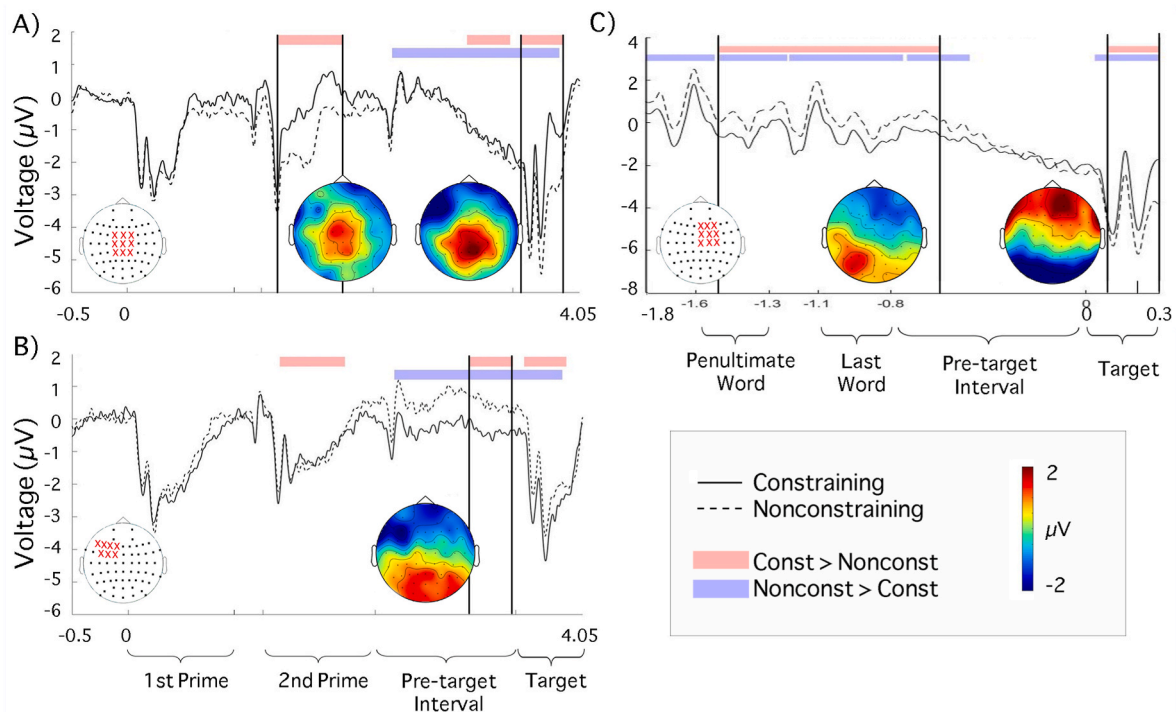


Fig. 5. Event related potentials displayed for A) nonverbal experiment averaged over central channels, B) nonverbal experiment averaged over left anterior channels, and C) verbal experiment averaged over right anterior channels. In the nonverbal and verbal experiments, there were clusters indicating amplitude differences between the constraining and nonconstraining condition (highlighted by red and blue bars). Five time periods where there were prominent differences between conditions are highlighted by vertical black bars for which top plots of the difference (const – nonconst) are displayed. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

post target picture onset ($p = 0.012$), and the nonconstraining condition had higher amplitude in the posterior channels starting from 35 to 300 ms post target picture onset ($p = 0.016$).

3.5. EEG effects correlate with RTs but not with cloze probability

In the nonverbal experiment, the correlation analysis for the alpha-beta power with the RTs did not show a statistically significant correlation for either constraining ($p = 0.152$) or nonconstraining condition ($p = 0.351$). For the verbal experiment, the correlation analysis between alpha-beta power and the RTs showed a positive relation in the constraining condition (i.e., RTs are shorter when alpha-beta power is lower, $p = 0.004$), replicating *Roos and Piai (2020)*. This relationship was most prominent from -550 ms to -150 ms relative to target picture onset, for the frequency range from 8 to 14 Hz (*Fig. 6A*). No relationship was found in the nonconstraining condition ($p = 1$).

