On the Boundaries between Decision and Action: Effector-selective Lateralization of Beta-frequency Power Is Modulated by the Lexical Frequency of Printed Words

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Abstract

■ Current computational and neuroscientific models of decision-making posit a discrete, serial processing distinction between upstream decisional stages and downstream processes of motor-response implementation. We investigated this framework in the context of two-alternative forced-choice tasks on linguistic stimuli, words and pseudowords. In two experiments, we assessed the impact of lexical frequency and action semantics on two effector-selective EEG indexes of motor-response activation: the lateralized readiness potential and the lateralization of beta-frequency power. This allowed us to track potentially continuous streams of processing progressively mapping the evaluation of linguistic stimuli onto corresponding response channels. Whereas action semantics showed no influence on EEG indexes of motor-response activation, lexical frequency affected the lateralization of response-locked beta-frequency power. We argue that these observations point toward a continuity between linguistic processing of word input stimuli and implementation of corresponding choice in terms of motor behavior. This interpretation challenges the commonly held assumption of a discrete processing distinction between decisional and motor-response processes in the context of decisions based on symbolic stimuli. ■

INTRODUCTION

Our daily lives are full of decisions. Their primary component is thought to be a deliberative process, where relevant alternatives or available evidence are considered and weighted against one another. Most decisions only become effective, however, if and when they are translated into a motor act: changing, starting, or stopping a movement; speaking one's mind overtly; and so forth. This intuitive description points to a functional distinction between deliberation and action, in keeping with a widespread view in cognitive science, including neuroscience.

As a paradigmatic case, consider the standard two-alternative forced-choice tasks requiring mutually exclusive responses as a function of stimulus evaluation. The canonical view maintains a serial processing chain in which actions are implemented once the decisional stages have terminated. Prominent models (e.g., Ratcliff, Smiath, Brown, & McKoon, 2016) describe the decisional stage in terms of evidence accumulating continuously over time until reaching a threshold triggering the delivery of the corresponding behavior. Motor processes would merely reflect the stereotypical implementation of an action selected at an upstream decisional stage. Models of this class are extremely successful in capturing, in terms of psychologically meaningful parameters, the benchmark effects and fine-grained features of human behavior across a variety of experimental paradigms (including those pertaining to language processing: Ratcliff, Gomez, & McKoon, 2004).

The hypothesis of a thresholded boundary between decision and action has also received support from neuroscientific evidence (reviewed in Calderon, Gevers, & Verguts, 2018) and, in particular, from experiments showing that EEG components such as the P300 and the centroparietal positivity may reflect neural signatures of abstract decision formation and evidence accumulation (Twomey, Kelly, & O'Connell, 2016). These components display a gradual and evidence-dependent buildup until they reach a fixed amplitude just before response execution, irrespective of specific stimulus modality or motor requirements (Twomey et al., 2016; Twomey, Murphy, Kelly, & O'Connell, 2015; Kelly & O'Connell, 2013; O'Connell, Dockree, & Kelly, 2012). Notably, the rate at which these components rise accounts for RT variance and scales with the difficulty of the decision (Twomey et al., 2015). These characteristics are akin to those of an abstract decision variable accumulating evidence up to a threshold.

However, previous research also suggests that accumulation dynamics can be traced downstream in the processing chain, within effector-selective activity in the motor cortices. The lateralized readiness potential (LRP;

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Coles, 1989) is an ERP obtained by subtracting the EEG activity recorded from sites ipsilateral to the effector from those recorded on homologous contralateral sites. It thus captures the asymmetries in cortical activity related to the activation of specific response effectors. Since the early studies of this component, evidence suggested that the execution of an overt behavioral response is controlled by a processing stream where evidence stemming from stimulus processing is continuously represented in response channels (Spencer & Coles, 1999; Cohen, Servan-Schreiber, & McClelland, 1992; see also Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988). The same can be said about desynchronizations in the beta-frequency band (13–30 Hz), which have been systematically linked to motor programming and execution (Kilavik, Zaepffel, Brovelli, MacKay, & Riehle, 2013), with a stronger reduction of beta oscillatory power over sites contralateral to the effector involved in the response (e.g., Doyle, Yarrow, & Brown, 2005). In the context of sensory decisions, this effector-selective asymmetry of beta power builds over time, presumably on a par with continuously accumulating sensory evidence, blurring the separation between decision and motor stages (e.g., Pape & Siegel, 2016; de Lange, Rahnev, Donner, & Lau, 2013; Kubanek, Snyder, Brunton, Brody, & Schalk, 2013; Donner, Siegel, Fires, & Engel, 2009; but see Steinemann, O'Connell, & Kelly, 2018; Twomey et al., 2016). Furthermore, recent developments in computational modeling invite to overcome the strong distinction between cognitive-decisional stages and motor response implementation, either by allowing motor-response activation to occur before a final commitment to a decision is reached (Servant, White, Montagnini, & Burle, 2015) or by implementing decisional processes as a continuous flow of activation up to the level of the primary motor cortex (Calderon et al., 2018; see also Servant, White, Montagnini, & Burle, 2016).

