RESEARCH ARTICLE

Effortful verb retrieval from semantic memory drives beta suppression in mesial frontal regions involved in action initiation

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Abstract

The contribution of the motor cortex to the semantic retrieval of verbs remains a subject of debate in neuroscience. Here, we examined whether additional engagement of the cortical motor system was required when access to verbs semantics was hindered during a verb generation task. We asked participants to produce verbs related to presented noun cues that were either strongly associated with a single verb to prompt fast and effortless verb retrieval, or were weakly associated with multiple verbs and more difficult to respond to. Using power suppression of magnetoencephalography beta oscillations (15–30 Hz) as an index of cortical activation, we performed a whole-brain analysis in order to identify the cortical regions sensitive to the difficulty of verb semantic retrieval. Highly reliable suppression of beta oscillations occurred 250 ms after the noun cue presentation and was sustained until the onset of verbal response. This was localized to multiple cortical regions, mainly in the temporal and frontal lobes of the left hemisphere. Crucially, the only cortical regions where beta suppression was sensitive to the task difficulty, were the higher order motor areas on the medial and lateral surfaces of the frontal lobe. Stronger activation of the premotor cortex and supplementary motor area accompanied the effortful verb retrieval and preceded the preparation of verbal responses for more than 500 ms, thus, overlapping with the time window of verb retrieval from semantic memory. Our results suggest that reactivation of verb-related motor plans in higher order motor circuitry promotes the semantic retrieval of target verbs.

KEYWORDS

beta oscillations, embodied cognition, magnetoencephalography (MEG), motor system, supplementary motor area (SMA), verb generation

1 | INTRODUCTION

A major claim of the embodied approach to language is that semantic/conceptual processing critically depends on the same neural

systems that are directly involved in the perception or execution of the relevant experience (e.g., Binder, Desai, Graves, & Conant, 2009; Kemmerer, 2015; Pulvermüller & Fadiga, 2010). Thus, the concept of embodiment directly links access to word semantics to reactivation of

sensory and/or motor representations implied by the word meaning. This hypothesis has inspired a multitude of neuroimaging studies examining the relationship between activation of the cortical motor system and the conceptual processing of action-related language.

Verbs that denote movements of specific body parts were considered crucial for experimental testing of the embodied semantics theory. The somatotopic organization of the motor cortex allows precise predictions regarding the activation of specific regions of the primary motor cortex in response to verbs implying movement of the respective body parts (Fischer & Zwaan, 2008; Pulvermüller, 2005). In a study measuring action verb-related brain activation with functional magnetic resonance imaging (fMRI), Hauk, Johnsrude, and Pulvermüller (2004) observed that passive reading of face, hand, and leg-related action verbs (e.g., "lick," "pick," or "kick") activated the left primary motor cortex in a roughly somatotopic manner. However, the somatotopic pattern of this verb-induced motor activation has not been replicated in subsequent fMRI studies (Tomasino, Werner, Weiss, & Fink, 2007; Willems, Toni, Hagoort, & Casasanto, 2010; Zhang, Sun, & Wang, 2018). Transcranial magnetic stimulation (TMS) research has also provided inconsistent results. While some authors found facilitated processing of body part-related verbs after single-pulse TMS stimulation of body part-specific regions of the primary motor cortex (Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005), others failed to replicate these findings (Papeo, Vallesi, Isaja, & Rumiat, 2009; Tomasino, Fink, Sparing, Dafotakis, & Weiss, 2008) unless the task required additional motor imagery (Tomasino et al., 2008) or TMS pulses were delivered at late, post-semantic stages of word processing (Papeo et al., 2009).

The available evidence is not sufficient to prove that body part-related verbs somatotopically activate the corresponding regions of the "motor homunculus" in the primary motor cortex. However, this does not rule out the motor embodiment concept for verb semantic retrieval. Meteyard, Cuadrado, Bahrami, and Vigliocco (2012) argued that integration of features within and between modalities produces more holistic representations than those neurally located in primary cortical areas. Accordingly, if sensory and motor information have a representational role in language, semantic retrieval might partially depend on neural circuits of sensory and motor systems, but not in the primary areas. Indeed, mounting evidence from neuroimaging studies indicates that action language processing recruits mainly higher order areas of the motor cortex that represent motor programs in a more abstract way than the primary motor cortex. For instance, in a study conducted by Postle, McMahon, Ashton, Meredith, and de Zubicaray (2008), the only cortical region sensitive to action verbs (leg, arm, and mouth-related verbs taken together) compared with non-action lexical stimuli was the supplementary and pre-supplementary motor areas (SMA and pre-SMA, respectively) related to action initiation (Nachev, Kennard, & Husain, 2008). In the same vein, Moseley and Pulvermüller (2014) reported that the left premotor cortex was equally activated by concrete action verbs, abstract verbs, and abstract nouns, but not by concrete object-related nouns. These results fit well with embodied models, claiming that abstract verbs, similarly to concrete ones, are linked to motor experience, either via

typical instances of their abstract meaning or associations with concrete, already embodied words (Barsalou & Wiemer-Hastings, 2005; Cangelosi, Greco, & Harnad, 2002; Meteyard et al., 2012).

However, even if verb processing is accompanied by activation of the cortical motor system, this does not prove that motor representations play a causal role in semantic processing (Caramazza, Anzellotti, Strnad, & Lingnau, 2014; Chatterjee, 2010; Mahon & Caramazza, 2008). The observed motor activation may be epiphenomenal and reflect processes occurring after word meaning has been successfully retrieved, such as mental imagery or post-retrieval enrichment of semantic representations. This is particularly easy to argue with respect to fMRI studies, which have poor temporal resolution and may capture semantic and post-semantic processes alike. In this regard, findings from electroencephalographic (EEG) and magnetoencephalographic (MEG) studies which have millisecond temporal resolution, may uncover whether verb-elicited motor activation occurs at the processing stage overlapping with the timing of semantic retrieval.

