

Beta Oscillations Reflect Memory and Motor Aspects of Spoken Word Production

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Abstract: Two major components form the basis of spoken word production: the access of conceptual and lexical/phonological information in long-term memory, and motor preparation and execution of an articulatory program. Whereas the motor aspects of word production have been well characterized as reflected in alpha-beta desynchronization, the memory aspects have remained poorly understood. Using magnetoencephalography, we investigated the neurophysiological signature of not only motor but also memory aspects of spoken-word production. Participants named or judged pictures after reading sentences. To probe the involvement of the memory component, we manipulated sentence context. Sentence contexts were either constraining or nonconstraining toward the final word, presented as a picture. In the judgment task, participants indicated with a left-hand button press whether the picture was expected given the sentence. In the naming task, they named the picture. Naming and judgment were faster with constraining than nonconstraining contexts. Alpha-beta desynchronization was found for constraining relative to nonconstraining contexts pre-picture presentation. For the judgment task, beta desynchronization was observed in left posterior brain areas associated with conceptual processing and in right motor cortex. For the naming task, in addition to the same left posterior brain areas, beta desynchronization was found in left anterior and posterior temporal cortex (associated with memory aspects), left inferior frontal cortex, and bilateral ventral premotor cortex (associated with motor aspects). These results suggest that memory and motor components of spoken word production are reflected in overlapping brain oscillations in the beta band. *Hum Brain Mapp* 36:2767–2780, 2015. © 2015 Wiley Periodicals, Inc.

Key words: beta oscillations; context; left temporal cortex; lexical retrieval; magnetoencephalography; phonological encoding; phonetic encoding; picture naming; sentential constraint; word production



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The study of the human ability to speak has been approached from two different perspectives, a psycholinguistic and a motor-control perspective [Hickok, 2012]. Whereas the psycholinguistic approach has been largely preoccupied with the memory aspects of language production, that is, the access of conceptual, lexical, and phonological information in long-term memory, the motor-control approach has mainly focused on aspects of motor preparation and execution of an articulatory program.

The vast majority of the electrophysiological studies with a psycholinguistic approach examined event-related brain potentials [see for review Ganushchak et al., 2011] whereas only a few studies investigated oscillatory activity [Laaksonen et al., 2012; Piai et al., 2014a,b; Rommers et al., 2013c]. The motor-control approach has booked substantial progress in understanding the neurophysiology of speech production in terms of neuronal oscillations [e.g., Herman et al., 2013; Jenson et al., 2014; Salmelin and Sams, 2002]. However, this research direction has often deliberately opted for bypassing the “confounding effects of lexical [...] processes” [Herman et al., 2013, p. 5440]. The present study investigated neuronal oscillations as measured by magnetoencephalography (MEG) to identify the neurophysiological signature of not only the motor but also the memory aspects of overt word production. To probe the involvement of the memory component, we manipulated sentence context, because semantic contextual cues guide the access to memory and the activation of word candidates associated with that semantic context [e.g., Griffin and Bock, 1998; Levelt, 1989].

According to psychological models of spoken-word production [e.g., Dell, 1986; Levelt, 1989; Roelofs, 2014], the planning of spoken words proceeds through a series of stages varying in their degree of involvement of memory and motor processes. The earlier stages rely mainly on retrieval of conceptual, lexical, and phonological information from long-term memory. By contrast, the subsequent stages rely increasingly more on motor programming, such as the incremental clustering of speech sounds into syllabic patterns, the transformation of syllables into motor plans, and articulation. Picture naming involves all the memory and motor components of spoken-word production and, therefore, has been a particularly useful task to study the cognitive architecture of speaking [cf. Levelt et al., 1999]. On an anatomical level, the retrieval of conceptual information has been associated with the (anterior) inferior and middle temporal cortex and angular gyrus [e.g., Binder et al., 2009; Lambon Ralph, 2014; Patterson et al., 2007; Price, 2012]. For word production in particular, the memory components have been largely associated with the mid- to anterior portion of the left middle temporal gyrus [Schwartz et al., 2009; Walker et al., 2011] and posterior superior and middle temporal gyrus, whereas the motor components have been associated with left inferior frontal gyrus (LIFG) and bilateral ventral premotor cortex [for reviews, see Indefrey, 2011; Indefrey and Levelt, 2004; Price, 2012; Roelofs, 2014]. Importantly, most of

this knowledge comes from studies of the brain’s hemodynamic responses [but see Roelofs, 2014], which is very useful for the purpose of localization, but not for identifying the neurophysiological mechanisms underlying cognitive computations. This is where neuronal oscillations become relevant, as they are argued to provide the link between cognitive and neurophysiological computations [see for further discussion Cohen, 2014].

The oscillatory dynamics of motor and general memory systems has been well characterized. In the motor domain, the preparation and execution of movement is accompanied by alpha-beta power decreases over the sensorimotor cortex contralateral to the side of movement [reviewed in Cheyne, 2013]. In this case, the active engagement of the sensorimotor system in the preparation and execution of movement is associated with neuronal desynchronization [Pfurtscheller and Lopes da Silva, 1999]. Retrieval of information from long-term memory has also been associated with the alpha-beta band [see for review Hanslmayr et al., 2012; Nyhus and Curran, 2010], where *desynchronization* in the alpha-beta band is assumed to reflect memory retrieval processes [e.g., Hanslmayr et al., 2012; Khader and Rösler, 2011].

OSCILLATIONS IN PREVIOUS OVERT WORD PRODUCTION STUDIES

Studies of speech production with a motor-control approach have mainly used pseudoword repetition and word naming tasks [Herman et al., 2013; Jenson et al., 2014]. These studies have found power decreases in the alpha-beta band (7–30 Hz) pre-speech onset, localized to left motor and premotor cortex and LIFG [Herman et al., 2013]. These studies provide evidence that motor aspects of speech production are associated with power decreases in the alpha-beta band [see also Saarinen et al., 2006; Salmelin and Sams, 2002]. However, since words can be read aloud via grapheme-phoneme correspondence rules [Coltheart et al., 2001] and pseudowords do not exist in memory, these studies do not tap into the memory aspects of word production.

Picture-naming studies, in turn, do tap into the memory aspects of word production since conceptual, lexical, and phonological information must be retrieved from long-term memory. In a picture-naming MEG study [Laaksonen et al., 2012], power modulations were found between 7–12 Hz and 17–22 Hz relative to a baseline period (fixation cross). Modulations between 7–12 Hz were observed bilaterally in visual, parietal, and temporal areas, and in premotor cortex. Modulations between 17–22 Hz were also bilateral in visual, parietal, and premotor cortices, but left-lateralized in middle and superior temporal regions. Importantly, this MEG study compared brain activity measured during active spoken word planning relative to a low-level passive baseline (i.e., fixation cross). This is different from two EEG studies in which we compared

activity between two task conditions that differed with respect to the involvement of spoken-word planning [Piai et al., 2014b; Rommers et al., 2013c]. Our participants read sentences that were either constraining or nonconstraining toward the last word of the sentence, which was presented as a picture [Griffin and Bock, 1998]. Participants were instructed to name the picture. We reasoned that, with a constraining context, conceptual, lexical, and phonological information from memory can already be retrieved before the picture is presented, whereas with nonconstraining contexts, word planning can only start after picture presentation. Thus, the difference in activity between these two conditions pre-picture onset reflects the difference in the engagement of the language production system (memory and motor components) during active performance in the task (as opposed to activity relative to a baseline). In both studies, we found between 10% and 15% oscillatory power decreases for constraining relative to nonconstraining sentence contexts in the alpha-beta range (7–30 Hz) already in the interval prior to picture presentation.

In these two EEG studies, we suggested that the alpha-beta power decreases reflected the assembly of a motor-speech plan (phonetic encoding), keeping with the evidence in the literature that motor aspects of word production are reflected in beta desynchronization. Moreover, Rommers et al. considered the possibility that the alpha-beta power decreases might reflect the generation of an abstract code of speech sounds (phonological encoding) in addition. Shortcomings in those studies, however, limited their conclusions. First, we could not firmly exclude the possibility that our alpha-beta power decreases reflected attentional/expectation processes [e.g., Klimesch et al., 1998; van Ede et al., 2011], rather than motor aspects of language production processes (phonetic encoding), as we tried to argue. Importantly, the two EEG studies did not provide a source localization of the alpha-beta power decreases, making a functional interpretation of the desynchronization difficult. As such, it remains unclear whether the alpha-beta desynchronization reflects only motor aspects of word production, as previous studies have shown, or also memory aspects.

