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 programme. Whereas the motor aspects of word production have been well characterised as reflected in alpha-beta desynchronisation, 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 towards the final word, presented as a picture. In the judgement 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 judgement were faster with constraining than nonconstraining contexts. Alpha-beta desynchronisation was found for constraining relative to nonconstraining contexts pre-picture presentation. For the judgement task, beta desynchronisation 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 desynchronisation 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.

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 programme.

The vast majority of the electrophysiological studies with a psycholinguistic approach examined event-related brain potentials (ERPs, see for review Ganushchak et al. 2011) whereas only a few studies investigated oscillatory activity (Laaksonen et al. 2012; Piai, Roelofs, Jensen, Schoffelen and Bonnefond 2014; Piai, Roelofs and Maris 2014; Rommers et al. 2014). 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 (LMTG) (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 localisation, but not for identifying the neurophysiological mechanisms underlying cognitive computations. This is where neuronal oscillations become relevant, since 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 characterised. 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 *de*synchronisation (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 *de*synchronisation 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, localised 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-lateralised 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, Roelofs and Maris 2014; Rommers et al. 2014). Our participants read sentences that were either constraining or nonconstraining towards 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 10-15% 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 desynchronisation. 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. Firstly, 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 localisation of the alpha-beta power decreases, making a functional interpretation of the desynchronisation difficult. As such, it remains unclear whether the alpha-beta desynchronisation 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 localise the brain sources of the alpha-beta desynchronisation. 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 judgement (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 judgement 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, Roelofs and Maris 2014; Rommers et al. 2014), 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 desynchronisation we previously observed is specific to the picture naming task, thus reflecting word production rather than attention and expectation processes. Moreover, if alpha-beta desynchronisation 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 judgement 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 analysed 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 familiarised 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, Roelofs and Maris (2014) and Rommers et al. (2014), seven constraining sentences from Rommers, Dijkstra and Bastiaansen (2013), 13 constraining sentences from Rommers, Meyer, Praamstra and Huettig (2013), and 22 constraining and 42 nonconstraining sentences from Van de Meerendonk, Indefrey, Chwilla and Kolk (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 .9 in the constraining sentences and of .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 judgement 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 judgement task was randomised over five main lists. The pairing of a specific picture with its corresponding sentence was also randomised 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-randomised with one unique final list per participant using Mix (van Casteren and Davis 2006). The randomisation 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.

Behavioural 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, see below), participants read the instructions and were familiarised with the pictures and their names using a booklet. They were instructed to keep fixation on the centre of the screen, to minimise (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 judgement task, to press one of four buttons indicating the degree to which the present 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 practised with three trials per task (naming and judgement) 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 hours.

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 kΩ). Three localisation coils were fixed to the nasion, left, and right ear canal to monitor the position of participants' heads relative to the gradiometers. Head localisation was performed in real-time (Stolk et al. 2013) and head position was re-adjusted 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), digitised 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: .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 (.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 s pre-stimulus to 1.4 s post-stimulus.

MEG preprocessing. All MEG epochs were inspected individually for artefacts (these were mainly SQUID jumps and ocular artefacts; on average, 5.4% of the trials were excluded). Excessively noisy channels were also removed. For analysing 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 judgement 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 (dpss) 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 centred 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, since we analysed 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 .05 means that we can reject the null hypothesis of no global differences between the conditions in favour 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 .05 for each task separately. Spatial clustering was performed on the basis of a neighbourhood structure in which sensors had on average 6 neighbours. 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 1,000) 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 localising 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 15-25 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 3-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 non-parametric 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 alternative hypothesis is favoured 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 analysed. 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, $t(13) = 1.7$, $p = .117$, nor for the judgement task, $t(13) < 1$, $p = .5$.