The neural oscillations in the beta frequency band (15–30 Hz) of EEG/MEG provide a suitable measure to track the temporal dynamics of motor system activation during verb processing. Beta oscillations are generated in cortico-basal ganglia-thalamo-cortical loops, and are inherently tied to motor functioning (Engel & Fries, 2010; Gilbertson et al., 2005). They are prominent during postural maintenance and are suppressed (or desynchronized) during preparation, initiation and execution of new motor sequences (Leocani, Toro, Manganotti, Zhuang, & Hallett, 1997; Pfurtscheller, Graimann, Huggins, Levine, & Schuh, 2003; Zhang, Chen, Bressler, & Ding, 2008). Although beta suppression (or beta event-related desynchronization [ERD]) is highly characteristic for activation of the motor system, it can also be observed in other cortical regions during tasks requiring the integration of complex, information-rich neural representations with a motor output (Leventhal et al., 2012).

Recent EEG/MEG studies of motor-language interaction in the brain employed beta ERD to characterize brain activation elicited by action verbs (Klepp, Niccolai, Buccino, Schnitzler, & Biermann-Ruben, 2015; Niccolai et al., 2014; Schaller, Weiss, & Müller, 2017; van Elk, van Schie, Zwaan, & Bekkering, 2010). Comparison of their results highlights the advantage of MEG over EEG in capturing verb-related beta oscillations (15–30 Hz) and their modulations that were previously reported for synchronous MEG and EEG recordings (Nikulin, Nikulina, Yamashita, Rossi, & Kähkönen, 2005). MEG studies (Klepp et al., 2015; Niccolai et al., 2014) demonstrated that action verb processing was accompanied by suppression of sensorimotor oscillations within beta frequency band (15–25 Hz), starting 250 ms after verb presentation. Whereas in EEG studies, the changes in sensorimotor oscillatory activity during action verb presentation were reported mainly for the mu/alpha frequency range (van Elk et al., 2010), with no reliable beta suppression in the EEG electrodes positioned over the motor cortex (Schaller et al., 2017). The MEG findings support the claim that motor activation is part of action verb semantic retrieval as it occurs within the time frame of lexico-semantic processes. Niccolai et al. (2014) attempted to relate MEG-recorded beta ERD elicited by verbs denoting body part movements to the selective activation of

the somatotopically organized motor cortex. However, the expected left hemispheric somatotopic activation was mainly observed for hand verbs compared with abstract verbs, and less so for foot verbs. Interestingly, in this study, all three categories of the presented verbs (hand, foot, or abstract) elicited strong beta suppression, over the left anterior cortical region, overlapping with hand area, although, for abstract verbs, the suppression was less prominent. These results corroborate previous fMRI findings on the recruitment of motor cortical areas in the processing of abstract words and suggest common neural ground for “embodiment” of action and abstract verbs in the motor system.

Still, the functional meaning of beta ERD during verb processing remains a debatable topic. The topology of observed beta suppressions can be influenced by anticipatory motor preparation, as the above MEG studies required responses given by using the right hand (Klepp et al., 2015) or by changing the gaze direction (Niccolai et al., 2014). As hand/eye motor output is unusual for speech processing, anticipatory preparation of the predefined motor responses may be advantageous to performance and elicit beta ERD in the lateral motor areas, even in trials that did not require overt motor actions. To ensure that beta suppression in the motor regions is elicited by verbs' semantic processing, one should eliminate any potentially confounding effect of the early motor preparation by switching to the most natural response—verbal word production. The available electrocorticographic studies indicate that the articulatory preparation starts not earlier than 300–250 ms before the overt speech production (e.g., Brumberg et al., 2016; Edwards et al., 2010). Furthermore, the above-mentioned MEG studies focused on the contrast between action-related verbs and abstract verbs, implicitly assuming that the motor system is much less involved in semantic processing of latter ones, an idea that has already been challenged in existing literature.

Another way to examine the role of the motor system in verb semantics is prompted by the “weak embodiment” approach. This suggests that additional association with higher order modal-specific representations is preferentially required for deep semantic processing of related language (see, e.g. Meteyard et al., 2012). The hindered access to a target word may pre-activate a limited subset of words representations, though not be sufficient for successful retrieval. The model predicts that each linguistic network is associated with a given modality-specific representation, and the top-down enhancement of additional associations may bias the competition between interfering word representations through tuning-up the linguistic neural representations via backward connections. Thus, the motor system could be strongly recruited under conditions that make semantic access to the verb difficult. If this is true, then the depth of verb processing should modulate the power of beta oscillations within motor regions.

Interestingly, a number of MEG studies have investigated beta suppression using experimental paradigms, which allows explicit manipulation of the difficulty gaining semantic access to a target verb, for example, a verb generation (VG) task (Martin & Cheng, 2006; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). VG is a semantic association task in which participants are asked to produce related verbs in response to visually presented noun cues. The difficulty of

semantic retrieval varies with the number of verbs associated with a particular noun cue; nouns are either strongly associated with a single verb and, thus, are easy to respond to, or weakly associated with many appropriate verbs and require additional effort to retrieve a related verb from memory (see for a discussion Martin & Cheng, 2006; Snyder & Munakata, 2008). However, previous MEG studies using VG examined beta suppression, mainly in the context of expressive speech lateralization (Findlay et al., 2012; Fisher et al., 2008; Pang, Wang, Malone, Kadis, & Donner, 2011; Youssofzadeh, Williamson, & Kadis, 2017). During VG, the task-related beta suppression typically started 250–500 ms after noun presentation in widespread and mostly left-lateralized cortical networks (Findlay et al., 2012; Fisher et al., 2008; Pang et al., 2011; Youssofzadeh et al., 2017). The contribution of the observed beta suppression to the difficulty of verbs' semantic retrieval fell outside the scope of these studies.