THE PRESENT STUDY

In the present study, participants also read constraining or nonconstraining sentences with the last word of the sentence presented as a picture. However, we used MEG, which allowed us to localize the brain sources of the alpha-beta desynchronization. Moreover, two different active tasks had to be performed on the pictures that followed the constraining and nonconstraining context sentences (in different task blocks): picture naming and picture judgment (manually indicate whether the picture was expected). Since both active tasks had the same materials presented with the same procedure (only instructions

on how to respond to the picture differed), predictive processing during comprehension and anticipation of the picture was similar across tasks. Thus, crucially, participants planned a spoken word in the naming task, surely engaging the memory and motor processes of word production, whereas they planned a button press in the judgment task. Finally, we examined the interval preceding picture presentation, rather than following picture presentation. In doing so, we expected to tap especially into the early (memory) stages of spoken word planning, in addition to subsequent stages prior to articulation.

In accordance with our previous findings [Piai et al., 2014b; Rommers et al., 2013c], we expected to replicate the alpha-beta power decreases pre-picture presentation for constraining relative to nonconstraining contexts. By comparing the relative power decreases between the two tasks, we assessed to what extent the desynchronization we previously observed is specific to the picture naming task, thus reflecting word production rather than attention and expectation processes. Moreover, if alpha-beta desynchronization also reflects memory aspects of word production, we should find alpha-beta modulations in left temporal cortex (extending more anteriorly) in the naming but not in the judgment task, in addition to the motor-related brain areas (LIFG and premotor cortex).

METHOD

The present experiment was approved by the Ethics Committee for Behavioural Research of the Social Sciences Faculty at Radboud University Nijmegen in compliance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

Participants

Fifteen native speakers of Dutch voluntarily participated in the experiment for monetary compensation or for course credits (6 male, mean age = 23, *sd* = 3.2). The datasets of four additional participants were not analyzed due to excessive blinking resulting in the loss of a large number of trials (< 70% of the trials remaining).

Materials

One hundred and sixty-eight depictable target words were chosen. For each target word, two line drawings were selected. This procedure was adopted in order to decrease the likelihood that participants would predict the visual features of a specific picture after having been familiarized with all pictures in the experiment (see below). We used line drawings from the picture database of the International Picture-Naming Project [Szekely et al., 2004], from the picture database of the Max Planck Institute for Psycholinguistics, Nijmegen, and public domain line drawings from the internet. Each word was paired with two

sentences for which the target word was the last word of the sentence, presented as a picture. Following the sentence, no specific word was expected as the final word of the sentence (nonconstraining context) or the target word was highly expected (constraining context). These sentences comprised the 126 sentence pairs of constraining and nonconstraining sentences previously used by Piai et al. [2014b] and Rommers et al. [2013c], seven constraining sentences from Rommers et al. [2013a], 13 constraining sentences from Rommers et al. [2013b], and 22 constraining and 42 nonconstraining sentences from van de Meerendonk et al. [2011]. The mean sentence length was 7.4 words. Where possible, the sentences associated with the same target word differed only in a few words between conditions. In most cases, a function word (a determiner or a possessive pronoun) preceded the target word in the sentence. In the remaining sentences, the word preceding the target was always an adjective, and care was taken that the adjective used was either the same across the two sentences, or matched for frequency and number of letters. The target words had a mean cloze probability of 0.9 in the constraining sentences and of 0.02 in the nonconstraining sentences (see the original articles for details). The sentences in the nonconstraining condition did not have a high-cloze probability for any word.

Design

Half of the constraining and half of the nonconstraining sentences were presented to participants in the naming task and the other half of the sentences were presented in the judgment task, resulting in 84 trials per condition in each task. Each picture appeared only once in the experiment. Each target word appeared once in one sentential constraint condition in one task and in another sentential constraint condition and task for the second time. Whether a specific sentence would appear in the naming or judgment task was randomized over five main lists. The pairing of a specific picture with its corresponding sentence was also randomized over five main lists. There was no significant difference in sentence length among sentential constraint conditions and tasks (mean number of words ranged between 7.1 and 7.7 for all main lists). All 168 sentences in each task were pseudo-randomized with one unique final list per participant using Mix [Van Casteren and Davis, 2006]. The randomization was constrained such that the same condition appeared at most in five consecutive trials. Moreover, 48 comprehension questions were interleaved randomly between the experimental sentences to make sure that participants were paying attention to the meaning of the sentences.

Behavioral Procedure

Participants were tested individually in an electrically, acoustically, and magnetically shielded room. The experimenter provided non-magnetic clothes to the participants.

Prior to entering the shielded room, while electrodes were being attached (for the electrocardiogram, electrooculogram, and electromyogram (EMG), see below), participants read the instructions and were familiarized with the pictures and their names using a booklet. They were instructed to keep fixation on the center of the screen, to minimize (head) movement during the experimental blocks, and to blink only at the appropriate interval (blinking intervals, see below). They were also instructed to read the sentences silently for comprehension and to respond to the comprehension questions by saying “yes” or “no.” Moreover, for the naming task specifically, they were instructed to name the picture according to the label they had learnt and for the judgment task, to press one of four buttons indicating the degree to which the presented picture was expected given the sentence they had just read (from left to right: not at all, not so much, somewhat, totally). After that, they were brought to the shielded room. Participants rested their left hand on the button box and used the little, ring, middle, and index fingers to press the buttons. Using the left hand is expected to predominantly activate right hemisphere regions, whereas naming will predominantly engage the left hemisphere.

Stimuli were presented through an overhead projector on a screen placed 90 cm in front of the participants. The stimuli subtended 2° to 2.5° of the participants’ visual angle. The tasks were practiced with three trials per task (naming and judgment) and another three trials were used in case participants did not follow the instructions. The experiment proper followed. The words (Arial font, size 20) and line drawings were presented in white on a black background. Figure 1 shows an example of a trial in each sentential constraint condition. A trial began with a fixation cross presented for 500 ms, followed by the first word of the sentence. Each word of the sentence was presented for 300 ms, interleaved with a black screen for 300 ms, except for the last word of the sentence for which the black screen was presented for 800 ms prior to picture presentation. The picture was then presented for 2 sec, followed by *** for 2 sec, which was the blinking interval. The 168 experimental trials of each task were divided into four blocks with self-paced breaks in between and participants always performed two blocks of each task before alternating to the other task (task-order was counterbalanced across participants). The whole session, including participant preparation, lasted approximately 2 h.

MEG and EMG Procedure

The MEG system (CTF VSM MedTech) contained 274 axial gradiometers. Pairs of Ag/AgCl-electrodes were used to record the electrocardiogram, the horizontal and vertical electrooculogram, and the surface electromyogram from the orbicularis oris muscle (impedance below 15 k Ω). Three localization coils were fixed to the nasion, left, and right ear canal to monitor the position of participants’

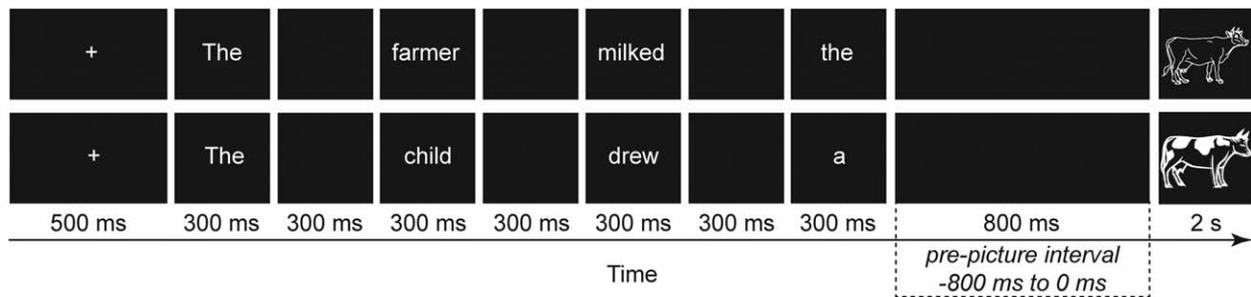


Figure 1.