The results of the correlation test between ERP amplitude and RTs in the nonverbal constraining condition showed a positive relationship (i.e. higher amplitude is related to faster RTs) in the anterior electrodes (appearing as two separate clusters: $p = 0.004$ and $p = 0.004$), and a negative relationship in the posterior electrodes (appearing as two separate clusters: $p = 0.004$ and $p = 0.004$). Both the positive and the negative correlations were most pronounced between -680 and 0 ms relative to target-picture onset. These two opposite correlations are found at overlapping time points but in different channels (*Fig. 6B*). In the nonverbal nonconstraining condition, there was no significant correlation ($p = 0.631$). By contrast, in the verbal experiment, no statistically significant correlation was found between pre-picture ERP amplitude and subsequent RTs for the constraining ($p = 0.070$) or the nonconstraining condition ($p = 0.012$), after correction for multiple comparisons (assuming an alpha level of 0.006).

We found no significant correlations between EEG effects and cloze probabilities. This was true for the correlations with alpha-beta power

(verbal constraining: $p = 0.614$; verbal nonconstraining: $p = 0.164$; nonverbal constraining: $p = 0.583$), as well as for the correlations with ERP amplitude (verbal constraining: $p = 0.164$; verbal nonconstraining: $p = 0.18$; nonverbal constraining: $p = 0.108$; note that all cloze probabilities were zero for the nonverbal nonconstraining trials).

4. Discussion

In a novel picture-naming experiment, we investigated electrophysiological signatures of conceptual and lexical retrieval from semantic memory when retrieval follows a nonverbal setting. For contrast, in the verbal experiment, we tried to replicate electrophysiological signatures associated with conceptual and lexical retrieval following verbal materials (i.e. alpha-beta desynchronization) in the same participants.

We replicated the finding that participants respond faster in constraining than nonconstraining contexts following verbal settings (*Griffin and Bock, 1998; Piai et al., 2014b; Piai et al., 2015*). Crucially, the same facilitation effect also holds following nonverbal settings. This shows that spreading activation following verbal and nonverbal information facilitates retrieval from semantic memory. A between-experiment statistical comparison and inspection of RT distributions indicated that participants responded faster following verbal compared to nonverbal settings, and that the difference between the constraining and nonconstraining contexts was larger following verbal compared to nonverbal settings. This suggests that conceptual and lexical retrieval unravels more slowly following nonverbal compared to verbal settings. The difference in word planning onset following the verbal versus nonverbal settings should be considered when evaluating our electrophysiological results.

As expected, in the verbal experiment, we replicated the desynchronization in the alpha-beta range in constraining as compared to the nonconstraining condition that started to emerge before the last word of the sentence and persisted throughout the pre-target interval (*Piai et al,*