The empirical research challenging the assumption of a clear separation between decision and motor stages mostly focused on sensorimotor tasks involving perceptual and sensory decisions. Decisions relying on linguistic stimuli, instead, provide the chance to assess the transition from decision onto action in the context of higher-order processing based on symbolic input. The lexical decision task, in particular, offers a perfect litmus test. It is a two-alternative forced-choice task coupled to specific effectors, in which participants have to respond on the basis of the lexical status (word vs. pseudoword) of visually presented letter strings, typically by pressing one of two buttons with their left versus right hand. Computational models of lexical decision rely on the dynamic accumulation of abstract evidence until an action-triggering threshold is reached (e.g., Dufau, Grainger, & Ziegler, 2012; Wagenmakers, Ratcliff, Gomez, & McKoon, 2008; Ratcliff et al., 2004; Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001), thus postulating, once again, a strong distinction between language-driven decisions and motor-response activation.

The current research investigated the discrete versus continuous transition from cognitive decisional stages onto motor response implementation within lexical decision tasks by assessing the impact of linguistic variables on specific EEG indexes of motor-response activation. Two lexical decision experiments were devised, one comparing high- versus low-frequency words and the other comparing hand-action verbs with mental-state verbs.

Word frequency, one of the major determinants of performance in lexical decision tasks (Yap & Balota, 2009), serves as pointer toward preexisting lexical representations and is generally assumed to influence decisional stages via the activation levels of orthographic lexical representations (e.g., Coltheart et al., 2001; but see Besner & Risko, 2016; Balota & Chumbley, 1984) and, in the framework of the diffusion model, via the rate of accumulation of lexical evidence (Ratcliff et al., 2004). The contrast between hand-action and mental-state verbs, instead, tackles the influence of conceptual processing on response implementation when the semantic representation of the stimuli involves the effector engaged in the response. Evidence suggests that action words, and verbs in particular, can activate the motor cortex in a somatotopic fashion, pointing toward a distributed and interactive representation of meaning across multiple neural assemblies (e.g., Pulvermüller, 2005). Consistently, neuroscientific models of semantic processing maintain that conceptual knowledge includes multimodal sensorimotor information that is integrated within supramodal hubs (Lambon-Ralph, Jefferies, Patterson, & Rogers, 2017; Patterson, Nestor, & Rogers, 2007) or convergence zones (Binder & Desai, 2011). Although the reflection of semantically driven sensorimotor processing on motor behavior remains controversial, evidence suggests that the processing of action semantics can be reflected within response channels, for example, in terms of an effector-specific interference produced by action verbs referring to the same effector involved in the behavioral response (e.g., Klepp, Niccolai, Buccino, Schnitzler, & Biermann-Ruben, 2015; Boulenger et al., 2006).

In this study, multiple neural indexes of motor-response activation were considered. In the time domain, we focused on the LRP and, in addition, we examined separately the underlying activities unfolding over electrodes contralateral and ipsilateral to the response hand. Previous evidence has shown that, before response onset, a negative potential surfaces over the motor cortex contralateral to the effector capturing the activation of the response hand, whereas a positive potential unfolds over the ipsilateral cortex indexing the inhibition of the incorrect response hand (e.g., Vidal, Burle, & Hasbroucq, 2018; Vidal et al., 2015; Burle, Vidal, Tandonnet, & Hasbroucq, 2004). In the time–frequency domain, we assessed the lateralization of activity in the beta band, that is, the difference in the attenuation of beta-frequency power between electrodes contralateral versus ipsilateral to the responding hand (e.g., Twomey et al., 2016; Poljac

& Yeung, 2014; Donner et al., 2009; de Jong, Gladwin, & t'Hart, 2006; Doyle et al., 2005). Although both the LRP and beta-band lateralization focus on effector-selective asymmetries in EEG activity, current literature provides evidence for dissociations across the two measures. Whereas the lateralization of beta power seems to reflect more abstract motor goals and intentions, such as the selection of the proper response hand, the LRP would index the translation of these goals into a more specific motor program (Poljac & Yeung, 2014; de Jong et al., 2006). By considering these different measures, we sought to provide a better functional characterization of any potential linguistic effect on motor-response activation, in an effort to highlight whether such effect would be linked to the instantiation of a specific unimanual motor program, as indexed by the LRPs and the underlying motor-related potentials, or the settling of higher-order motor goals, as indexed by the lateralization of beta power decrease.