An example of a trial with constraining (upper) and nonconstraining (lower) sentence contexts. The width of the black boxes is proportional to the duration of the events in the trial, except for picture presentation. The *** presented for 2 sec after picture presentation are not shown.

heads relative to the gradiometers. Head localization was performed in real-time [Stolk et al., 2013] and head position was readjusted when it deviated for more than 9 mm from the initial position. The data were low-pass filtered by an anti-aliasing filter (300 Hz cutoff), digitized at 1200 Hz, and stored for offline analysis. A microphone in the magnetically shielded room was connected to a computer, which recorded the responses and the speech signal and controlled stimulus presentation with the software package Presentation (Neurobehavioral Systems). Anatomical T1-weighted magnetic resonance images (MRI) of the participants' brains were acquired with a 1.5 T Siemens Magnetom Sonata system using a magnetization-prepared, rapid-acquisition gradient echo sequence.

Response Time Analysis

Vocal responses were evaluated in real time and responses containing disfluencies or errors were coded as invalid and their corresponding trials excluded from all response time (RT) and MEG analyses (constraining: 0.95%, nonconstraining: 2.4%). Naming latencies were calculated manually using the speech waveform editor Praat [Boersma and Weenink, 2009] before being separated by sentential constraint condition. For the manual responses, trials were discarded for which no manual response was recorded (0.75% of the trials). We used paired-samples *t*-tests to evaluate the sentential constraint effect for each task separately. Confidence intervals (95% CI) are reported in addition. Moreover, group RT distributions were examined by rank-ordering the RTs for each participant, dividing them into 20% quantiles, and then computing quantile means.

MEG and EMG Data Analysis

The analyses were performed using FieldTrip version 20130515 [Oostenveld et al., 2011] in MatlabR2011b. The data were down-sampled offline to 600 Hz and segmented into epochs from 1.5 sec pre-stimulus to 1.4 sec post-stimulus.

MEG preprocessing

All MEG epochs were inspected individually for artefacts (these were mainly SQUID - superconducting quantum interference device - jumps and ocular artefacts; on average, 5.4% of the trials were excluded). Excessively noisy channels were also removed. For analyzing the effect of interest, we focused on the time window during which response planning was likely to start for the constraining condition (pre-picture interval henceforth), defined between -800 ms (last black screen before picture onset) and 0 ms (picture onset), indicated in Figure 1. All trials containing artefacts within this time window were discarded. Artefact- and error-free data comprised on average 80 and 75 trials for the naming task and 80 and 81 for the judgment task, for the constraining and nonconstraining contexts, respectively.

Sensor-level analysis

To facilitate the interpretation of sensor-level topographies, synthetic planar gradients were calculated [Bastiaansen and Knösche, 2000]. With planar gradients, the amplitude of the signal is largest at sensors located above the sources. We estimated spectral power from the signal in the pre-picture interval using a multitaper approach, involving discrete prolate spheroidal sequences as tapers. Frequencies between 1 and 45 Hz were estimated with 2 Hz smoothing (two tapers). We report on results obtained with time-resolved spectral power estimates (i.e., spectral power as a function of time) in the Supplement only. For several reasons, the time-averaged spectral power estimates are to be preferred over the time-resolved estimates. Firstly, temporal smearing is an inherent property of time-resolved power estimation. Therefore, signal components elicited by the picture will also affect power estimates for time intervals that are centered around the pre-picture interval. As a result, it is difficult to derive conclusions that depend on the temporal specificity of the measured oscillatory activity. Moreover, as we analyzed the activity prior to picture onset,

there is substantial uncertainty regarding when exactly different stages of response planning would have started. As such, the inclusion of the temporal dimension would contribute little to the interpretation of our findings. Finally, we opted for multitaper-based spectral power estimates because these allow for a precise control of the spectral smoothing. We note that we conducted additional analyses on time-resolved spectral power estimates and these yielded highly similar results as we report here. Power spectra were averaged over trials per participant, separately for each task and sentential constraint condition. Relative power change was calculated as the difference between the power in the two sentential constraint conditions divided by their average. The differences in spectral power between conditions (i.e., the simple effect of sentential constraint within each task) were evaluated using a non-parametric cluster-based permutation approach [Maris and Oostenveld, 2007]. Note that, under this approach, the P -value pertains to the global null hypothesis of no differences between the two conditions. A P -value below the alpha level of 0.05 means that we can reject the null hypothesis of no global differences between the conditions in favor of the alternative hypothesis that the conditions differ from each other. However, this probability is non-specific with respect to the spatial-spectral patterns in the data, that is, we cannot assign a probability to the spatial or spectral extent of the condition difference [see Maris, 2012, for a discussion as to why it is not possible to make spatially specific statistical inferences with electrophysiological data]. All parameters were the default settings of the Fieldtrip toolbox (version 20130515), unless otherwise stated. The largest cluster in size of adjacent sensors and frequencies exhibiting a similar difference across conditions was identified by means of dependent-samples t -tests thresholded at an alpha level of 0.05 for each task separately. Spatial clustering was performed on the basis of a neighborhood structure in which sensors had on average 6 neighbors. Using a Monte Carlo method with 1,000 random permutations, P -values of the observed clusters were calculated as the proportion of random partitions (out of 1000) that yielded a larger effect than the observed effect. Only the sensors that were available for all participants were entered in the analyses (262 in total).

Source-level analysis

To construct the forward model, for each participant, the anatomical MRI was segmented using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/>). From the segmented MRI, a corrected-sphere model of the inside of the skull was constructed [Nolte, 2003], which served as the volume conduction model. Next, the participant-specific MRI was first warped to a template MRI (Montreal Neurological Institute [MNI], Montreal, QC, Canada) and then the inverse of that warp was applied to the dipole grid (a 3D grid with 1 cm resolution). In this way, for every participant, a grid in MNI coordinates is obtained, allowing us to directly compare grid points across participants in MNI space

without the need to co-register participant-specific source reconstructions. The volume conduction model was then used to compute the lead field matrix for each grid point in the source model [Nolte, 2003]. For each participant, source-level power was estimated in the pre-picture interval using the dynamic imaging of coherent sources method [Gross et al., 2001], which is an appropriate method for localizing oscillatory activity [Liljeström et al., 2005]. For each task, combining the data of the two sentential constraint conditions, the sensor-level cross-spectral density matrix was computed between 15 and 25 Hz (i.e., spectral smoothing of 10 Hz). This frequency window was selected on the basis of the sensor-level results (see the Results section). The cross-spectral density matrices were then used in combination with the leadfields to compute the common spatial filters at each location of the three-dimensional grid. The common spatial filters were then applied to the Fourier transformed data from each sentential constraint condition separately, and this resulted in source-level spectral power estimate for each grid point. Per participant, these source-level spectral power estimates were then averaged over all trials in each of the two sentential constraint conditions. Relative power change was calculated as the difference between the power in the two conditions divided by their average. The differences in spectral power between conditions (i.e., the simple effect of sentential constraint within each task) were evaluated using a nonparametric cluster-based permutation test, as explained above, resulting in a cluster of adjacent cortical locations exhibiting a similar difference across conditions (all parameters set to default).

Interaction analysis

To investigate whether there is a difference between the two tasks with respect to the sources that are associated with the sentential constraint effect, we tested for an interaction between task and sentential constraint. For the sensor-level analysis, we compared the constraint-dependent relative power changes between the two tasks using a cluster-based permutation test (as explained above for the simple effects). For the source-level analysis, we calculated common spatial filters for the four experimental conditions being compared in this interaction effect. More specifically, the common spatial filters were calculated from a cross-spectral density matrix obtained by averaging the four condition-specific cross-spectral density matrices. To test the interaction effect, we first calculated the constraint-dependent relative power changes for the two tasks and then compared these values between the two tasks using a cluster-based permutation test (as explained above for the simple effects). This interaction effect analysis at the source level evaluates the exact same null hypothesis as the one at the sensor level, that is, that the two simple effects within each task do not differ from each other. If this null hypothesis is rejected, the