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 judgement (right) tasks. Naming responses were on average 286 ms faster with constraining than with nonconstraining contexts, $t(14) = 16.2$, $p < .001$, 95% CI [249, 324] and judgement responses were on average 445 ms faster with constraining than with nonconstraining contexts, $t(14) = 10.7$, $p < .001$, 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' judgements 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 judgement)

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 judgement (lower) tasks averaged over six groups of 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 naming (top) and judgement (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 judgement task, power modulations were strongest between 8-25 Hz over central sensors bilaterally. The reliability of these changes were supported by the cluster-based permutation tests, which confirmed the power decreases for both the naming ($p = .004$) and the judgement ($p = .002$) 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 left sensors for the naming task, and 8-25 Hz over left posterior and bilateral central sensors for the judgement task, as shown in Figure 4). Note that the effect of sentential constraint is also significant when evaluated for the time-resolved spectra (ps < .004, see Supplementary Materials 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 localisation of the context effect was conducted in that frequency range. Figure 5 shows the results, masked by the statistically significant clusters, and with the colour scale indicating the percentage of power changes. Power decreases were statistically significant for the naming ($p = .002$, top) and judgement ($p = .002$, 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 judgement 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 judgement 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=.048) but not at the sensor level ($p = .078$)[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). The source-level clusters associated with this interaction are shown in the Supplementary Materials.

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 centred 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 neighbouring 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 judgement 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 > .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 judgement 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, $t(14) < 1$, $p = .454$.

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 judgement 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 judgement 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 judgement 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 judgement 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 judgement 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. Firstly, we found no differences in EMG amplitude as a function of sentential constraint and task. Secondly, 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). Thirdly, the beamformer technique used for the source localisation 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 *de*creases. In sum, the present effects cannot be the result of artefactual myogenic activity from the mouth.

The present results nicely replicate the scalp-EEG findings of Piai, Roelofs and Maris (2014) and Rommers et al. (2014) showing alpha-beta power decreases in the pre-picture interval for the picture naming task. Moreover, by introducing an active control task (picture judgement), we could better determine that the alpha-beta desynchronisation we observed was spatially distinct between the tasks. This finding provides evidence against an explanation of the alpha-beta desynchronisation in these tasks in terms of expectation and attention processes. Finally, by improving the spatial resolution with MEG, our results provide a further characterisation 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 co-localised 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 conceptualising 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 judgement task, the left posterior beta desynchronisation was spatially more restricted, likely not encompassing the anterior portion of the temporal cortex. This task-dependent spatial extent of the left posterior beta desynchronisation 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 desynchronisation

in anterior temporal cortex in picture naming but not in picture judgement suggests stronger involvement of conceptualising processes, including the retrieval of concepts from memory, in naming than in judgement.

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 judgement 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 (judgement task) suggests that a motor plan could be prepared generally to respond either vocally (naming task) or manually (judgement task, left hand) already during the pre-picture interval.

The interaction effect confirmed the more extended beta desynchronisation for the naming task, but it did not show any pattern of desynchronisation specific to the judgement task. This finding is unexpected, as the simple effect of sentential constraint in the judgement task suggests a beta desynchronisation over right motor cortex. The right motor cortex beta desynchronisation in the judgement task did show up as a separate cluster in the interaction effect analysis (see Supplementary Materials) 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 desynchronisation 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 characterisation, 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 & 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 judgement, so under this interpretation, we should also have found inferior frontal cortex involvement in the judgement 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 desynchronisation 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 characterised 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 programme for future research. The evidence so far supports this view with respect to the motor processes (e.g., Herman et al. 2013; Jenson et al. 2014; Saarinen et al. 2006; Salmelin and Sams 2002). The present findings of beta desynchronisation in the inferior frontal cortex and bilateral ventral premotor cortex corroborate this evidence. Regarding the memory aspects, the present findings of beta desynchronisation 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 judgement 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 desynchronisation was found in brain areas related to conceptual/semantic processing. However, only in the picture naming task, beta desynchronisation 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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Footnote

[1] When this threshold was increased to .1, the interaction-effect clusters became larger such that

they became significant in the cluster-based permutation test ($p = .02$). 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.

Figure captions

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 seconds after picture presentation are not shown.

Figure 2. (A) Group mean response times (bottom) and cumulative response-time distribution as a function of sentential constraint for the naming (left) and judgement (right) tasks. (B) Judgement responses as a function of sentential constraint in total number and as a percentage.

Figure 3. Group-level power spectra as a function of sentential constraint for the naming (upper) and judgement (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.

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 localisation of the power differences between 15-25 Hz as a function of sentential constraint for the naming (upper) and judgement (lower) tasks. The colour bars show relative power changes, masked by the statistically significant clusters.

| + | The | | farmer | | milked | | the | | |

| + | The | | child | | drew | | a | | |

500 ms 300 ms 300 ms 300 ms 300 ms 300 ms 300 ms 300 ms 800 ms 2 s

Time

pre-picture interval
-800 ms to 0 ms

Naming Task

Judgement Task