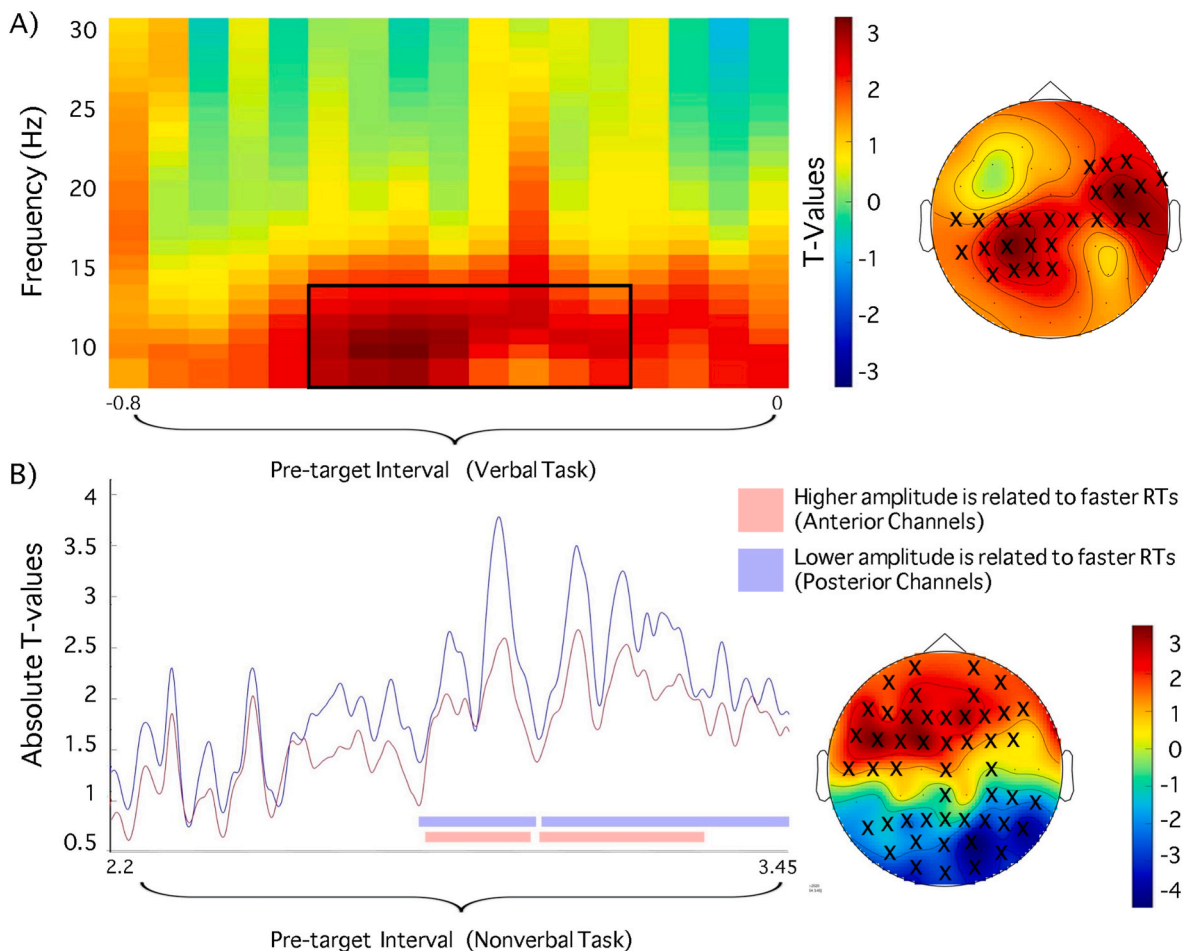


Fig. 6. Correlations of neural signatures with response times (RT). A) Depicts positive correlations between RTs and alpha-beta power for the verbal experiment. The correlation plot shows in which time interval and frequency range there are most prominent correlations (extreme t-values are represented by darker colors). The correlation plot is averaged over the channels with highest t-values highlighted with x in the topo plot. B) Depicts both positive correlations between RTs and ERP amplitude for the anterior channels and negative correlations in the posterior channels in the nonverbal experiment. The correlation plot shows the absolute t-values separately for the anterior channels (red) and posterior channels (blue). The correlation plot is averaged over the channels with significant t-values highlighted with x in the topo plot. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

2015, 2017, 2018, 2015; Piai et al., 2014b). In line with previous research (Klaus et al., 2020; Piai et al., 2015; Roos and Piai, 2020), this desynchronization originated from the language-dominant left hemisphere, more specifically from inferior temporal gyrus, temporo-parietal areas and premotor cortex. These results were paralleled by the correlations with RTs, which showed that the alpha-beta desynchronization is related to RTs on a single-trial level (discussed in more detail below). Most crucially, in the nonverbal experiment, we expected to show that alpha and beta desynchronization would be more pronounced in the constraining compared to the nonconstraining condition as well. To our surprise, this was not the case, and we did not find any significant desynchronization (or synchronization) pattern. The effect sizes of the 8–25 Hz power decreases following the constraining versus the nonconstraining conditions were larger in the verbal compared to the nonverbal experiment, which is in line with the finding of a significant interaction between condition and experiment. We note that the interaction analysis as well as the comparison of the effect sizes between experiments should be interpreted with caution. This is because the timing of the tasks was different across the two experiments, which makes it somewhat difficult to directly compare the EEG results. Nevertheless, the between-experiment analyses further corroborate the within-experiment findings, where we replicated the previously observed effect in the verbal experiment, whereas we found a weaker (or absent) effect in the nonverbal experiment in the same participants.