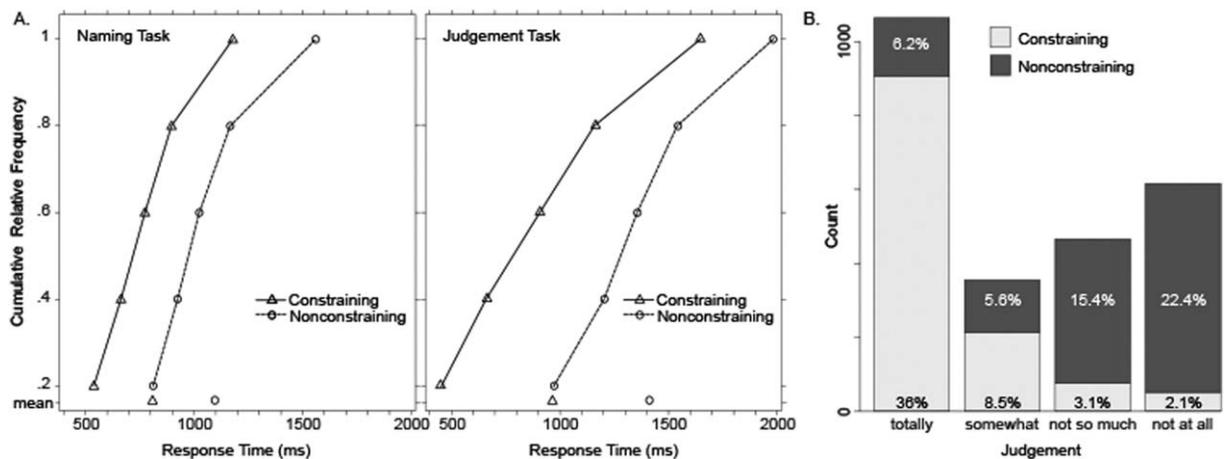


Figure 2.

(A) Group mean response times (bottom) and cumulative response-time distribution as a function of sentential constraint for the naming (left) and judgment (right) tasks. (B) Judgment responses as a function of sentential constraint in total number and as a percentage.

alternative hypothesis is favored that the sentential constraint effect differs between the two tasks.

EMG preprocessing and analysis

To ensure that the brain activity of interest during the pre-picture interval is not the result of participants' muscle activity while preparing to articulate the picture name, the EMG was analyzed. For one participant, EMG recordings failed so this analysis comprised 14 participants. The same trials that entered in the MEG analyses were selected for the EMG analysis, comprising the whole segment, i.e., -1.5 pre- to 1.4 s post-picture onset. Prior to segmentation, the EMG data were high-pass filtered at 15Hz (Butterworth filter, FieldTrip default settings), as this bandwidth is optimal for recording surface EMG of the orbicularis oris muscle [van Boxtel, 2001]. The EMG was then Hilbert-transformed and rectified. After segmentation, the EMG was averaged over trials per participant for each task and condition separately. To quantify the difference in EMG amplitude between the two sentential constraint conditions during the pre-picture interval (-800 ms to picture onset), we averaged the signal within that interval for each condition separately and compared the averaged amplitude with a dependent-samples *t*-test. No differences in EMG amplitude were observed between the two conditions for the naming task, $t(13) = 1.7$, $P = 0.117$, nor for the judgment task, $t(13) < 1$, $P = 0.5$.

RESULTS

Sentential Constraint Modulates Response Latencies

Figure 2A shows the mean RTs and their cumulative distribution as a function of sentential constraint for the

naming (left) and judgment (right) tasks. Naming responses were on average 286 ms faster with constraining than with nonconstraining contexts, $t(14) = 16.2$, $P < 0.001$, 95% CI [249, 324] and judgment responses were on average 445 ms faster with constraining than with nonconstraining contexts, $t(14) = 10.7$, $P < 0.001$, 95% CI [356, 534]. The cumulative RT distributions show that, for both tasks, the effect is the result of a shift of the entire curve as a function of sentential constraint. This means that the difference in response times were not due to a subset of trials in one of the two conditions being much longer or much shorter than in the majority of the trials. Instead, these results provide evidence that constraining sentence contexts enabled the (spoken word and manual) response planning stages to have a head start in general, for both fast and slow responses. Figure 2B presents the participants' judgments on the pictures as a function of sentential constraint. As expected, with constraining contexts, participants responded that they could predict the picture in a large portion of the trials, whereas with nonconstraining contexts, most of the pictures could not be predicted at all.

Spatially Distinct Pre-Picture Power Modulations as a Function of Task (naming versus judgment)

For the presentation of the MEG results, we focus on the two simple effects of sentential constraint within each task as well as on the interaction between sentential constraint and task.

Sensor-level analysis

Figure 3 shows the time-averaged power spectra as a function of sentential constraint for the naming (upper) and judgment (lower) tasks averaged over six groups of

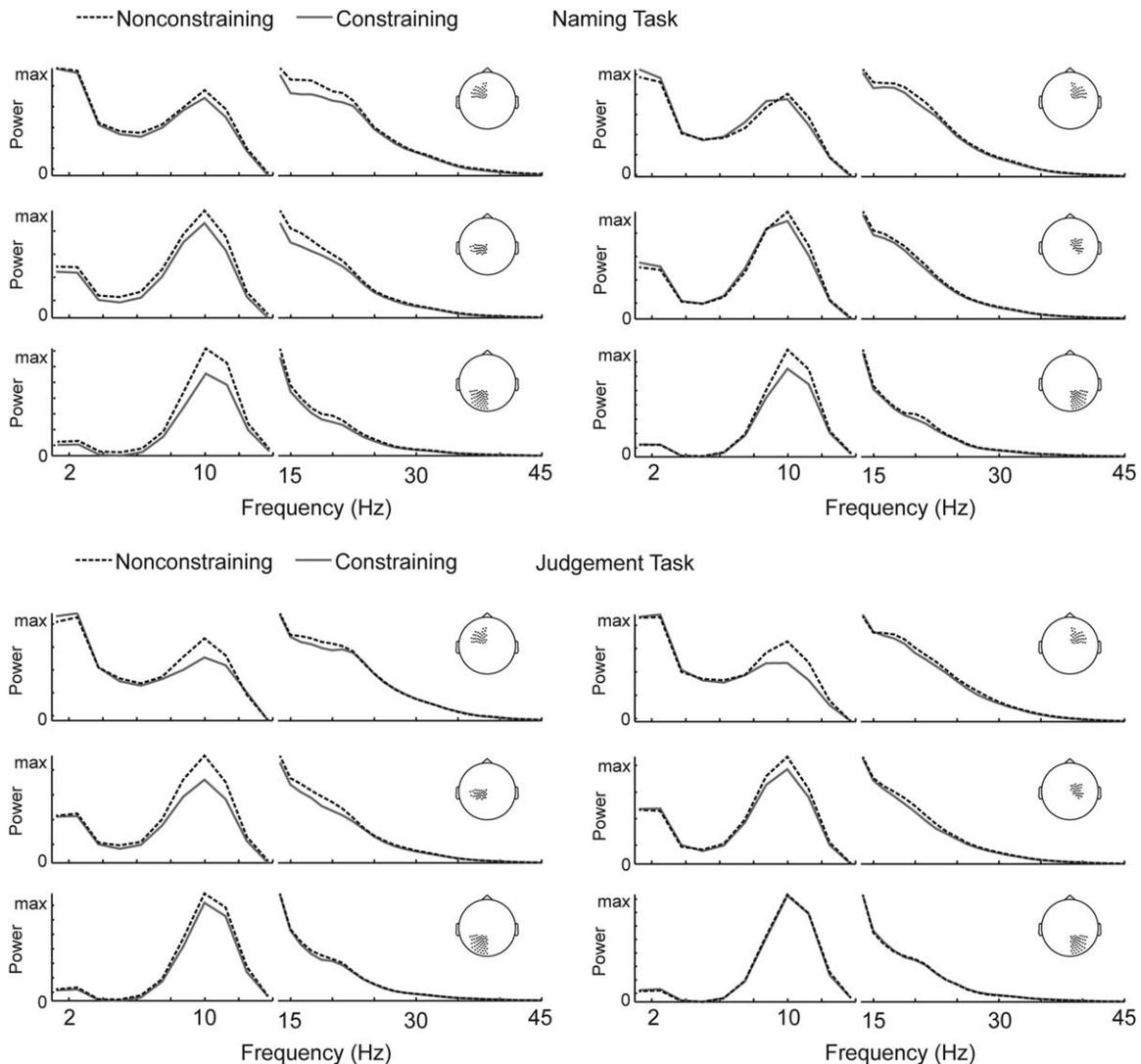


Figure 3.