Specifically, effector-selective lateralization of EEG activity may scale with the amount/quality of the available lexical evidence as indexed by word frequency, consistent with a continuous processing stream mapping lexical evidence accumulation onto effector-selective motor goals (beta lateralization) and/or effector-specific motor programs (LRP). In addition, the semantically driven motor activation triggered by the processing of action verbs may percolate and interfere with response processing, for example, by reducing lateralized activity because of the activation of task-irrelevant motor representations either at the levels of higher-order motor goals (beta lateralization) or via the activation of competing and incompatible motor programs (LRPs; Buccino et al., 2005). The motor-related ERPs underlying the LRP may further shed light on whether incompatible and/or erroneous motor programs triggered by reduced lexical evidence or action semantic representations are actively inhibited at the level of the motor programs for the effector not involved in the response. In turn, this should modulate the positive potential unfolding ipsilaterally to the response hand. Taken together, the two manipulations and the different EEG indexes should provide a description of the transition from lexical–semantic processing of input word stimuli onto the implementation of motor goals and motor programs for the corresponding behavioral response.

To increase the accuracy of our temporal descriptions, in the experiments, all EEG indexes were time-locked to the actual onset of the motor response, as indexed by the EMG signal recorded from the muscle responsible of the motor response.

METHODS

Two lexical decision experiments were devised and conducted with Italian materials and Italian native speakers. The first experiment used high-frequency (e.g., the Italian translations of *month* and *church*) and low-frequency (e.g., the Italian translations of *breeze* and *cork*) nouns as word stimuli, to probe the effect of lexical frequency on EEG indexes of motor response preparation. The second experiment used hand-action verbs (e.g., *to caress*, *to clap*) and mental-state verbs (e.g., *to think*, *to ignore*) in their Italian infinitive form (e.g., *accarezzare, applaudire, pensare, ignorare*) as stimuli to ascertain the presence of action-related semantic effects on motor-response preparation. In addition, each experiment included pseudowords that resembled the word stimuli. Further details are presented hereinafter.

Participants

Thirty right-handed, Italian native speakers were recruited (18 women, $M_{age} = 24.47$ years, $SD_{age} = 4.95$). All participants performed both experiments, and the order of administration was counterbalanced across them. All participants had normal or corrected-to-normal vision and reported no history of neurological problems or learning disabilities. Participation was compensated either with course credit or a €10 stipend. All the procedures received approval from the ethical committee of the University of Trento, and participants signed an informed consent document before the experiment. The data from two participants were discarded: in one case because of poor signal quality and in the other because of an excessive alpha-wave activity. Data and scripts for the analyses are stored at osf.io/mdw3e/ and can be accessed by submitting a request at the same Web page.

Stimuli

The psycholinguistic properties of the stimuli are listed in Table 1. For the lexical decision experiment focusing on word frequency manipulation, 50 high-frequency nouns and 50 low-frequency nouns were selected from SUBTLEX-IT database (Crepaldi, Keuleers, Mandera, & Brysbaert, 2013). The words from the two frequency categories were comparable on a series of other psycholinguistic variables, as detailed in Table 1. One hundred filler pseudowords were created. Pseudowords were all phonotactically legal in Italian and comparable with words with respect to the length in terms of number of letters (see Table 1).

For the experiment focusing on hand-action semantics, 54 hand-action and 54 mental-state verbs were selected. All the verbs were presented in their infinitive form. The two categories were comparable in terms of a series of psycholinguistic variables reported in Table 1. All verbs were pretested to ensure that they differed on them being (or not being) associated to hand actions. Twenty participants (not purposely all women, $M_{age} = 25.80$ years, $SD_{age} = 3.72$; none participated in the EEG experiment) took part in the pretest. They were asked to rate on a 7-points scale the extent to which each verb made

Table 1. Psycholinguistic Variables Controlled across Stimulus Categories of the Two Experiments

Variables	HF	LF	Action Verbs	Mental Verbs	Words	PWs
Frequency	8.62 (0.95)	4.93 (1.24)	5.14 (1.67)	5.78 (2.28)	–	–
N. of letters	6.88 (1.68)	6.90 (1.89)	8.59 (1.61)	8.29 (1.55)	7.70 (1.84)	7.75 (1.39)
Orth. N.	3.22 (4)	3.06 (4.61)	2.91 (5.18)	2.39 (4.82)	–	–
Concreteness	7.13 (1.30)	7.33 (0.98)	–	–	–	–
Imageability	7.57 (0.91)	7.46 (0.89)	–	–	–	–
Familiarity	7.27 (0.80)	6.47 (1.13)	–	–	–	–
Hand-action	–	–	6.08 (0.35)	1.45 (0.18)	–	–