The current study, in order to answer the questions pertaining to the role of the motor system in verb semantic processing, utilized a VG task and manipulated the difficulty of verb semantic retrieval by presenting the noun cues strongly associated with a single verb and weakly associated with multiple verbs. Participants were instructed to vocally produce an associated verb. We examined the temporal dynamics of motor-related beta oscillations in response to the increasing difficulty of verb semantic retrieval and localized cortical sources based on individual MRI images. Considering that the search for a target verb in semantic memory is a protracted process with an uncertain and variable onset, but uniform termination at response production, we concentrated on the time period preceding the response onset. This was in contrast with the majority of previous VG studies, which analyzed stimulus-related neural activity. Assuming an essential role in higher order motor circuitry for the conceptual representation of verbs, we expected that more effortful verb retrieval would elicit greater beta suppression in the motor areas of the frontal lobe. However, unlike previous MEG research of beta ERD in the context of action verb processing, we employed whole-brain analysis with rigorous statistics to determine all cortical regions in which beta ERD is sensitive to semantic load. We expected that if reactivation of verb-motor associations indeed promote semantic retrieval of a target verb, more demanding verb retrieval would be accompanied by stronger beta ERD, not only in classical language-related areas, but also in cortical motor regions.

2 | METHODS

2.1 | Participants

Thirty-five volunteers (age range 20–48 years, mean age 26 years, 16 females) took part in this study. Participants were native Russian speakers, who were right-handed, with normal or corrected-to-normal vision. All subjects had either complete or incomplete higher education and reported no neurological diseases or dyslexia. One participant was subsequently excluded from the analysis due to an extremely low number of correct responses and another due to an MEG acquisition error. The final sample comprised 33 subjects. Written and informed consent was obtained from all subjects. The study was conducted

according to the principles of the Declaration of Helsinki and was approved by the Ethics Committee of the Moscow State University of Psychology and Education.

2.2 | Materials

The stimuli list comprised 65 Russian nouns with a single strong verb associate and 60 nouns that were weakly associated with many verbs (see a list of nouns in Supplementary Appendix S1). The nouns were selected using an independent norming study (for details, see Butorina

same response, the noun was assigned to the Weak Association (WA) category (e.g., “bumaga—goryt, mnetsya, rvetsya/paper—burns, becomes crumpled, is torn”). The mean word length, word frequency, and number of lexical associations were matched between the SA and WA categories (Table 1). Word frequency was taken from Lyashevskaya and Sharov's (2009) frequency dictionary (Lyashevskaya & Sharov, 2009). A number of lexical associations were taken from Russian Associative Thesaurus (Karaulov, Cherkasova, Ufimtseva, Sorokin, & Tarasov, 2002).

TABLE 1 Means (and SD) for psycholinguistic parameters of the nouns in SA and WA conditions

	SA	WA
Length in letters	5.6 (± 1.6)	5.7 (± 1.45)
Word form frequency (occurrence per million)	50.6 (± 87.3)	49.1 (± 65.8)
Number of lexical associates ^a	72.9 (± 52.6)	85.6 (± 59)

Abbreviations: SA, strong association; WA, weak association.

^aIrrespective of associates' grammatical class.

et al., 2017). If the majority of the norming sample (from 58 to 90%) responded with the same verb to a presented noun, the noun was included into the Strong Association (SA) category (e.g., “solovey—poyet/nightingale—sings”). If less than 23% of participants agreed on the

2.3 | Design

The noun cues were presented in white font with a black background, on a screen placed 1.5 m in front of participants. The size of the stimuli did not exceed 5° of visual angle. Participants were required to overtly produce a verb associated with a presented noun by answering a question—“What this noun does?”. Each noun appeared on the screen for 3,500 ms and was preceded by a white fixation cross presented for 300–500 ms (Figure 1a).

Subjects performed the task continuously within 16 blocks; each block contained eight stimuli of the same category presented in random order. Blocks comprising SA and WA nouns were alternated with 16-s intervals. Block design was chosen for further comparison of MEG and fMRI data that will be published elsewhere. The experiment was implemented in the Presentation software (Neurobehavioral Systems, Inc., Albany, CA).

FIGURE 1 (a) Verb generation task design. Subjects were required to name a verb in response to a noun cue, which had either a single strong association (SA) verb or many weakly associated (WA) ones. Time point 0 is the onset of the vocal response. The other time points represent the group means of time intervals between noun cue presentation and verb production under WA and SA conditions. The blue rectangle represents the time window of interest used in the subsequent analysis. (b) Statistical Parametric Mapping space-frequency statistical maps show scalp topography and frequency range of magnetoencephalography power suppression ($p < .05$, family wise error corrected). A—anterior, P—posterior, L—left, and R—right parts of the sensor array. The dashed lines correspond to 15–30 Hz frequency range, which showed significant suppression against the baseline. (c) Reconstructed cortical sources of beta suppression (15–30 Hz) for SA and WA trials pooled together. The color bar represents the strength of beta suppression in arbitrary units. The colored areas indicate the cortical regions with significant differences from baseline ($p < .05$, Bonferroni corrected) [Color figure can be viewed at wileyonlinelibrary.com]

2.4 | Behavioral responses

During the course of the VG session, participants' vocal responses were tape recorded and checked offline for response errors. Trials with semantically unrelated or no responses, grammatical mistakes or incomprehensible verbalization were considered as erroneous and were excluded from subsequent analyses. In addition, trials in which a prestimulus interval overlapped with the vocal response to the previous stimulus were rejected.