Group-level power spectra as a function of sentential constraint for the naming (upper) and judgment (lower) tasks averaged over groups of sensors shown on the right of each spectrum. The y-axis is scaled from 0 to maximum power for each spectrum.

sensors, indicated on the right of each panel. Since the power of brain signals tends to decrease with increasing frequency (i.e., the $1/f$ phenomenon) and power differs substantially across sensor groups, the power axis was scaled to span from 0 to maximum. The discontinuity between the lower (2–14 Hz) and higher (15–45 Hz) frequencies in the figure is the result of this scaling procedure. It is evident from the figure that spectral power is largely concentrated in the alpha and beta bands (combined, 8–25 Hz) across all depicted sensor groups. Also the differences between the sentential constraint conditions are predominantly in these bands. Figure 4 shows the scalp distribution of the time-averaged relative power changes as a function of sentential constraint for the nam-

ing (top) and judgment (bottom) tasks for different frequency bands. In the naming task, relative power changes were strongest over (left) posterior sensors between 4–25 Hz and additionally over left anterior sensors between 15–25 Hz. In the judgment task, power modulations were strongest between 8–25 Hz over central sensors bilaterally. The reliability of these power changes was supported by the cluster-based permutation tests, which confirmed the power decreases for both the naming ($P = 0.004$) and the judgment ($P = 0.002$) tasks. The statistically significant effect in each task can be attributed to the spatio-spectral cluster of adjacent frequencies and sensors that exhibited a similar difference between the constraining and nonconstraining conditions (i.e., 4–25 Hz over the majority of the

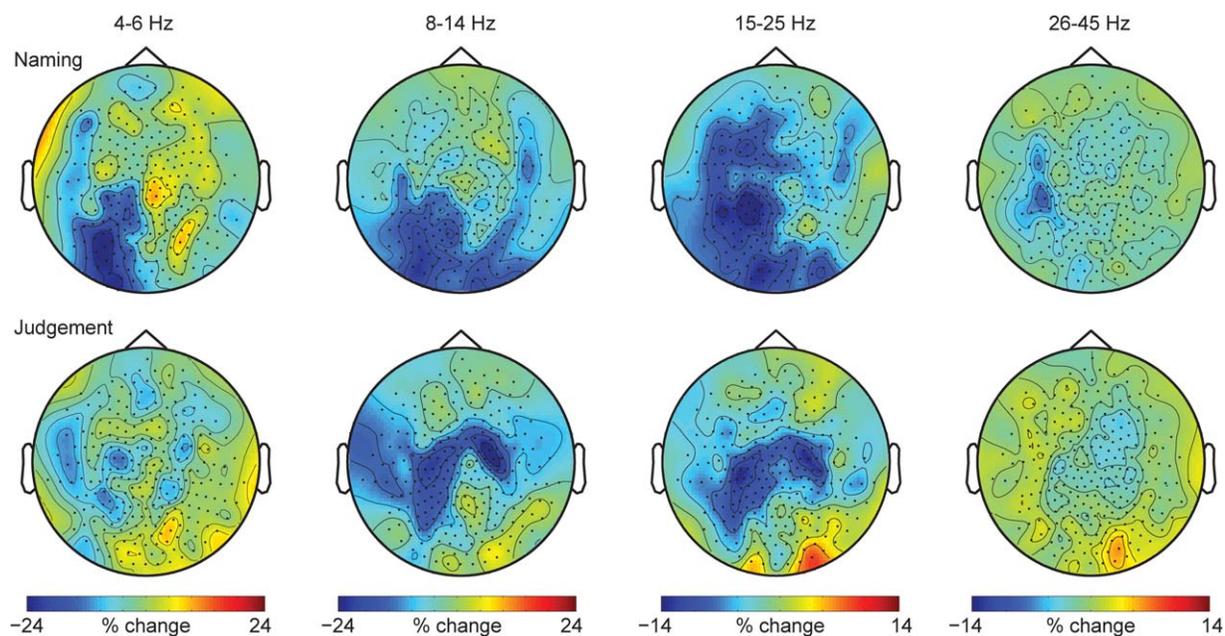


Figure 4.

Group-level scalp distribution of the power changes for the constraining relative to the nonconstraining condition for frequencies between 4 and 45 Hz.

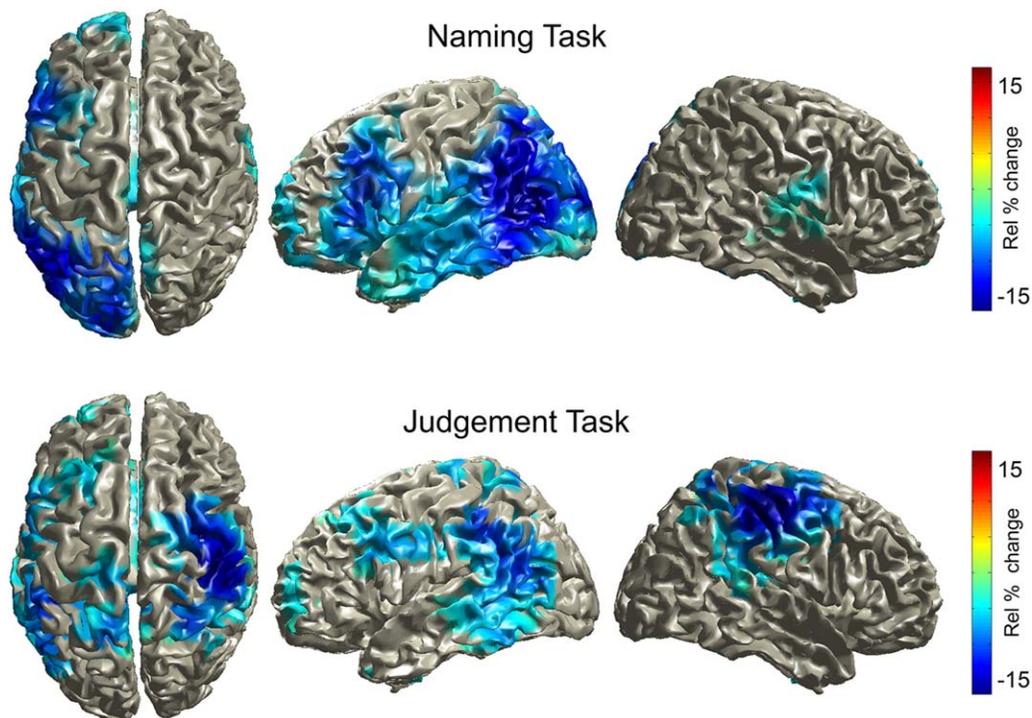


Figure 5.

Group-level source localization of the power differences between 15 and 25 Hz as a function of sentential constraint for the naming (upper) and judgement (lower) tasks. The color bars show relative power changes, masked by the statistically significant clusters. Rel = relative.

left sensors for the naming task, and 8–25 Hz over left posterior and bilateral central sensors for the judgment task, as shown in Fig. 4). Note that the effect of sentential constraint is also significant when evaluated for the time-resolved spectra ($ps < 0.004$, see Supporting Information for figures of the time-resolved spectra).

Source-level analysis

The effect with the broadest scalp distribution was observed around 20 Hz (in the beta band), indicating the engagement of a larger network of sources than the effect between 8–14 Hz (in the alpha band). Therefore, the source localization of the context effect was conducted in that frequency range. Figure 5 shows the results, masked by the statistically significant clusters, and with the color scale indicating the percentage of power changes. Power decreases were statistically significant for the naming ($P = 0.002$, top) and judgment ($P = 0.002$, bottom) tasks.

In the naming task, beta-power decreases were observed predominantly in the left hemisphere. The strongest power decreases were observed around the posterior temporal cortex and angular gyrus, and around the inferior frontal cortex. The power decreases in the temporal cortex further extended dorsally, ventrally, and anteriorly. In the right hemisphere, only the ventral premotor cortex showed very moderate beta-power decreases. In the judgment task, beta-power decreases were also observed in the left angular gyrus but, in contrast to the naming task, these extended only moderately into the left posterior temporal cortex. In the right hemisphere, strong beta-power decreases were observed around the post-central gyrus (around the hand area in the motor cortex). Given that in the judgment task, participants had to respond with their left hand, the decreases around the right post-central gyrus most likely reflect preparatory motor activity.

Interaction analysis

The interaction effect was significant at the source level ($P = 0.048$) but not at the sensor level ($P = 0.078$).¹ Because exactly the same null hypothesis was tested as at the source level, the larger P -value of the sensor-level analysis must be due to a lower sensitivity of this analysis. We therefore reject the null hypothesis that the effect of sentential constraint is identical in the two tasks. This statistically significant interaction can be attributed to the sources that show the largest between-task differences of the within-task sentential constraint effects (see Fig. 5).