For each variable, mean values are reported (*SD* within parentheses). Frequency values (log-transformed) and orthographic neighborhood size were taken from the SUBTLEX-IT database (Crepaldi et al., 2013). Concreteness, imageability, and familiarity scores for high- and low-frequency words (HF and LF, respectively) were taken from the Italian adaptation (Montefinese, Ambrosini, Fairfield, & Mammarella, 2014) of the Affective Norms for English Words database (Bradley & Lang, 1999). PW = pseudoword; N. of letters = number of letters; Orth. N. = orthographic neighborhood size.

them think about an action performed with the hands. Hand-action and mental-state verbs were significantly different for these scores. One hundred eight legal filler pseudowords were created for this experiment. Care was taken to create pseudowords with a (pseudo) inflected endings marking the Italian infinitive form (*-are, -ere, -ire*). The different inflections appeared equally often across words and pseudowords. Words and pseudowords were comparable in terms of number of letters.

Apparatus and Procedure

Participants were first asked to complete a questionnaire collecting demographic information. Then, after installation of the EEG cap, they performed the two lexical decision experiments in sequence, in a counterbalanced order across participants. As the two experiments used the same procedure and changed only with respect to the stimuli, they are described together in the remainder of this section.

The experimental procedures and the acquisition of behavioral data were controlled using the E-Prime 2 software (Version 2.0.10.356, Psychology Software Tools) running on a laptop computer. Participants sat in an armchair in front of the computer screen at a distance of about 40 cm, holding a joypad in their hands with their thumbs resting on the upper triggers. They were instructed to classify letter strings as words or pseudowords performing thumb button presses with the right or left hand on the joypad trigger. Each experiment was divided into two blocks. The mapping between stimulus type (word vs. pseudoword) and response hand (left vs. right) was reversed across the two blocks, to have an equal number of left- and right-hand responses for each category of stimuli within each participant. The order of the two stimulus–response hand mappings across blocks was counterbalanced. Before each block, there were eight practice trials to familiarize with the response mapping. Participants could take self-terminated breaks halfway

within each block. The whole experimental session (including both experiments) lasted about 40 min, excluding the time for installation of EEG cap and EMG electrodes.

Stimuli were presented in uppercase 14-point Courier New font, in white against a black background. Each trial began with a fixation cross (+) for 800 msec, followed by the target string that remained on-screen for 1500 msec or until a response was made. Immediately after, a screen displaying a blink stimulus [(−)] was shown for 2500 msec; participants were instructed, whenever possible, to blink only during this interval. Trials were separated by a blank screen lasting 300 msec.

EEG/EMG Recording and Processing

EEG data were acquired via an eego sports system (ANT Neuro), from 64 Ag–AgCl electrodes placed according to the International 10–10 system referenced online to CPz at a sampling rate of 1000 Hz (filters: DC to 260 Hz, third-order sinc filter). An additional electrode was placed below the left eye to serve as an EOG. Impedance at each electrode site was kept below 20 kΩ.

Two pairs of bipolar electrodes were placed ~2 cm apart on the thenar eminences of both hands to record the EMG activity of the flexor pollicis brevis.

EMG Processing and Onset Detection

EMG data were high-pass (10 Hz; Order 2 Butterworth filters) and notch (50 Hz) filtered. Stimulus-locked epochs (−600 to 1500 msec) were extracted. EMG onsets were detected using an automated algorithm. Specifically, the envelope of the EMG signal was obtained by computing the absolute values of the Hilbert transform (Schoffelen, Poort, Oostenveld, & Fries, 2011) and smoothing them using a centered moving-average procedure with a window of 50 msec. The resulting data were then transformed to z scores, on the basis of the average and standard

deviation of the activity of the whole epoch. The algorithm marked as the onset of the EMG activity the first of a series of at least 50 samples in which $z > 1$. The onsets detected were visually inspected on raw EMG data, and epochs in which the algorithm detection failed manifestly, epochs with partial errors (i.e., covert activation of the incorrect response hand before the final correct response), or false starts (multiple covert activations of the correct response hand before the final response) were all marked for rejection (5.06% of the trials).