The onset of participants' overt responses was registered by a three-axis accelerometer placed on the participant's throat (ADXL330 iMEMS Accelerometer, Analog Devices, Norwood, MA). Speech onsets were marked using an automated algorithm (Zakharova et al., 2012) that detected increases in the accelerometer signal (z axis) above baseline by three *SD* within a 3,500 ms poststimulus time window, they were then visually inspected for false positives. The resulting reaction times (RT) and error rates were subjected to a paired *t* test.

2.5 | MEG data acquisition

MEG data were acquired inside a magnetically shielded room (AK3b; VACUUMSCHMELZE GmbH, Hanau, Germany), using a dc-SQUID Neuromag Vector View system (Elekta Neuromag, Helsinki, Finland) with 204 planar gradiometers and 102 magnetometers. Data were sampled at 1,000 Hz and filtered with a band-passed 0.03–333 Hz filter. Participants' head shapes were measured using a 3SPACE ISOTRACK II System (FASTRAK Polhemus, Colchester, VA) by digitizing three anatomical landmark points (nasion, left, and right preauricular points) and additional randomly distributed points on the scalp. While recording, the position and orientation of the head were monitored by four head position indicator coils. The electrooculogram was registered with two pairs of electrodes located above and below the left eye, and at the outer canthi of both eyes for the recording of vertical and horizontal eye movements, respectively.

After MEG data acquisition, 28 participants underwent MRI scanning with a 1.5T Philips Intera system to obtain head geometry for later reconstruction of the cortical surface.

2.6 | MEG preprocessing

Raw data were subjected to the temporal signal space separation method (Taulu, Simola, & Kajola, 2005) embedded in MaxFilter program (Elekta Neuromag software); which aims to suppress magnetic interference coming from sources distant to the sensor array. Biological artifacts (cardiac fields, eye movements, and myogenic activity), were corrected using the SSP algorithm implemented in Brainstorm software (Tadel, Baillet, Mosher, Pantazis, & Leahy, 2011). To compensate for the within-block head movement (as measured by head position indicator coils), a movement compensation procedure was applied. For sensor-space analysis, data were converted to a standard head position ($x = 0$ mm; $y = 0$ mm; $z = 45$ mm) across all blocks.

Data were divided into epochs of 1,500 ms, 500 ms before the stimulus presentation, and 1,000 ms before vocal response onset.

Epochs were rejected if the peak-to-peak value over the epoch exceeded 3×10^{-10} T/m (gradiometers) and 12×10^{-10} T/m (magnetometers). The average number of VG trials finally taken for the analysis was 63 ± 2 in the SA condition and 53 ± 5 in the WA condition.

2.7 | MEG data analysis

Sensor-space data were analyzed using MATLAB toolboxes SPM12 (Statistical Parametric Mapping software, Wellcome Trust Centre for Neuroimaging, London, UK). For time-frequency analysis, we used a multitaper power spectrum estimation (Thomson, 2000), implemented in SPM12. We estimated the spectra in overlapping windows of 400 ms (shifted by 50 ms) with the frequency resolution set to 2.5 Hz for the frequency range 1–25 Hz, to $0.1 \times$ frequency for 25–50 Hz, and then to a constant 5 Hz resolution. These settings resulted in a single taper being used for 2.5–30 Hz, two tapers for 32.5–42.5 Hz, and three tapers for 45 Hz or above.

The epoched time-frequency images were averaged over trials using a robust averaging procedure (Holland & Welsch, 1977). To normalize power changes across different frequency bands, the averaged power was log transformed and baseline corrected using a period of 300–0 ms before noun cue onset as the baseline (LogR option in SPM). Planar channels were then combined by adding time-frequency data for pairs of channels corresponding to orthogonal sensors at the same location.

We chose the period –700 to –200 ms before vocal response as a time window of interest to study the response-related suppression. Considering the difference in the response times between SA and WA conditions (1.22 and 1.89 s, respectively), the chosen time window is well suited for a between-condition comparison of verb retrieval period. The lower boundary allows for omitting an early time interval devoted to noun cue processing (≈ 500 –600 ms after cue onset), even for the SA condition, while the upper boundary excludes an articulation preparatory period within approximately 200 ms before a vocal response onset (Bouchard, Mesgarani, Johnson, & Chang, 2013; Brumberg et al., 2016).

To define the frequency boundaries of beta suppression, we performed statistical analysis of the response-related spectra in each experimental condition (SA and WA) in order to detect significant differences from the baseline. To this end, we averaged the time-frequency data over the period from –700 to –200 ms before the vocal response. The three-dimensional files of space (32×32 pixels) and frequency (60) dimensions were converted to Neuroimaging Informatics Technology Initiative format and smoothed using a Gaussian smoothing kernel with full width at half maximum of $8 \text{ mm} \times 8 \text{ mm} \times 3 \text{ Hz}$ to ensure that the images conformed to the assumptions of random field theory (Kilner & Friston, 2010). The smoothed images were then subjected to a single-sample *t* test with a reference value of zero. A family wise error (FWE) correction with the cluster-level threshold of $p < .05$ was applied to control for multiple comparisons.

The adjacent frequency bins that showed significant spectral power suppression under both experimental conditions were collapsed into a single band of interest, for which power time courses

were computed for both experimental conditions. To ensure that the power suppression within the band of interest occurred throughout the entire verb retrieval period (and was not restricted to its later part which could overlap with motor preparation period), we subjected the scalp $\times$ time images under each condition to a single-sample t test (FWE corrected at the cluster-level threshold of $p < .05$).