The EEG results should be interpreted in light of the behavioral results. Shorter RTs in the constraining compared to the nonconstraining condition indicate that the participants must have engaged in conceptual activation before target-picture onset in each experiment. However, the degree to which the semantic information in the experiments guides the participants towards a selection of a single concept differs depending on the settings. One interpretation of the results could be that the set-up of the verbal experiment funnels the lexical possibilities of the participant until one (or only a few at most) final concept can be retrieved from semantic memory, even before target picture presentation. For example, the sentence “The farmer milked a ...” leads participants to only retrieve the concept “cow”. In the nonverbal experiment, the longer RTs and smaller alpha-beta power decreases indicate that conceptual and lexical retrieval occur differently. Yet the different RTs between constraining and nonconstraining conditions show evidence for the presence of conceptual retrieval as a function of the context. We believe that the broader context in the nonverbal experiment leads to activation of many target-related concepts (before the target picture presentation). These activated concepts set a semantic space, but it is not resolved further (or at least not consistently, as is the case for the verbal experiment). This means that after presentation of both primes, participants cannot narrow down the retrieved concepts (e.g., nest, feather, egg, bird, tree, etc.) to a single one, which is going to appear as the target (e.g., bird), possibly leading to the longer RTs following nonverbal settings. Hence,

the alpha-beta desynchronization, found in the verbal experiment, appears to be associated with conceptual and lexical retrieval of a single concept, as the broad conceptual activation, taking place in the nonverbal experiment, does not seem sufficient to elicit this desynchronization.

These desynchronization results can also be interpreted in light of the prediction literature. Word prediction aids prompt language production as well as comprehension (Pickering and Garrod, 2007) and is thought to be associated with beta desynchronization (e.g., Meyer, 2018). For example, according to the predictive coding framework, beta desynchronization is thought to be associated with sending target predictions from higher-to lower-level processing hierarchy, where these predictions can be compared with incoming linguistic information (Lewis and Bastiaansen, 2015; Lewis et al., 2016), or in our case, the picture names. In the verbal experiment, we simply describe such predictions as conceptual and lexical retrieval. In the nonverbal experiment, the context modality may lead to different types of predictions, which are not associated with alpha-beta desynchronization. This interpretation would be in line with the predictive coding framework, as it postulates that one of the functions of beta desynchronization is to propagate the target predictions to lower hierarchical levels for error monitoring (Lewis and Bastiaansen, 2015), which is only useful if a specific prediction has been made.

If participants are engaging in conceptual activation following constraining but not nonconstraining contexts in the nonverbal experiment, it should be reflected in the electrophysiological signatures. For language, oscillations reflect only some cognitive processes while others are more apparent in the ERPs (e.g., Davidson and Indefrey, 2007; Piai et al., 2014a,b). It should be noted that the nonverbal experiment has discrete events that further constrain the context, while the verbal experiment does not have one discrete event and the constraining effect is more cumulative; this difference could potentially lead to ERP differences between experiments, but this is contrary to what we found.

Here we will provide a tentative interpretation of the ERP effects, although it should be noted that it is rather speculative at this stage. We observed amplitude differences between the constraining and nonconstraining condition in three time intervals in the nonverbal experiment and in two time intervals in the verbal experiment. In the nonverbal experiment, we observed a negative deflection approximately 300 ms after the second prime onset (time point of 1.5 s in Fig. 5A), which was more pronounced in the nonconstraining condition. This component may be an N300, which may reflect category membership and semantic similarity (Barrett and Rugg, 1990; Franklin et al., 2007; Ganis et al., 1996; McPherson and Holcomb, 1999). This indicates that participants were aware of the semantic similarity of the two primes and were therefore more likely to start retrieving conceptual candidates from semantic memory before the target picture onset. Throughout the pre-target interval of the nonverbal experiment, the amplitude of the nonconstraining condition was more extreme in left anterior and posterior electrodes. The same pattern was seen in the verbal experiment after the penultimate word onset throughout the beginning of the pre-target interval. Similar slow ERP waveforms have been found in various studies investigating working memory (WM) load, where high memory load conditions were associated with more extreme amplitudes (Löw et al., 1999; Ruchkin et al., 1990; Vogel and Machizawa, 2004). Hence, there could be higher WM demands in the nonconstraining than in the constraining conditions. Finally, in each experiment, we found a positive deflection peaking around 300 ms after target picture onset, which was more pronounced in the constraining condition. This positive deflection likely represents the P300 component. The same effect was found in a previous study that utilized the verbal experiment (Piai et al., 2014b). The amplitude of the P300 increases with target predictability (Roehm et al., 2007), in line with the claim that in the constraining condition, participants could expect some properties of the upcoming target picture.