EEG Preprocessing

EEG data were band-pass (0.1–70 Hz; Order 2 Butterworth filters) and notch (50 Hz) filtered. Epochs going from 800 msec before target onset until 1850 msec after target onset were extracted. Note that larger epochs were extracted, compared to the EMG analysis, to allow an appropriate time–frequency decomposition for the time windows of interest. Noisy channels were interpolated via spherical interpolation (3.3 channels on average per participant), and the resulting data were rereferenced to the average activity of all the electrodes (excluding EOG, M1, and M2). A first artifact rejection was conducted to discard the epochs contaminated by excessive noise (2.97% of the total, on average). Afterward, independent component analysis was performed (algorithm: AMICA; Palmer, Makeig, Kreutz-Delgado, & Rao, 2008), and the components corresponding to blinks were removed. A second artifact rejection was performed to remove the remaining noisy epochs. Furthermore, epochs with incorrect behavioral responses and those marked during EMG onset detection were discarded. On average, across the two experiments, 13.51% of the epochs were thus discarded, leaving an average of 45.54 epochs for each experimental condition (high frequency: $M = 48$, $SD = 4.33$; low frequency: $M = 47$, $SD = 4.89$; hand-action verbs: $M = 45$, $SD = 4.03$; mental-state verbs: $M = 43$, $SD = 3.52$). A prestimulus baseline (-200 to 0 msec before target onset) was then applied by subtraction. Finally, response-locked epochs (-1000 to 350 msec centered on EMG onset) were extracted.

All analyses were conducted on Laplacian-transformed data to increase the spatial resolution (Babiloni, Cincotti, Carducci, Rossini, & Babiloni, 2001; see also Cohen, 2015) and gain a better spatiotemporal differentiation for EEG indexes of motor response preparation both in the time (Vidal et al., 2015) and time–frequency (e.g., Twomey et al., 2016) domains. The surface Laplacian was computed with the spline interpolation method (Perrin, Pernier, Bertrand, & Echallier, 1989) as implemented by Cohen (2014; order of splines = 4, maximal degree of Legendre polynomial = 10, lambda parameter = 10^{-5}).

ERP Analyses

Response-locked lateralized ERPs related to motor-response preparation were isolated by separately averaging (within participants and conditions) EEG activity recorded within sites contralateral versus ipsilateral to the responding hand. Specifically, to isolate the contralateral negative potential and the ipsilateral positive one, activities recorded from electrodes over the left hemisphere for right-hand responses were averaged together with those from right electrodes for left-hand responses. Symmetrically, the activity recorded over left electrodes during left-hand responses was averaged with those recorded from right electrodes during right-hand responses (Burle, Van den Wildenberg, Spieser, & Ridderinkhof, 2016). The LRPs were calculated by subtracting ipsilateral activity from the contralateral one. After previous research, analyses in the time domain were limited to activities recorded from electrodes C3 and C4 (e.g., Burle et al., 2016; Vidal et al., 2015; Tandonnet, Burle, Vidal, & Hasbroucq, 2003, 2006; Gratton et al., 1988).

Time–Frequency Analyses

To compute the single-trial time–frequency representations, a 500-msec Hanning window was applied in frequency steps of 2 Hz (from 2 to 34 Hz) and at time steps of 10 msec. Epochs were zero-padded to the length of 4 sec to obtain integer frequency values. The single-trial time–frequency representations were averaged within participants and conditions.

Whereas the ERP analyses were focused a priori on signals recorded from C3 and C4 on the basis of prior literature, the spatial and frequency coordinates of effector-selective time–frequency modulations are not standardized. To corroborate indications from previous literature (e.g., Twomey et al., 2016) in the context of our experiment, the contrast between left- and right-hand responses (collapsed across conditions and across experiments) was exploited as a functional localizer to confirm the spatial, temporal, and frequency coordinates related to effector-selective oscillatory modulations in a manner that was independent from the comparisons between the experimental conditions at stake (i.e., word frequency and verbs' action semantics; see Cohen, 2014, for the usefulness of this general approach; for a similar application, see Twomey et al., 2016; Donner et al., 2009). Specifically, left- and right-hand responses (irrespective of experimental conditions) were compared using a cluster-based permutation test conducted on response-locked data considering all the channels, all the frequencies between 4 and 34 Hz (to fully encompass alpha and beta frequencies between 8 and 30 Hz with an additional 4-Hz margin to accommodate potential smearing in frequency estimation), and all the samples in a time window going from -700 to 100 msec centered on EMG onset (the cluster-based permutation test is detailed in the next section). The assessment of linguistic manipulations was restricted to the motor-related asymmetries of oscillatory

activities within such functionally identified time–frequency coordinates.