The final step was to contrast the power suppression within the band of interest under SA and WA conditions in space and time dimensions. The scalp $\times$ time images were subjected to a paired t test and the resulting spatial-temporal clusters of significant differences were FWE corrected for multiple comparisons. For the sensors with maximal statistical between-condition differences, we reconstructed power time courses of the frequency band of interest for both experimental conditions. The amplitudes of maximal power changes against baseline were subjected to a Wilcoxon signed-rank test (with Bonferroni corrections for the number of the sensors).

2.8 | MEG source localization

Individual structural MRIs were used to construct single-layer boundary-element models of cortical gray matter with a watershed segmentation algorithm (FreeSurfer 4.3 software; Martinos Center for Biomedical Imaging, Charlestown, MA). Induced power in the source space was computed using a dynamic statistical parametric mapping localization method (Dale et al., 2000) and Morlet wavelets with 2 cycles per wavelet implemented in MNE Python open-source software (<http://www.nmr.mgh.harvard.edu/martinos>). This method provided time courses of the induced power changes within the selected frequency band at each cortical location for each participant in each experimental condition. The individual data were then morphed into a common cortical model to allow a group comparison.

In order to examine which cortical regions displayed the verb retrieval-related suppression in the selected frequency band, the data from two experimental conditions were collapsed and averaged within a -700 to -200 pre-response time window. Using a paired t test, they were then contrasted with the pre-stimulus baseline. Results of statistical test were adjusted by using Bonferroni correction for multiple comparisons.

In order to localize between-condition effects, the spatiotemporal data from SA and WA conditions were contrasted in the source space. Statistical analysis was restricted to time windows that demonstrated significant SA-WA differences at the sensor level. The statistical threshold was set to uncorrected $p < .05$ in combination with a cluster extent of 10 adjacent voxels, providing that the sensor-space results had been corrected for multiple comparisons.

3 | RESULTS

3.1 | Behavioral results

Consistent with previous VG studies (e.g., Snyder, Banich, & Munakata, 2011; Thompson-Schill et al., 1997), responses were faster and more accurate when the noun cues had a single dominant verb association

($M = 1.22 \pm 0.17$ s; $1.76 \pm 2.28\%$ errors) compared with when the cues were weakly associated with multiple verbs ($M = 1.89 \pm 0.23$ s, $11.76 \pm 5.51\%$ errors). Paired t test revealed a highly significant effect of association strength on reaction times ($t(32) = -18.02$; $p < .0001$) and error rate ($t(32) = -9.1$; $p < .0001$).

3.2 | MEG results

Frequency boundaries and spatial-temporal features of response-related beta suppression:

3.2.1 | Sensor-level analysis

As beta frequency range varies between VG studies (Findlay et al., 2012; Fisher et al., 2008; Youssofzadeh et al., 2017), at the first step, we explored the frequency boundaries for VG task-induced beta suppression under SA and WA conditions. To this end, the data in each experimental condition were averaged across a -700 to -200 ms time window before the onset of vocal response, and compared to the respective baselines using scalp-frequency SPM analysis. This time interval was characterized by a highly significant oscillatory power suppression, of which frequency boundaries largely overlapped between SA and WA conditions: 15–25 Hz for SA and 18–30 Hz for WA (both p 's $< .0001$, FWE corrected; see Figure 1b). The above frequency ranges generally complied with the definition of beta oscillations (e.g., Engel & Fries, 2010). The beta ERD was characterized by a widespread, predominantly left-lateralized scalp topography, which was also similar for SA and WA (see Figure 3a,b, left panels). For the subsequent analyses, we chose a beta frequency band of 15–30 Hz, which covered all frequencies that underwent significant power attenuation under either task condition.

Next, we examined the temporal dynamics of the beta ERD using space-time SPM analysis. These analyses revealed that beta oscillations, both under SA and WA conditions, were reliably suppressed at each consecutive 50 ms interval throughout the entire -700 to -200 -time window preceding vocal response (p 's $< .0001$, FWE corrected). The comparison of response-related and stimulus-related beta ERD time courses (Figure 2b) showed that the selected pre-response period captured the maximum gradually developing beta suppression. The reliable beta ERD started at 250 ms post-stimulus under both SA and WA conditions (single-sample t test for baseline-normalized beta power; both p 's $< .0001$, FWE corrected) and did not attenuate until the vocal response onset.

3.2.2 | Source-level analysis

Figure 1c represents the cortical regions exhibiting robust beta ERD under the VG task ($p < .05$, Bonferroni corrected), the SA and WA conditions were pooled together for this analysis. In accordance with previous findings (Findlay et al., 2012; Fisher et al., 2008; Pang et al., 2011; Youssofzadeh et al., 2017), the beta-band suppression was strongly lateralized to the left hemisphere, and comprised a widely distributed cortical network, including areas of the temporal lobes involved in language processing, as well as regions of the medial and lateral surface on the frontal lobe subserving initiation, planning, and execution of motor programs

FIGURE 2 Differences in beta suppression between strong (SA) and weak association (WA) trials. (a) Sensor-based Statistical Parametric Mapping space-time images show three statistical clusters demonstrating significantly stronger response-related beta suppression in WA compared to SA trials ($p < .05$, family wise error corrected). A—anterior, P—posterior, L—left, and R—right parts of the sensor array. (b) Time courses of baseline-normalized beta (β) power changes under SA and WA conditions calculated from the sensors nearest to the maxima of the two most significant clusters. The grand average time courses are aligned to the onset of the noun cue (left panel) and to the onset of the vocal response (right panel). The shaded areas denote the SE of the mean. Note. Stronger beta suppression corresponds to lower (more negative) values of beta power change. The light orange rectangle denotes the time period where beta suppression was significantly stronger under WA than under SA condition. (c) The individual peak values of beta suppression at the same sensors under SA and WA conditions. The thick black line represents the group medians (Wilcoxon matched pairs test, $p < .05$). (d) The reconstruction of cortical sources corresponding with the three sensor-space spatio-temporal clusters. The images were thresholded at $p < .05$ (uncorrected) [Color figure can be viewed at wileyonlinelibrary.com]