¹When the clustering threshold was increased to .1, the interaction-effect clusters became larger such that they became significant in the cluster-based permutation test ($P = 0.02$). However, this is a post hoc and data-dependent choice of the threshold used for defining the clusters, and therefore the false alarm rate is not controlled using this procedure.

The source-level clusters associated with this interaction are shown in the Supporting Information.

The origin of the task-dependent spatial extent of the source-reconstructed beta-power decrease

In principle, the task-dependent spatial extent of the angular-gyrus centered beta-power decrease could be due to a different effect size in the two tasks. In fact, our source-reconstruction method is probably unable to reconstruct the source-level neural activity in a spatially unbiased way. Therefore, without additional evidence, we cannot rule out that source sites get a higher reconstructed neural activity merely as a result of an increased neural activity at neighboring sites. We investigated whether it is likely that this type of spatial leakage is responsible for the difference between the two tasks in the spatial extent of the beta-power decrease. The most relevant information for this question is whether the task-dependent spatial extent occurs with or without a task-dependent difference in the maximum effect size. We examined this both at the sensor- and the source-level. First, at the sensor-level, we selected sensors that showed the largest beta-power decrease in the judgment task, and tested whether the average beta power over these sensors was different from the one in the naming task. We did this for 10, 15, 20, and 25 sensors. We found that for none of these sets there was a significant difference in the beta-power decrease between the two tasks, all $ts(14) < 1$, all $ps > 0.740$. Next, at the source-level, we used the Automated Anatomical Labeling atlas [Tzourio-Mazoyer et al., 2002] to find the location in the left angular gyrus that showed the largest beta-power decrease in the judgment task. We then tested whether the average beta power decrease in this left angular gyrus source location was different from the one in the naming task, which was not the case, $t(14) < 1$, $P = 0.454$.

These null results with respect to the maximum beta-power decrease due to sentential constraint must be combined with the significant interaction between sentential constraint and task. Thus, this significant interaction must be due to a more broadly distributed beta-power decrease in the naming as compared to the judgment task, rather than to a different maximum effect size in the two tasks.

DISCUSSION

Evidence suggests that motor aspects of spoken word production are reflected in beta (and alpha) oscillations. However, at present, the neurophysiology of the memory aspects of word production has remained poorly investigated. In the present study, we examined the oscillatory dynamics of spoken word planning processes by comparing a picture naming with a picture judgment task. We manipulated sentential constraint to examine memory access during spoken word planning. Semantic cues provided by the sentential context are known to facilitate the

access to (lexical) information in long-term memory [Griffin and Bock, 1998], also affecting fluency in spontaneous language production [Levelt, 1989].

Our manipulation of sentential constraint clearly facilitated access to memory, as evidenced by the sizable difference in picture naming and judgment RTs as a function of sentential constraint throughout the RT distribution. This finding is consistent with the idea that conceptual and lexical information could be retrieved from long-term memory already pre-picture onset in the constraining condition, but not in the nonconstraining condition.

During the pre-picture interval, alpha-beta power decreases were observed in both tasks for constraining relative to nonconstraining contexts, with the beta band showing the maximal differences between the two tasks and the broadest involvement of the left hemisphere. Crucially, although the relative power decreases were of similar magnitude in the naming and judgment tasks, they were also spatially distinct, with different scalp distributions indicating different neuronal generators of the context effect. Whereas beta power decreases in the naming task were largely distributed over left anterior and posterior sensors, in the judgment task, alpha and beta power decreases were distributed over central sensors only. The source-level results, discussed below, supported the claim of spatial differences between tasks.

The contamination of the electrophysiological signal by muscle artefacts is a well-known problem for research employing overt speech production [e.g., Goncharova et al., 2003]. Although we report brain activity measured before picture onset, and therefore hundreds of milliseconds before speech onset, studies have shown that some EMG activity may be detected prior to speech onset [e.g., Riès et al., 2012]. However, for several reasons, we can rule out myogenic activity as a confound for our effects. First, we found no differences in EMG amplitude as a function of sentential constraint and task pre-picture onset. Second, the scalp distribution and frequency bands of our effects do not have the characteristics of myogenic activity in the MEG signal [e.g., Laaksonen et al., 2012; Muthukumaraswamy, 2013]. Third, the beamformer technique used for the source localization is suitable for attenuating myogenic artefacts since it suppresses signals whose spatial scalp distribution cannot be explained by a dipolar source in the brain. Most importantly, however, artefacts on the scalp from increased myogenic activity in the constraining condition should increase spectral power for the constraining relative to the nonconstraining condition. Yet, our results from 4–25 Hz show power decreases. In sum, the present effects cannot be the result of artefactual myogenic activity from the mouth.

The present results clearly replicate the scalp-EEG findings of Piai et al. [2014b] and Rommers et al. [2013c] showing alpha-beta power decreases in the pre-picture interval for the picture naming task. Moreover, by introducing an active control task (picture judgment), we could better determine that the alpha-beta desynchronization we

observed was spatially distinct between the tasks. This finding provides evidence against an explanation of the alpha-beta desynchronization in these tasks in terms of expectation and attention processes. Finally, by improving the spatial resolution with MEG, our results provide a further characterization of the oscillatory brain dynamics associated with the memory and motor components of spoken word planning.

Functional Significance of Neuroanatomical Effects

With respect to the functional neuroanatomy, it is important to note that existing functional claims have been largely constructed based on blood-oxygen-level dependent (BOLD) measures, so a comparison between our findings of alpha-beta power decreases and the existing functional neuroanatomy literature remains somewhat indirect. However, a few observations may help us link the two measures. For example, in a visual attention task, BOLD activity correlated negatively with alpha and beta power, that is, BOLD increases were associated with alpha-beta power decreases [Scheeringa et al., 2011]. A similar relation was observed in a motor task, for which alpha/beta-power decreases and increased BOLD during hand movement colocalized to the primary sensorimotor cortex [Yuan et al., 2010]. Analogously, in a memory task, successful memory encoding was associated with beta-power decreases and increased BOLD in LIFG [Hanslmayr et al., 2011]. Thus, for both a motor and a memory task, BOLD increases were associated with beta-power decreases in those cortical areas previously associated with motor and memory function, respectively. This observation invites us to draw a parallel between our findings of beta-power decreases and the existing functional neuroanatomy literature.

Common to both tasks during the pre-picture interval are processes related to language comprehension, such as conceptual processing and semantic integration, picture anticipation, and processes related to motor preparation (although different effectors are involved for speech vs. finger movement). We observed a beta-power decrease in the left angular gyrus for both tasks. The involvement of the left angular gyrus in both tasks is consistent with its putative role in the integration of semantic information [Binder et al., 2009]. However, the beta-power decrease in the naming task was more broadly distributed over the left temporal cortex, extending more anteriorly to temporal areas strongly associated with conceptualizing and lexical retrieval in word production [e.g., Baldo et al., 2013; Indefrey, 2011; Indefrey and Levelt, 2004; Lambon Ralph, 2014; Roelofs, 2014; Schwartz et al., 2009], as also confirmed by the interaction effect. By contrast, in the judgment task, the left posterior beta desynchronization was spatially more restricted, likely not encompassing the anterior portion of the temporal cortex. This task-dependent spatial

extent of the left posterior beta desynchronization is not a by-product of a possible task-dependent effect size (see the Results section The origin of the task-dependent spatial extent of the source-reconstructed beta-power decrease).

Accumulating evidence suggests that the anterior temporal lobe is involved in both language production and comprehension, and in the comprehension of nonverbal stimuli [e.g., Patterson et al., 2007]. Much evidence suggests that the anterior temporal lobe is implicated in the representation and retrieval of abstract or “transmodal” conceptual structures [see for a review Lambon Ralph, 2014]. The evidence comes from patients with semantic dementia, functional neuroimaging, and repetitive transcranial magnetic stimulation, among others. The presence of beta desynchronization in anterior temporal cortex in picture naming but not in picture judgment suggests stronger involvement of conceptualizing processes, including the retrieval of concepts from memory, in naming than in judgment.