Given that conceptual and lexical retrieval were reflected differently

in the electrophysiological signatures in the two experiments (i.e., oscillations and ERPs in the verbal experiment and only ERPs in the nonverbal experiment), we investigated whether these signatures are related to naming latencies and cloze probabilities on a single-trial level and, thus, have behavioral relevance. Firstly, we examined how alpha-beta power and ERP amplitude in the critical pre-target interval (when participants are likely planning their response) are related to subsequent naming RTs within conditions. In line with previous findings (Roos and Piai, 2020), we found that in the verbal experiment, the alpha-beta desynchronization correlated with the RTs in the constraining but not in the nonconstraining condition. In the nonverbal experiment, only ERP amplitude correlated with the RTs. This correlation was only found in the constraining condition and it persisted throughout the majority of the pre-target interval. Thus, the ERP amplitude may be better at reflecting the broad conceptual activation thought to be taking place here. This suggests that the different neural mechanisms employed across the two modalities are predictive of the naming latencies, which depend on how and when conceptual and lexical retrieval occurs. Secondly, we examined how alpha-beta power and ERP amplitude in the critical pre-target interval are related to cloze probabilities of the individual items within conditions. The correlational analysis between the EEG effects and cloze probability did not reveal any significant results in either experiment. This finding is in itself interesting because the contextual manipulation in each experiment leads to vast effects of cloze probability. Yet, within conditions, it does not consistently relate to the EEG effects while the RTs do. Trial to trial, as compared to cloze probability, the RTs more closely reflect conceptual and lexical retrieval in the verbal experiment and conceptual activation in the nonverbal experiment, which drive the EEG effects.

It should be noted that it was not possible to control for the level of constraint between the verbal and nonverbal experiments. We examined the alpha-beta power in a subset of trials with comparable cloze probabilities. We again only found significant power decrease in the constraining relative to nonconstraining condition in the verbal experiment. Thus, disparities in cloze probability do not readily explain power differences between nonverbal and verbal experiments. Crucially, the two experiments differ in the amount of context that drives the planning of the target word. It is likely that the verbal constraining context funnels the lexical possibilities of the participant until one or a few final concepts are retrieved from semantic memory. The nonverbal constraining context seems to be less confining and allows for wider interpretation. The electrophysiological differences between the two experiments are qualitatively too different to be only driven by the different levels of constraint. Thus, we interpret our findings as indicating that the context modality is the driving force behind these differences, which then modulates both cloze probabilities and EEG signatures (rather than cloze probabilities being the driving force behind the EEG signatures). It should be noted that inclusion of syntax (or structure) seems essential to reach the funneling of lexical possibilities, which was only present in the verbal experiment. Hence, future research should examine conceptual and lexical retrieval following verbal settings that exclude syntactic cues.

In summary, our behavioral results indicate that conceptual and lexical retrieval unravels more slowly following nonverbal compared to verbal settings. The alpha-beta desynchronization, which has been associated with conceptual and lexical retrieval, was observed following the verbal settings. This pattern was not observed after the semantic processing of nonverbal settings. However, we did find faster RTs in the constraining relative to the nonconstraining condition of the nonverbal experiment, which suggests that at least the initial stage of conceptual activation must have occurred before target presentation. This is further supported by the attenuated N300 response in the constraining condition, which shows that participants were aware of the semantic similarity of the two primes and they were therefore more likely to start activating conceptual candidates before the target picture onset. However, the conceptual preparation of multiple concepts does not seem

enough to elicit the alpha-beta desynchronization. We conclude, thus, that the alpha-beta desynchronization must be related to conceptual and lexical retrieval of a single word, or at least of a more specific representation. These findings contribute to our understanding of the relationship between brain oscillations, and alpha-beta desynchronization in particular, and retrieval of information from semantic memory.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuropsychologia.2021.107988>.