(see Table 2 for the MNI coordinates and anatomical labels). The beta ERD was also highly significant at the medial aspect of the temporal lobe and at the posterior cingulate/retrosplenial cortex, which are closely interconnected and thought to support memory retrieval (Vann, Aggleton, & Maguire, 2009). No spatial clusters on the lateral surface of the right hemisphere survived the correction for multiple comparisons.

3.3 | SA versus WA

3.3.1 | Sensor-level analysis

In order to analyze the effect of verb retrieval demands on beta-band oscillations, we contrasted the beta ERD in SA and WA conditions using space-time SPM analysis. As expected, the more difficult WA condition was accompanied by significantly greater beta suppression at approximately -700 to -550 ms before the response onset ($p < .05$, FWE corrected; see Figure 2a). The SA-WA difference in the beta ERD clustered around frontal midline sensors. Figure 3(a-c) (right panels) represents the time-frequency plots for each condition separately as well as for their contrast at the sensor 0622, which is the closest to the local maximum of the most significant cluster of SA-WA differences.

To track the temporal dynamics of this difference, we reconstructed time courses of the beta ERD for both stimulus and response onsets at the sensors representing the local maxima of the significant clusters. Under both SA and WA conditions, beta suppression was highly reliable starting from 250 ms after the stimulus onset, up to the vocal response (Figure 2b). As the latency of vocal responses were significantly longer for WA than SA noun cues (1.89 and 1.22 s, respectively, $p < .0001$), the duration of beta suppression was prolonged for the WA condition.

The between-condition differences built up with time, while noun cues produced comparable beta ERD under both conditions up to 500 ms poststimulus, the beta suppression in WA trials reached greater values (Figure 2b). The observed difference in beta-ERD strength between WA and SA conditions could be a mere artifact of a shift in response time that was an inevitable consequence of uneven SA-WA reaction times. In order to refute this explanation, we performed an additional between-condition analysis of beta ERD peak values at the maximal sensors (Figure 2c). Results of this analysis were significant (Wilcoxon signed-rank test; $p < .017$; a p value of .05 Bonferroni corrected for three maximal sensors), indicating that the greater beta ERD values in WA conditions could not be fully explained by the response time shift.

TABLE 2 Brain regions showing robust suppression of beta oscillations under VG task compared to the baseline ($p < .05$, Bonferroni corrected). MNI coordinates and BA are given for the most significant vertexes within the standard anatomical labels^a

Brain region	BA	MNI		
		x	y	z
On the lateral surface				
L central sulcus	4	−45	−14	30
L precentral sulcus	6	−20	−13	53
L inferior frontal sulcus	44	−36	8	24
L postcentral sulcus	40	−31	−39	41
L intraparietal sulcus	7	−27	−51	36
L superior temporal sulcus	21	−52	−38	−5
L inferior temporal sulcus	37	−46	−59	−7
L insula	13	−35	6	8
On the medial surface				
L superior frontal gyrus (SMA)	6	−7	−16	53
L paracentral lobule	5	−6	−30	50
L middle cingulate gyrus	24	−12	−18	45
L posterior cingulate gyrus dorsal	23	−4	−34	28
L posterior cingulate gyrus ventral (retrosplenial cortex)	30	−17	−43	1
L precuneus	31	−9	−56	44
L fusiform gyrus	37	−36	−45	−20
L parahippocampal gyrus	36	−23	−35	−10
R margin of the cingulate sulcus	31	7	−28	49
R middle/posterior cingulate gyrus	23	12	−25	36
R posterior cingulate gyrus dorsal	23	6	−34	32
R precuneus	31	7	−45	42

Abbreviations: BA, Brodmann areas; SA, strong association; SMA, supplementary motor area; VG, verb generation; WA, weak association.

^aBased on the FreeSurfer aparc parcellation.

3.3.2 | Source-level analysis

Based on the sensor-level results, we restricted the MNE source reconstruction to -700 to -550 ms prior to response onset. Figure 2d shows the cortical regions demonstrating statistically significant differences in beta suppression between SA and WA conditions ($p < .05$, uncorrected). The differential neural response involved cortical regions lying at the mesial aspects of frontal lobe bilaterally: anterior cingulate cortex, middle cingulate gyrus/sulcus with motor cingulate area, adjacent region of superior frontal gyrus comprising pre-SMA and SMA, and the entire precentral gyrus/sulcus on the lateral surface of the left hemisphere (see Table 3 for the MNI coordinates).

4 | DISCUSSION

The aim of the present study was to test the hypothesis that verb retrieval from semantic memory engages the motor circuitry related to initiation and programming of motor acts, and that this engagement

FIGURE 3 Response-locked analysis of spectral power in strong and weak association trials. (a) Topographical maps at the left represent grand averages of baseline-normalized spectral power within beta range (15–30 Hz) for both conditions (a,b) and their contrasts (c). A sensor showing maximal statistical difference between conditions is marked in white. Time-frequency plots from this sensor are shown at the right panels. For the contrast plot, non-significant time-frequency tiles are masked (also note the change in amplitude). Time point 0 marks response onset. (d) The grand average root mean square (RMS) from the orthogonal channels of the accelerometer placed on the throat for both conditions. Paired t test at each time point within -1 to $+0.25$ s time interval of RMS time courses showed no significant differences between conditions ($p < .05$, uncorrected) [Color figure can be viewed at wileyonlinelibrary.com]

plays a functional role in access to verb semantics. Therefore, we expected that more demanding memory search would recruit the motor system more heavily. We used suppression of MEG beta oscillations (15–30 Hz) to evaluate the degree of cortical activation related to motor system involvement in the VG task, while manipulating the difficulty of verb retrieval.