Specifically, akin to the analyses in the time domain, we separately averaged oscillatory power within sites ipsilateral versus contralateral to the responding hand (e.g., Twomey et al., 2016; Pape & Siegel, 2016). Lateralization of oscillatory power was computed, within each participant and each condition, by subtracting ipsilateral activity from the contralateral one and normalizing by their sum.

All the EEG/EMG signal processing procedures were conducted using MATLAB toolboxes EEGLAB (Delorme & Makeig, 2004), ERPLAB (Lopez-Calderon & Luck, 2014), and FieldTrip (Oostenveld, Fries, Maris, & Schoffelen, 2011) together with custom routines.

Statistical Analyses

Behavioral analyses on chronometric measures were conducted using linear mixed effects models and on response accuracy using generalized mixed models via the library lme4 (Bates, Mächler, Bolker, & Walker, 2015) in R (R Core Team, 2015). EMG-onset and RT analyses included only the correct responses on which the algorithm of onset detection succeeded (see the section EMG Processing and Onset Detection above). Accuracy analyses (correct vs. error) included all the responses, irrespective of their neurophysiological features. All the models included by-participant and by-item (i.e., for each word stimulus) random intercepts. The significance of the fixed effects was assessed using log-likelihood tests to compare the model featuring the fixed term under examination with the null model featuring solely the random effects structure.

Analyses of EEG signals were performed via cluster-based permutation tests. In the time domain, the amplitudes of the LRPs and of the lateralized potentials of motor-response preparation across conditions (high- vs. low-frequency words; hand-action vs. mental-state verbs) were compared by a series of paired t tests conducted at each sample from −200 msec before to 100 msec after EMG onset. The t values surpassing a predefined threshold ($p < .05$) were selected and aggregated into clusters as a function of their temporal adjacency. Cluster statistics were then computed by summing all the t values included within the identified clusters. Cluster p values are finally computed on the basis of a null distribution of t values obtained via permutations ($n = 1500$) where observations are shuffled across conditions. The cluster p value was represented by the proportion of permutations featuring a larger test statistics compared to the observed one (Groppe, Urbach, & Kutas, 2011; Maris & Oostenveld, 2007). The threshold for statistical significance was set as the two-tailed alpha level of .025.

In the time–frequency domain, the procedure was the same, except for the fact that the initial series of paired t tests included the spatial and frequency dimensions. The t values surpassing the threshold ($p < .05$) were thus

aggregated into clusters as a function of their adjacency in terms of frequency, time, and space. These analyses assessing the impact of linguistic manipulations on beta-band lateralization were restricted to the spatial, temporal, and frequency coordinates identified via the functional localizer analyses comparing left- and right-hand responses, that is, within the coordinates capturing effector-selective lateralization of beta power modulations.

RESULTS

Behavioral Data

For measures of EMG onset, the model including the fixed effect of word frequency (EMG Onset ~ Word Frequency + (1|Subject) + (1|Item)) significantly increased the goodness of fit, χ^2 (1) = 33.47, $p < .001$, compared to a null model including only random effects (EMG Onset ~ (1|Subject) + (1|Item)). We thus replicated the classic effect of word frequency, with faster response onsets for high- compared to low-frequency words ($b = -65.61$, $SE = 10.48$, $t = -6.26$). The fixed effect of action semantics (i.e., action semantics vs. mental-state verbs; EMG Onset ~ Action Semantics + (1|Subject) + (1|Item)), instead, failed to highlight any significant contribution, $\chi^2(1) = 0.47$, $p = .49$, over the null model (EMG Onset ~ (1|Subject) + (1|Item)). There was in fact no significant difference between hand-action and mental-state verbs ($b = 7.97$, $SE = 11.71$, $|t| < 1$). The aforementioned pattern of results was fully replicated when the analyses were conducted on the more standard RTs (i.e., the latency of the actual button press). Of note, EMG onset latencies were detected 81 msec on average ($SD = 47$) before the actual button press. Accuracy analyses revealed a significant contribution, $\chi^2(1) = 13.56$, $p < .001$, of the model including the factor Word frequency (Accuracy ~ Word Frequency + (1|Subject) + (1|Item), family = "binomial"), compared to the null model (Accuracy ~ (1|Subject) + (1|Item), family = "binomial"). Accuracy was indeed significantly lower for low- compared to high-frequency words ($b = -1.21$, $SE = 0.32$, $z = -3.74$). There was no significant contribution, $\chi^2(1) = 0.08$, $p = .78$, when the factor Action semantics was considered (Accuracy ~ Action Semantics + (1|Subject) + (1|Item), family = "binomial") in comparison with the corresponding null model (Accuracy ~ (1|Subject) + (1|Item), family = "binomial"). There were in fact no significant differences in accuracy between hand-action and mental-state verbs ($b = -0.07$, $SE = 0.26$, $|z| < 1$). These behavioral results are plotted in Figure 1.