References

- Barrett, S.E., Rugg, M.D., 1990. Event-related potentials and the semantic matching of pictures. *Brain Cognit.* 14 (2), 201–212. [https://doi.org/10.1016/0278-2626\(90\)90029-N](https://doi.org/10.1016/0278-2626(90)90029-N).
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Software* 67 (1), 1–18. <https://doi.org/10.18637/jss.v067.i01>.
- Boersma, P., Weenink, D., 2013. Praat: Doing Phonetics by Computer. Retrieved from, Version 6.1.16. www.praat.org.
- Bögels, S., 2020. Neural correlates of turn-taking in the wild: response planning starts early in free interviews. *Cognition* 203 (1), 104347. <https://doi.org/10.1016/j.cognition.2020.104347>.
- Brodeur, M.B., Guérard, K., Bouras, M., 2014. Bank of standardized stimuli (BOSS) phase II: 930 new normative photos. *PLoS One* 9 (9), e106953. <https://doi.org/10.1371/journal.pone.0106953>.
- Buzsáki, G., Anastassiou, C.A., Koch, C., 2012. The origin of extracellular fields and currents — EEG, ECoG, LFP and spikes. *Nat. Rev. Neurosci.* 13 (1), 407–420. <https://www.nature.com/articles/nrn3241>.
- Chiang, H.S., Eroh, J., Spence, J.S., Motes, M.A., Maguire, M.J., Krawczyk, D.C., Kraut, M.A., 2016. Common and differential electrophysiological mechanisms underlying semantic object memory retrieval probed by features presented in different stimulus types. *Int. J. Psychophysiol.* 106 (1), 77–86. <https://doi.org/10.1016/j.ijpsycho.2016.06.011>.
- Davidson, D.J., Indefrey, P., 2007. An inverse relation between event-related and time-frequency violation responses in sentence processing. *Brain Res.* 1158 (1), 81–92. <https://doi.org/10.1016/j.brainres.2007.04.082>.
- Dell, G.S., 1986. A spreading-activation theory of retrieval in sentence production. *Psychol. Rev.* 93 (3), 283–321. <https://doi.org/10.1037/0033-295X.93.3.283>.
- Düzel, E., Habib, R., Schott, B., Schoenfeld, A., Lobaugh, N., McIntosh, A.R., Heinze, H.J., 2003. A multivariate, spatiotemporal analysis of electromagnetic time-frequency data of recognition memory. *Neuroimage* 18 (2), 185–197. [https://doi.org/10.1016/S1053-8119\(02\)00031-9](https://doi.org/10.1016/S1053-8119(02)00031-9).
- Fellner, M., Hanslmayr, S., 2017. Brain oscillations, semantic processing, and episodic memory. *Neural Mechanisms of Language*, pp. 63–80. <https://doi.org/10.1007/978-1-4939-7325-5>.
- Franklin, M.S., Dien, J., Neely, J.H., Huber, E., Waterson, L.D., 2007. Semantic priming modulates the N400, N300, and N400RP. *Clin. Neurophysiol.* 118 (5), 1053–1068. <https://doi.org/10.1016/j.clinph.2007.01.012>.
- Ganis, G., Kutas, M., Sereno, M.I., 1996. The search for “common sense”: an electrophysiological study of the comprehension of words and pictures in reading. *J. Cognit. Neurosci.* 8 (2), 89–106. <https://doi.org/10.1162/jocn.1996.8.2.89>.
- Garrett, M.F., 1988. In: Newmeyer, F.J. (Ed.), *Processes in Language Production*. Cambridge University Press, New York, NY, US.
- Griffin, Z.M., Bock, K., 1998. Constraint, word frequency, and the relationship between lexical processing levels in spoken word production. *J. Mem. Lang.* 38 (1), 313–338. <https://doi.org/10.1006/jmla.1997.2547>.
- Gross, J., Kujala, J., Hamalainen, M., Timmermann, L., Schnitzler, A., Salmelin, R., 2001. Dynamic imaging of coherent sources: studying neural interactions in the human brain. *Proc. Natl. Acad. Sci. Unit. States Am.* 98 (2), 694–699. <https://doi.org/10.1073/pnas.98.2.694>.
- Hanslmayr, S., Spitzer, B., Bäuml, K., 2009. Brain oscillations dissociate between semantic and nonsemantic encoding of episodic memories. *Cerebr. Cortex* 19 (1), 1631–1640. <https://doi.org/10.1093/cercor/bhn197>.
- Hanslmayr, S., Staresina, B.P., Bowman, H., 2016. Oscillations and episodic memory: addressing the synchronization/desynchronization conundrum. *Trends Neurosci.* 39 (1), 16–25. <https://doi.org/10.1016/j.tins.2015.11.004>.
- Hart, J., Anand, R., Zoccoli, S., Maguire, M., Gamino, J., Tillman, G., Kraut, M.A., 2007. Neural substrates of semantic memory. *J. Int. Neuropsychol. Soc.* 13 (1), 865–880. <https://doi.org/10.1017/S135561770707110X>.
- Holmes, C.J., Hoge, R., Collins, L., Woods, R., Toga, A.W., Evans, A.C., 1998. Enhancement of MR images using registration for signal averaging. *J. Comput. Assist. Tomogr.* 22 (2), 324–333. <https://doi.org/10.1097/00004728-199803000-00032>.
- Homöle, S., Oostenveld, R., 2019. Using a structured-light 3D scanner to improve EEG source modeling with more accurate electrode positions. *J. Neurosci. Methods* 326, 108378. <https://doi.org/10.1016/j.jneumeth.2019.108378>.
- Klaus, J., Schutter, D.J.L.G., Piai, V., 2020. Transient perturbation of the left temporal cortex evokes plasticity-related reconfiguration of the lexical network. *Hum. Brain Mapp.* 41 (4), 1061–1071. <https://doi.org/10.1002/hbm.24860>.
- Klimesch, W., Doppelmayr, M., Pachinger, T., Ripper, B., 1997a. Brain oscillations and human memory: EEG correlates in the upper alpha and theta band. *Neurosci. Lett.* 238 (1), 9–12. [https://doi.org/10.1016/S0304-3940\(97\)00771-4](https://doi.org/10.1016/S0304-3940(97)00771-4).