Besides the beta-power decrease over the left temporal lobe, the two tasks also showed different beta-power modulations over other brain areas. In the naming task, we observed beta-power decreases in the inferior frontal cortex, possibly including the LIFG, an area implicated in phonological encoding/syllabification in word production (but see further discussion below). Furthermore, the source-level results also suggest a possible involvement of bilateral ventral premotor cortex, which has been associated with phonetic encoding [Indefrey and Levelt, 2004]. By contrast, for the judgment task, beta-power decreases were observed in the right motor cortex, most likely reflecting left finger-movement preparation. The finding of beta power decreases in bilateral premotor cortex (naming task) and right motor cortex (judgment task) suggests that a motor plan could be prepared generally to respond either vocally (naming task) or manually (judgment task, left hand) already during the pre-picture interval.

The interaction effect confirmed the more extended beta desynchronization for the naming task, but it did not show any pattern of desynchronization specific to the judgment task. This finding is unexpected, as the simple effect of sentential constraint in the judgment task suggests a beta desynchronization over right motor cortex. The right motor cortex beta desynchronization in the judgment task did show up as a separate cluster in the interaction effect analysis (see Supporting Information) but did not have a significant *P*-value. A likely explanation for this finding is that, in the interaction effect analysis, the right motor-cortex desynchronization is now a separate smaller cluster; given that the test statistic involves a sum over all voxels in a cluster, this smaller cluster is no longer significant.

Inferior Frontal Cortex Involvement

At this point, it may be asked how the observed modulations in the inferior frontal cortex relate to existing interpretations of LIFG function. In the literature, its functional interpretation depends on whether it is approached from

the domain of memory retrieval [e.g., Thompson-Schill et al., 1997; Wagner et al., 2001], action observation [e.g., Rizzolatti et al., 1996], language comprehension [e.g., Grodzinsky and Santi, 2008], including predictive comprehension [Lau et al., 2008], language production [e.g., Indefrey and Levelt, 2004], or language more broadly [e.g., Hagoort, 2005; Price, 2012; for a data-driven functional characterization, see Clos et al., 2013]. Our findings of inferior frontal cortex involvement in the naming task pre-picture onset as a function of context could be compatible with many of these views. For example, it could reflect (1) unification of retrieved lexical information into the sentence context [e.g., Hagoort, 2005], (2) predictive processing during comprehension [e.g., Lau et al., 2008], (3) controlled retrieval and selection of (competing) lexical information from long-term memory [memory component, e.g., Thompson-Schill et al., 1997], or (4) the clustering of a phonological code into syllabic units [motor component, e.g., Indefrey and Levelt, 2004]. However, the interpretation in terms of unification can be rejected based on the fact that the unification of retrieved information into the ongoing context, which is presumably easier in the constraining than in the nonconstraining condition, was required in both tasks. All else being equal, this account would predict power differences in inferior frontal cortex as a function of sentential constraint in both tasks. Although we acknowledge that the integration of retrieved information does play a role in our tasks, it cannot be the sole explanation for the involvement of the inferior frontal cortex in picture naming only. Similarly, with respect to the predictive processing interpretation, predictive processes should be involved in both picture naming and judgment, so under this interpretation, we should also have found inferior frontal cortex involvement in the judgment task. The other two functional interpretations (i.e., controlled retrieval/selection and syllabification) are both compatible with our results. However, at this point, we cannot conclude whether beta desynchronization in the inferior frontal cortex reflects only motor or memory aspects of word production, or both.

Beta-Band Oscillations in Spoken Word Production

Alpha- and beta-band dynamics have been well characterized in the motor and memory domains [see for reviews, respectively, Cheyne, 2013; Hanslmayr et al., 2012]. The extent to which beta (and alpha) oscillations provide a brain signature of memory and motor aspects of language production provides an important program for future research. The evidence so far supports this view with respect to the motor processes [e.g., Herman et al., 2013; Jensen et al., 2014; Saarinen et al., 2006; Salmelin and Sams, 2002]. The present findings of beta desynchronization in the inferior frontal cortex and bilateral ventral premotor cortex corroborate this evidence. Regarding the memory aspects, the present findings of beta desynchronization in left temporal cortex (extending posteriorly and

anteriorly) and left angular gyrus, together with the findings of Laaksonen et al. [2012], provide unprecedented evidence that not only motor aspects but also memory aspects of spoken word production are reflected in the dynamics of beta (and alpha) oscillations [for a review of beta oscillations in language comprehension, see Weiss and Mueller, 2012]. Based on these findings, one could speculate about the possibility of a common frequency band through which memory and motor aspects in word production are linked, in order to enable speakers to talk about what they retrieve from memory. Future research could consider beta-band oscillations as a candidate neural mechanism that enables communication through the language production network and as a testbed for further studying interactions between these two aspects of spoken word production.

CONCLUSION

Our results show that constraining sentential contexts produce faster responses in both picture naming and picture judgment tasks, indicating facilitated access to long-term memory. In addition, in both tasks, sentential constraint modulated alpha-beta power in the pre-picture interval. Crucially, however, this effect originated from different brain areas in the two tasks. In both tasks, beta desynchronization was found in brain areas related to conceptual/semantic processing. However, only in the picture naming task, beta desynchronization was observed in core language-production areas, such as left anterior temporal cortex and inferior frontal cortex. These results suggest that beta oscillations in spoken word planning reflect both memory and motor components of word production.

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REFERENCES

Baldo JV, Arévalo A, Patterson JP, Dronkers NF (2013): Grey and white matter correlates of picture naming: Evidence from a voxel-based lesion analysis of the Boston Naming Test. *Cortex* 49:658–667.

Bastiaansen MCM, Knösche TR (2000): Tangential derivative mapping of axial MEG applied to event-related desynchronization research. *Clin Neurophysiol* 111:1300–1305.

Binder JR, Desai RH, Graves WW, Conant LL (2009): Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb Cortex* 19:2767–2796.

Boersma P, Weenink D (2013): Praat: doing phonetics by computer (Version 5.3.42). Available at <http://www.praat.org>, accessed on 2 March 2013.

Cheyne DO (2013): MEG studies of sensorimotor rhythms: A review. *Exp Neurol* 245:27–39.

Clos M, Amunts K, Laird AR, Fox PT, Eickhoff SB (2013): Tackling the multifunctional nature of Broca's region meta-analytically: Co-activation-based parcellation of area 44. *Neuroimage* 83:174–188.

Cohen MX (2014): A neural microcircuit for cognitive conflict detection and signaling. *Trends Neurosci* 37:480–490.

Coltheart M, Rastle K, Perry C, Langdon R, Ziegler J (2001): DRC: A dual route cascaded model of visual word recognition and reading aloud. *Psychol Rev* 108:204–256.

Dell GS (1986): A spreading-activation theory of retrieval in sentence production. *Psychol Rev* 93:283–321.

Ganushchak LY, Christoffels IK, Schiller NO (2011): The use of electroencephalography in language production research: a review. *Front Psychol* 2:208.

Goncharova II, McFarland DJ, Vaughan TM, Wolpaw JR (2003): EMG contamination of EEG: Spectral and topographical characteristics. *Clin Neurophysiol* 114:1580–1593.

Griffin ZM, Bock KJ (1998): Constraint, word frequency, and the relationship between lexical processing levels in spoken word production. *J Mem Lang* 38:313–338.

Grodzinsky Y, Santi A (2008): The battle for Broca's region. *Trends Cogn Sci* 12:474–480.

Gross J, Kujala J, Hämäläinen MS, Timmermann L, Schnitzler A, Salmelin R (2001): Dynamic imaging of coherent sources: Studying neural interactions in the human brain. *Proc Natl Acad Sci USA* 98:694–699.

Hanslmayr S, Staudigl T, Fellner M-C (2012): Oscillatory power decreases and long-term memory: The information via desynchronization hypothesis. *Front Hum Neurosci* 6:74.

Hanslmayr S, Volberg G, Wimber M, Raabe M, Greenlee MW, Bäuml K-HT (2011): The relationship between brain oscillations and BOLD signal during memory formation: a combined EEG-fMRI study. *J Neurosci* 31:15674–15680.

Herman AB, Houde JF, Vinogradov S, Nagarajan SS (2013): Parsing the phonological loop: Activation timing in the dorsal speech stream determines accuracy in speech reproduction. *J Neurosci* 33:5439–5453.

Hickok G (2012): Computational neuroanatomy of speech production. *Nat Rev Neurosci* 13:135–145.

Hagoort P (2005): On Broca, brain, and binding: A new framework. *Trends Cogn Sci* 9:416–423.

Indefrey P (2011): The spatial and temporal signatures of word production components: A critical update. *Front Psychol* 2:255.