EEG Data

EMG-locked LRPs

LRPs for the different conditions are reported in Figure 2 (first column). None of the comparisons (hand-action vs.
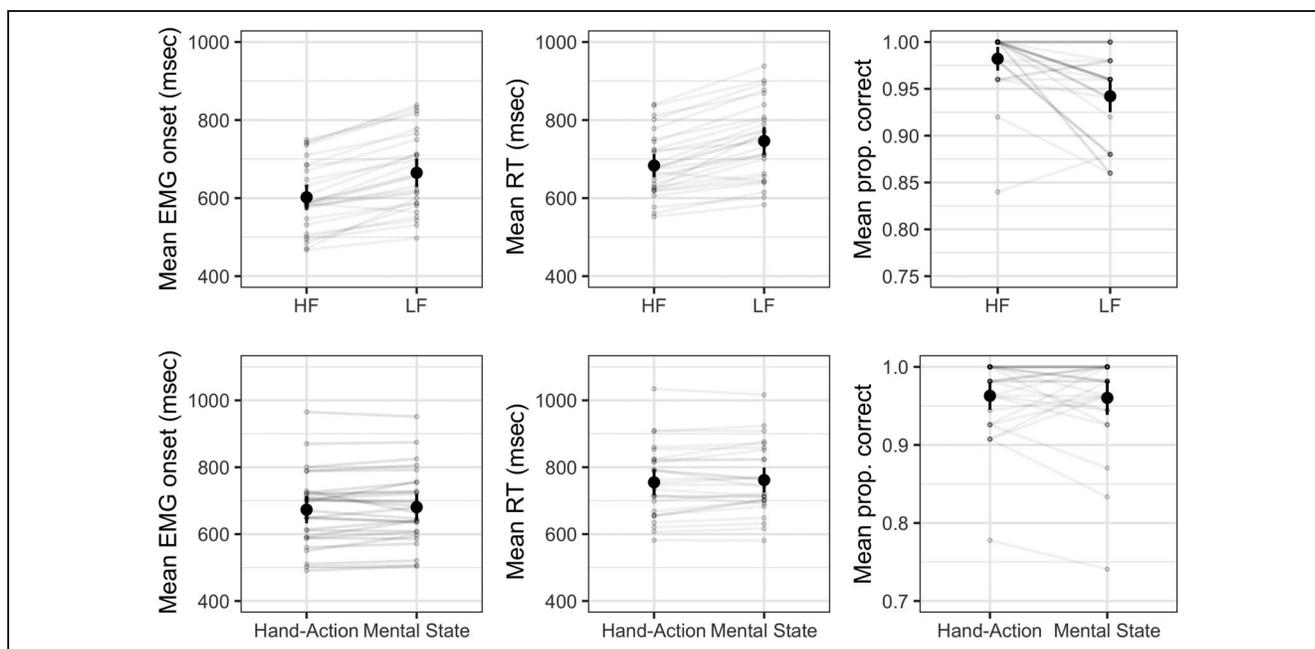
Figure 1. Behavioral results. Black points represent grand mean score, and error bars indicate 95% confidence intervals across individuals. Smaller gray points represent individual means, with lines connecting observations from the same participant. HF = high frequency; LF = low frequency; prop. = proportion.

mental-state verbs; high- vs. low-frequency nouns) revealed any significant difference.

EMG-Locked ERPs

For both negative ERP unfolding contralaterally to the responding hand (signaling activation of the response hand) and the positive one unfolding ipsilaterally (signaling inhibition of the hand not involved in the response), there were no differences between high- and low-frequency words (no cluster found) or between hand-action and mental-state verbs (no cluster found). The corresponding ERP traces are displayed in Figure 2 (second column).