- Klimesch, W., Doppelmayr, M., Pachinger, T., Russegger, H., 1997b. Event-related desynchronization in the alpha band and the processing of semantic information. *Cognit. Brain Res.* 6 (2), 83–94. [https://doi.org/10.1016/S0926-6410\(97\)00018-9](https://doi.org/10.1016/S0926-6410(97)00018-9).
- Kutas, M., Van Petten, C., 1990. Electrophysiological perspectives on comprehending written language. *Electroencephalogr. Clin. Neurophysiol. Suppl.* 41 (1), 155–167. <https://doi.org/10.1016/B978-0-444-81352-7.50020-0>.
- Kutas, M., van Petten, C.K., 1994. Psycholinguistics electrified. In: *Handbook of Psycholinguistics*, pp. 83–143. <https://doi.org/10.1016/B978-012369374-7/50018-3>.
- Laaksonen, H., Kujala, J., Hultén, A., Liljeström, M., Salmelin, R., 2012. MEG evoked responses and rhythmic activity provide spatiotemporally complementary measures of neural activity in language production. *Neuroimage* 60 (1), 29–36. <https://doi.org/10.1016/j.neuroimage.2011.11.087>.
- Lega, B.C., Jacobs, J., Kahana, M., 2012. Human hippocampal theta oscillations and the formation of episodic memories. *Hippocampus* 22 (4), 748–761. <https://doi.org/10.1002/hipo.20937>.
- Levelt, W.J.M., Roelofs, A., Meyer, A.S., 1999. A theory of lexical access in speech production. *Behav. Brain Sci.* 22 (1), 1–38. <https://doi.org/10.1017/S0140525X99001776>.
- Lewis, A.G., Bastiaansen, M., 2015. A predictive coding framework for rapid neural dynamics during sentence-level language comprehension. *Cortex* 68 (1), 155–168. <https://doi.org/10.1016/j.cortex.2015.02.014>.
- Lewis, A.G., Schoffelen, J.-M., Schriefers, H., Bastiaansen, M., 2016. A predictive coding perspective on beta oscillations during sentence-level language comprehension. *Front. Hum. Neurosci.* 10 (85), 1–6. <https://doi.org/10.3389/fnhum.2016.00085>.
- Löw, A., Rockstroh, B., Cohen, R., Hauk, O., Berg, P., Maier, W., 1999. Determining working memory from ERP topography. *Brain Topogr.* 12 (1), 39–47. <https://doi.org/10.1023/A:1022229623355>.
- Maris, E., Oostenveld, R., 2007. Nonparametric statistical testing of EEG- and MEG-data. *J. Neurosci. Methods* 164 (1), 177–190. <https://doi.org/10.1016/j.jneumeth.2007.03.024>.
- McPherson, W.B., Holcomb, P.J., 1999. An electrophysiological investigation of semantic priming with pictures of real objects. *Psychophysiology* 36 (1), 53–65. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/10098380>.
- Meyer, L., 2018. The neural oscillations of speech processing and language comprehension: state of the art and emerging mechanisms. *Eur. J. Neurosci.* 48 (7), 2609–2621. <https://doi.org/10.1111/ejn.13748>.
- Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.M., 2011. FieldTrip: open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comput. Intell. Neurosci.* 2011 (1), 1–9. <https://doi.org/10.1155/2011/156869>.
- Piai, V., Klaus, J., Rossetto, E., 2020. The lexical nature of alpha-beta oscillations in context-driven word production. *J. Neurolinguistics* 55 (1), 100905. <https://doi.org/10.1016/j.jneuroling.2020.100905>.
- Piai, V., Meyer, L., Dronkers, N.F., Knight, R.T., 2017. Neuroplasticity of language in left-hemisphere stroke: evidence linking subsecond electrophysiology and structural connections. *Hum. Brain Mapp.* 38 (6), 3151–3162. <https://doi.org/10.1002/hbm.23581>.
- Piai, V., Roelofs, A., Jensen, O., Schoffelen, J.-M., Bonnefond, M., 2014a. Distinct patterns of brain activity characterise lexical activation and competition in spoken word production. *PLoS One* 9 (2), e88674. <https://doi.org/10.1371/journal.pone.0088674>.
- Piai, V., Roelofs, A., Maris, E., 2014b. Oscillatory brain responses in spoken word production reflect lexical frequency and sentential constraint. *Neuropsychologia* 53 (1), 146–156. <https://doi.org/10.1016/j.neuropsychologia.2013.11.014>.
- Piai, V., Roelofs, A., Rommers, J., Maris, E., 2015. Beta oscillations reflect memory and motor aspects of spoken word production. *Hum. Brain Mapp.* 36 (7), 2767–2780. <https://doi.org/10.1002/hbm.22806>.
- Piai, V., Rommers, J., Knight, R.T., 2018. Lesion evidence for a critical role of left posterior but not frontal areas in alpha-beta power decreases during context-driven word production. *Eur. J. Neurosci.* 48 (7), 2622–2629. <https://doi.org/10.1111/ejn.13695>.
- Pickering, M.J., Garrod, S., 2007. Do people use language production to make predictions during comprehension? *Trends Cognit. Sci.* 11 (3), 105–110. <https://doi.org/10.1016/j.tics.2006.12.002>.
- Ratcliff, R., 1979. Group reaction time distributions and an analysis of distribution statistics. *Psychol. Bull.* 86 (3), 446–461. <https://doi.org/10.1037/0033-2909.86.3.446>.
- Roehm, D., Bornkessel-Schlesewsky, I., Rösler, F., Schlesewsky, M., 2007. To predict or not to predict: influences of task and strategy on the processing of semantic relations.