Our participants were presented with noun cues either strongly associated with a single verb (SA), that prompted the fast and effortless VG (mean RT = 1.22 s), or was weakly associated with multiple verbs (WA) that were more difficult to respond to (mean RT = 1.89 s).

TABLE 3 Brain regions showing significantly stronger beta suppression under WA compared to SA condition. MNI coordinates and BA are given for the most significant vertexes within the standard anatomical labels^a

Brain region	BA	MNI		
		x	y	z
On the medial surface				
L anterior cingulate gyrus	32	−8	25	26
L middle cingulate gyrus	24	−8	−11	38
L superior frontal gyrus (SMA)	6	−7	18	51
R anterior cingulate sulcus	32	7	44	25
R middle cingulate gyrus	24	9	−15	38
R superior frontal gyrus (SMA)	6	7	18	50
On the lateral surface				
L precentral gyrus	6	−35	3	29
L superior frontal gyrus	8	−17	40	38
R middle frontal gyrus	9	41	21	33

Abbreviations: BA, Brodmann areas; SA, strong association; SMA, supplementary motor area; VG, verb generation; WA, weak association.

^aBased on the FreeSurfer aparc parcellation.

We did not restrict the search for the differential activation to specific motor region of interest and performed a whole-brain analysis with rigorous statistics in anticipation that if our hypothesis was correct, we would find the effect to be present in the cortical motor regions.

Our findings demonstrate that beta suppression starts at around 250 ms after noun cue presentation and is sustained until the overt generation of the appropriate verb, regardless of response latency. Thus, the beta ERD spans the entire period dedicated to the search in semantic memory to obtain a target verb in the VG task. In spatial terms, the beta ERD during the search period was localized to a widely distributed left-hemispheric cortical network, comprising the higher order motor areas of the frontal lobe, as well as classical auditory speech areas of the temporal lobe and memory-related structures at the mesial temporal surface (Figure 1c, Table 2). Considering the involvement of the extensive language-related system, the beta ERD could reflect co-activation of structures involved in the recollection of target verbs. This assumption fits well with the view that suppression of beta oscillations reflects cortical activation beyond the motor domain, especially under the demands of encoding and retrieving memories (for review, see Hanslmayr, Staudigl, & Fellner, 2012).

Crucially, in accordance with our hypothesis, and despite the spread of beta suppression over the entire left hemisphere, the differential effect of verb retrieval demands was confined to a set of cortical areas tightly related with the initiating and planning of motor acts, with a noticeable exception of primary motor cortex implicated in action execution (Figure 2d). A significant effect of task difficulty on motor system activation was observed in the −700 to −550 ms pre-response time window, which substantially precedes the preparation of vocal response, and likely overlaps with the semantic search for the appropriate verb in the both conditions. Moreover, comparison of

accelerometer traces revealed no significant differences between the experimental conditions, suggesting that the observed modulations of beta power were not related to differences in downstream motor signals to the response muscles (Figure 3d).

Given that greater beta ERD characterized more difficult task, with a greater number of errors and prolonged response latency, we cannot rule out confounding domain-general factors related to difficulty/effort. For instance, greater attentional and/or memory resources allocated to the more difficult task could promote stronger brain activation (Dockstader, Cheyne, & Tannock, 2010; Pesonen, Hämäläinen, & Krause, 2007). However, had this been the case, the pattern of cortical activation indexing by beta suppression would have lacked motor specificity and would have comprised the entire large-scale network of the left hemisphere.

Another general factor, that putatively can account for greater beta ERD in the prefrontal areas during more difficult WA trials, is the functional interaction between associative retrieval and executive control in the VG task (Missier & Crescentini, 2011). As Missier and Crescentini proposed, in the case of weakly associated noun–verb pairs, the interference from task-irrelevant responses (e.g., from strongly semantically associated nouns instead of verbs) may require inhibitory processes, which are needed to suppress erroneous words after retrieval. Such inhibition of task-irrelevant word representations would appear to rely upon frontal cortex capacities, as evidenced by the impaired control of interference during a VG task in patients with focal frontal lesions (Thompson-Schill et al., 1998). However, findings from both frontal patients and healthy volunteers (Barch, Braver, Sabb, & Noll, 2000; Persson et al., 2004; Snyder et al., 2011; Thompson-Schill et al., 1997) indicate that the selection of task-relevant verbs in VG task is mainly linked to the left inferior frontal gyrus (mid/posterior ventrolateral prefrontal cortex), compared with other frontal regions. Thus, the executive control account is incompatible with the observed localization of differential activation in the mesial part of superior frontal gyrus, comprising SMA and pre-SMA as well as in the middle cingulate cortex, including cingulate motor area (Figure 2d).

Based on these considerations, the most plausible explanation of our findings is the one specifically implicating motor system with verb semantic retrieval. The effortful memory search for the appropriate verb requires greater allocation of processing resources in the higher order motor areas than the easy task, in which the suitable verb is deftly retrieved due to the automatic nature of the underlying associative memory processes. Thus, our data provided strong evidence to support the notion that the motor system contributes to the verb retrieval from semantic memory. However, the exact role of beta suppression in the mesial frontal motor areas and lateral premotor cortex in the access to verb meaning is still debatable.