Indefrey P, Levelt WJM (2004): The spatial and temporal signatures of word production components. *Cognition* 92:101–144.

Jenson D, Bowers AL, Harkrider A, Thornton D, Cuellar M, Saltuklaroglu T (2014): Temporal dynamics of sensorimotor integration in speech perception and production: Independent component analysis of EEG data. *Front Psychol* 5:656.

Khader PH, Rösler F (2011): EEG power changes reflect distinct mechanisms during long-term memory retrieval. *Psychophysiology* 48:362–369.

Klimesch W, Doppelmayr M, Russegger H, Pachinger T, Schwaiger J (1998): Induced alpha band power changes in the human EEG and attention. *Neurosci Lett* 244:73–76.

Laaksonen H, Kujala J, Hultén A, Liljeström M, Salmelin R (2012): MEG evoked responses and rhythmic activity provide spatio-temporally complementary measures of neural activity in language production. *Neuroimage* 60:29–36.

Lambon Ralph MA (2014): Neurocognitive insights on conceptual knowledge and its breakdown. *Philos T Roy Soc B* 369: 20120392.

- Lau EF, Phillips C, Poeppel D (2008): A cortical network for semantics: (de)Constructing the N400. *Nat Rev Neurosci* 9:920–933.
- Levelt WJM (1989): *Speaking: From Intention to Articulation*. Cambridge: MIT Press. 566 p.
- Levelt WJM, Roelofs A, Meyer AS (1999): A theory of lexical access in speech production. *Behav Brain Sci* 22:1–38.
- Liljeström M, Kujala J, Jensen O, Salmelin R (2005): Neuromagnetic localization of rhythmic activity in the human brain: A comparison of three methods. *Neuroimage* 25:734–745.
- Maris E, Oostenveld R (2007): Nonparametric statistical testing of EEG- and MEG-data. *J Neurosci Meth* 164:177–190.
- Muthukumaraswamy SD (2013): High-frequency brain activity and muscle artifacts in MEG/EEG: A review and recommendations. *Front Hum Neurosci* 7:138.
- Nolte G (2003): The magnetic lead field theorem in the quasi-static approximation and its use for magnetoencephalography forward calculation in realistic volume conductors. *Phys Med Biol* 48:3637–3652.
- Nyhus E, Curran T (2010): Functional role of gamma and theta oscillations in episodic memory. *Neurosci Biobehav Rev* 34:1023–1035.
- Oostenveld R, Fries P, Maris E, Schoffelen J-M (2011): FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comp Intell Neurosci* 2011:1–9.
- Patterson K, Nestor PJ, Rogers TT (2007): Where do you know what you know? The representation of semantic knowledge in the human brain. *Nat Rev Neurosci* 8:976–987.
- 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: e88674.
- Piai V, Roelofs A, Maris E (2014b): Oscillatory brain responses in spoken word production reflect lexical frequency and sentential constraint. *Neuropsychologia* 53:146–156.
- Price CJ (2012): A review and synthesis of the first 20 years of PET and fMRI studies of heard speech, spoken language and reading. *Neuroimage* 62:816–847.
- Pfurtscheller G, Lopes da Silva FH (1999): Event-related EEG/MEG synchronization and desynchronization: Basic principles. *Clin Neurophysiol* 110:1842–1857.
- Riès S, Legou T, Burle B, Alario F-X, Malfait N (2012): Why does picture naming take longer than word reading? The contribution of articulatory processes. *Psychon B Rev* 19:955–961.
- Riès S, Janssen N, Burle B, Alario F-X (2013): Response-locked brain dynamics of word production. *PLoS ONE* 8:e58197.
- Rizzolatti G, Fadiga L, Matelli M, Bettinardi V, Paulesu E, Perani D, Fazio F (1996): Localization of grasp representations in humans by PET: 1, observation versus execution. *Exp Brain Res* 2:246–252.
- Roelofs A (2014): A dorsal-pathway account of aphasic language production: The WEAVER++/ARC model. *Cortex* 59:33–48.
- Rommers J, Dijkstra T, Bastiaansen MCM (2013a): Context-dependent semantic processing in the human brain: Evidence from idiom comprehension. *J Cogn Neurosci* 25:762–776.
- Rommers J, Meyer AS, Praamstra P, Huettig F (2013b): The contents of predictions in sentence comprehension: Activation of the shape of objects before they are referred to. *Neuropsychologia* 51:437–447.
- Rommers J, Meyer AS, Piai V, Huettig F (2013c): Constraining the involvement of language production in comprehension: A comparison of object naming and object viewing in sentence context. Paper presented at the AMLaP conference in Marseille, France.
- Saarinén T, Laaksonen H, Parviainen T, Salmelin R (2006): Motor cortex dynamics in visuomotor production of speech and non-speech mouth movements. *Cereb Cortex* 16:212–222.
- Salmelin R, Sams M (2002): Motor cortex involvement during verbal versus non-verbal lip and tongue movements. *Hum Brain Mapp* 16:81–91.
- Scheeringa R, Fries P, Petersson K-M, Oostenveld R, Grothe I, Norris DG, Hagoort P, Bastiaansen MC (2011): Neuronal dynamics underlying high- and low-frequency EEG oscillations contribute independently to the human BOLD signal. *Neuron* 69:572–583.
- Schwartz MF, Kimberg DY, Walker GM, Faseyitan O, Brecher A, Dell GS, Coslett HB (2009): Anterior temporal involvement in semantic word retrieval: Voxel-based lesion-symptom mapping evidence from aphasia. *Brain* 132:3411–3427.
- Stolk A, Todorovic A, Schoffelen J-M, Oostenveld R (2013): Online and offline tools for head movement compensation in MEG. *Neuroimage* 68:39–48.
- Szekely A, Jacobsen T, D’Amico S, Devescovi A, Andonova E, Herron D, Lu CC, Pechmann T, Pléh C, Wicha N, Federmeier K, Gerdjikova I, Gutierrez G, Hung D, Hsu J, Iyer G, Kohnert K, Mehotcheva T, Orozco-Figueroa A, Tzeng A, Tzeng O, Arévalo A, Vargha A, Butler AC, Buffington R, Bates E (2004): A new on-line resource for psycholinguistic studies. *J Mem Lang* 51:247–250.
- Thompson-Schill SL, D’Esposito M, Aguirre GK, Farah MJ (1997): Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proc Natl Acad Sci USA* 94:14792–14797.
- Tzourio-Mazoyer B, Landeau B, Papathanassiou D, Crivello F, Etard O, Delcroix N, Mazoyer B, Joliot M (2002): Automated anatomical labeling of activations in SPM using a macroscopic Anatomical Parcellation of the MNI MRI single-subject brain. *Neuroimage* 15:273–289.
- Van Casteren M, Davis MH (2006): Mix, a program for pseudorandomization. *Behav Res Methods* 38:584–589.
- van Boxtel A (2001): Optimal signal bandwidth for the recording of surface EMG activity of facial, jaw, oral, and neck muscles. *Psychophysiology* 38:22–34.
- van Ede F, de Lange F, Jensen O and Maris E (2011): Orienting attention to an upcoming tactile event involves a spatially and temporally specific modulation of sensorimotor alpha- and beta-band oscillations. *J Neurosci* 31:2016–2024.
- van de Meerendonk N, Indefrey P, Chwilla DJ, Kolk HHJ (2011): Monitoring in language perception: Electrophysiological and hemodynamic responses to spelling violations. *Neuroimage* 54: 2350–2363.
- Wagner AD, Paré-Blagoev EJ, Clark J, Poldrack RA (2001): Recovering meaning: left prefrontal cortex guides controlled semantic retrieval. *Neuron* 31:329–338.
- Walker GM, Schwartz MF, Kimberg DY, Faseyitan O, Brecher A, Dell GS, Coslett HB (2011): Support for anterior temporal involvement in semantic error production in aphasia: New evidence from VLSM. *Brain Lang* 117:110–122.
- Weiss S, Mueller HM (2012): “Too many betas do not spoil the broth”: The role of beta brain oscillations in language processing. *Front Psychol* 3:201.
- Yuan H, Liu T, Szarkowski R, Rios C, Ashe J, He B (2010): Negative covariation between task-related responses in alpha/beta-band activity and BOLD in human sensorimotor cortex: An EEG and fMRI study of motor imagery and movements. *Neuroimage* 49:2596–2606.