- J. Cognit. Neurosci. 19 (8), 1259–1274. <https://doi.org/10.1162/jocn.2007.19.8.1259>.
- Roos, N.M., Piai, V., 2020. Across-session consistency of context-driven language processing: a magnetoencephalography study. *Eur. J. Neurosci.*, 14785 <https://doi.org/10.1111/ejn.14785>.
- Ruchkin, D.S., Johnson, R., Canoune, H., Ritter, W., 1990. Short-term memory storage and retention: an event-related brain potential study. *Electroencephalogr. Clin. Neurophysiol.* 76 (5), 419–439. [https://doi.org/10.1016/0013-4694\(90\)90096-3](https://doi.org/10.1016/0013-4694(90)90096-3).
- Strijkers, K., Holcomb, P.J., Costa, A., 2012. Conscious intention to speak proactively facilitates lexical access during overt object naming. *J. Mem. Lang.* 65 (4), 345–362. <https://doi.org/10.1016/j.jml.2011.06.002>. Conscious.
- Taylor, W.L., 1953. “Cloze procedure”: a new tool for measuring readability. *Journal. Q.* 30 (1), 415–433. <https://doi.org/10.1177/107769905303000401>.
- Van Casteren, M., Davis, M.H., 2006. Mix, a program for pseudorandomization. *Behav. Res. Methods* 38 (1), 584–589. <https://doi.org/10.3758/BF03193889>.
- Vogel, E.K., Machizawa, M.G., 2004. Neural activity predicts individual differences in visual working memory capacity. *Nature* 428 (6984), 748–751. <https://doi.org/10.1038/nature02447>.