One potential account is sensorimotor transformation, which links speech processing with speech production while a word is retaining in short-term memory in an active, readily available state (Cogan et al., 2014). Due to the process of the laborious decision-making occurring during the difficult VG task, the search for the semantically and grammatically correct verb may be accompanied by erroneous retrieval of

later rejected words (Missier & Crescentini, 2011), causing subvocal articulation which activates the cortical premotor areas. However, several convergent lines of evidence suggest that sensorimotor transformation cannot explain our data.

First, brain activity related to sensorimotor transformation was shown to occupy both lateral areas of the premotor cortex and the classical auditory language areas (Cogan et al., 2014; Piai, Roelofs, Rommers, & Maris, 2015), while the SA-WA difference in beta suppression data was restricted to higher-tier motor structures at the lateral and medial aspects of prefrontal cortex. Second, if caused by sensorimotor transformation, SA-WA differences would be solely linked to the duration of the beta ERD, whereas we observed not only prolonged but also greater beta ERD under WA condition (Figures 2b and 3a–c). Third, greater uncertainty in the anticipated vocal response has been shown to attenuate the beta suppression in the core language-production areas of the left hemisphere (Piai et al., 2015), whereas our experiment showed that the difficulty of verb retrieval modulates the beta ERD in the opposite direction (Figures 2b and 3c).

We suggest that the prefrontal beta suppression in the VG task could act to release task-relevant neural circuits that encode additional motor evidence needed for selecting the appropriate verb. Persistent activation of the motor system during verb retrieval may also be required for evidence accumulation as was found for phoneme discrimination (D'Ausilio et al., 2009). Specifically, the beta ERD in higher order motor areas of the frontal cortex may represent a partial reactivation of the motor circuitry involved in the initiation and planning of motor sequences implied by verb meaning. Such motor reactivation may be redundant for verbs strongly associated with their nouns. In this case, a noun-elicited activation propagates across the strong links of preformed purely linguistic associative network, and is sufficient for retrieving the intended verb almost synchronously with semantic processing of the presented noun (Butorina et al., 2017). When noun-verb association is weak, a failure of automatic verb retrieval triggers additional activation of shared motor representations that may play a supportive role in the selection of the weakly associated verbs from semantic memory. On the other hand, a competition between multiple simultaneously reactivated motor plans may also elicit greater sensorimotor beta suppression, as was previously shown for sensory-motor tasks (Grent-'t-Jong, Oostenveld, Jensen, Medendorp, & Praamstra, 2013). Our findings agree with both accounts, which are not mutually exclusive as they both imply that neural circuitry involved in action initiation and planning plays a role in verb retrieval from semantic memory.

In line with this, an fMRI whole-brain analysis performed by Postle et al. (2008), showed that pre-SMA and SMA were the only cortical areas that demonstrated a selectivity for action-related semantic representations, as their heightened activation clearly dissociated both action word reading and action observations from all the other categories of linguistic stimuli and visual scenes. It may, therefore, be relevant that in our study, the major verb-related differential activation in the beta band was coupled with mesial rather than lateral frontal cortical areas. It is also noteworthy that mesial frontal motor cortical areas are implicated in the initiation or changing of rules for selecting motor programs (Nachev et al., 2008), this generally complies with

their contribution to initiation and selection of the motor associations for sequentially retrieved verbs in VG task. Further insight into the specificity of the cortical architecture underlying verb semantics can be obtained from MEG studies, in which the participants are required to generate cue-related nouns or adjectives, conceivably revealing the unique contributions of the motor system into verb semantics.

One might argue that predominant involvement of higher-tier motor cortex in differential activation associated with more challenging VG task stems from our choice of beta band oscillations as a signal of interest. Indeed, the mechanisms underlying cortical oscillations in theta, alpha and beta ranges are highly sensitive to the specific task demands, and may differ substantially across cortical regions during linguistic and other cognitive processes (for a review, see Siegel, Donner, & Engel, 2012). For instance, frontotemporal theta oscillations are thought to be indicative of feedback loops between the neo-cortex and medial temporal lobe memory system (for reviews, see Bastiaansen & Hagoort, 2003; Kirk & Mackay, 2003), and are shown to be involved in VG task (Hermes et al., 2014). Alpha and low beta (up to 18 Hz) oscillations, on the other hand, seems to be more related to top-down attention-like mechanisms modulating cortical processing in a vast variety of cognitive tasks including those in language domain (Jensen, Gips, Bergmann, & Bonnefond, 2014; Klimesch, 2012). Accordingly, in linguistic tasks differential activation indexed by MEG alpha suppression and attributed to the task difficulty is usually observed in the core language cortical areas (Kielar, Meltzer, Moreno, Alain, & Bialystok, 2014; Wang et al., 2012; Wang, Hagoort, & Jensen, 2017). Therefore, although in our study, induced alpha power changes did not survive the correction for multiple comparisons (Figure 1b), we cannot exclude the possibility that focusing on alpha or theta responses would provide the different patterns of cortical activation than that we reported here.

5 | CONCLUSION

Our results show that the effortful extraction of the verbs from semantic memory accompanied by slower responses in VG task produces greater beta suppression confined to the higher order motor areas of mesial and lateral prefrontal cortex indicating contribution of motor system to an access to verbs' representations. Since the prefrontal motor areas are involved in maintaining abstract representations of actions during their initiating and planning, we argue that our finding provides strong evidence for the proposed role of linguistic-motor association in retrieval of verb semantics.

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CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

DATA AVAILABILITY

The data that support the findings of this study are available from the corresponding author upon a request.

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