Figure 2. Response-locked ERPs computed on Laplacian-transformed data from C3/C4 electrodes. First column: response-locked LRPs. Second column: lateralized ERPs related to motor-response preparation. I = ipsilateral to the response hand (dashed lines); C = contralateral to the response hand (solid lines); HF = high frequency; LF = low frequency.
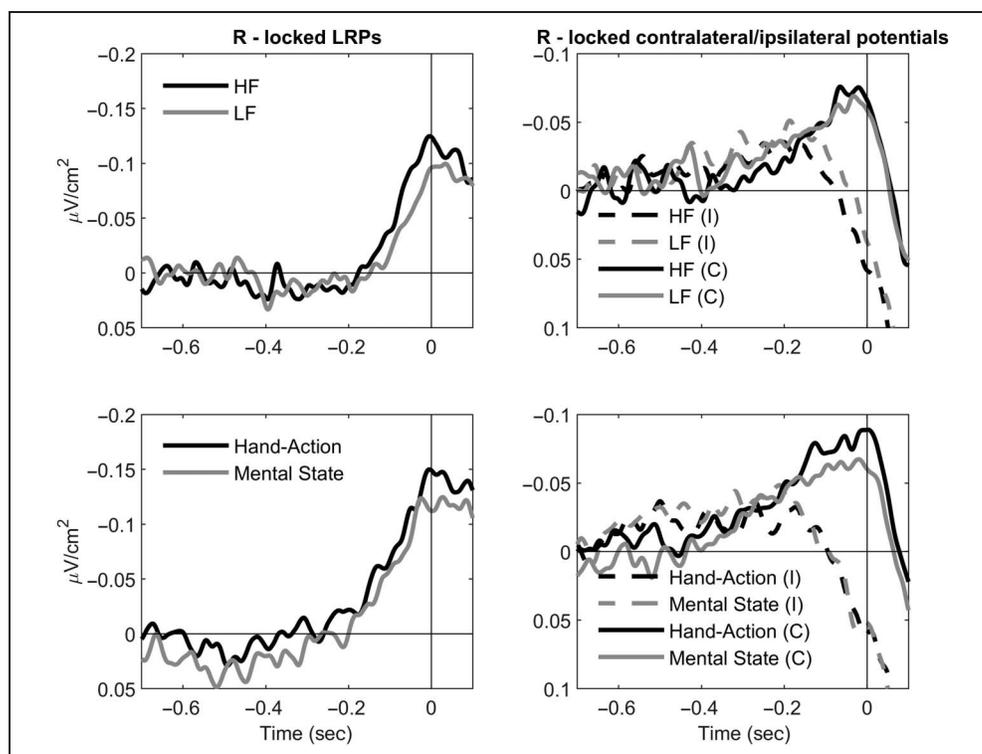
EMG-Locked Beta Power Lateralization

The comparison between activities linked to left- and right-hand responses (i.e., functional localizer) revealed the presence of one significant positive ($p = .005$) and one significant negative ($p < .001$) cluster. Maximal asymmetries in oscillatory power were present (a) on central recording sites, particularly the classic C3 and C4 electrodes, but extended to more posterior electrodes, and particularly to CP3 and CP4; (b) in a time window roughly corresponding to −175 to 100 msec around the EMG onset; and (c) across alpha- and beta-frequency bands (10–24 Hz). In these frequency, spatial, and temporal coordinates, electrodes contralateral to the responding hand showed reduced oscillatory power compared to ipsilateral ones. These differences are summarized in Figure 3.

Inferential claims on frequency and spatiotemporal features of the clusters are unwarranted (e.g., Sassenhagen & Draschkow, 2019; Maris, 2012; Groppe et al., 2011). Instead of strictly relying on the aforementioned features, we used them to loosely define the spatial, temporal, and frequency extension within which effector-selective asymmetries are maximal. The definition of these boundaries also considered the indications from the previous literature (e.g., Twomey et al., 2016; Wyart, Myers, & Summerfield, 2015; Kubanek et al., 2013).

Our search for an impact of linguistic manipulations on beta power desynchronization was thus limited to the coordinates exhibiting a stronger lateralization of oscillatory power in correspondence to effector-specific motor-response activation. Specifically, we ran a cluster-based permutation test comparing measures of lateralization (i.e., contralateral minus ipsilateral activity, normalized by their sum) across conditions as measured from channels C3, C4, CP3, and CP4, on frequencies from 8 to 32 Hz (thus encompassing both alpha and beta frequency bands) within a time window going from −200 to 100 msec centered on EMG onset. This analysis of the effect of linguistic variables on beta lateralization is equivalent, in essence, to a test of the interaction between the linguistic factors and the one coding hemispheres as a function of response hand (contralateral vs. ipsilateral). The results are summarized in Figure 4.

A significant difference surfaced in the contrast between high- and low-frequency words. The features of the positive cluster ($p = .015$) suggest that maximal differences between these conditions in terms of oscillatory

Figure 3. Results from the contrast between left- and right-hand responses, used as a functional localizer. (A) Time–frequency representation (power) of the difference between left- and right-hand responses normalized by their sum, centered on EMG onset (0; dashed lines). Contoured areas highlight time samples and frequencies identified as significant clusters. (B) Topography of the difference between left- and right-hand responses (normalized by their sum) in the −200 to +100 msec EMG-locked time window, for activity between 10 and 22 Hz.
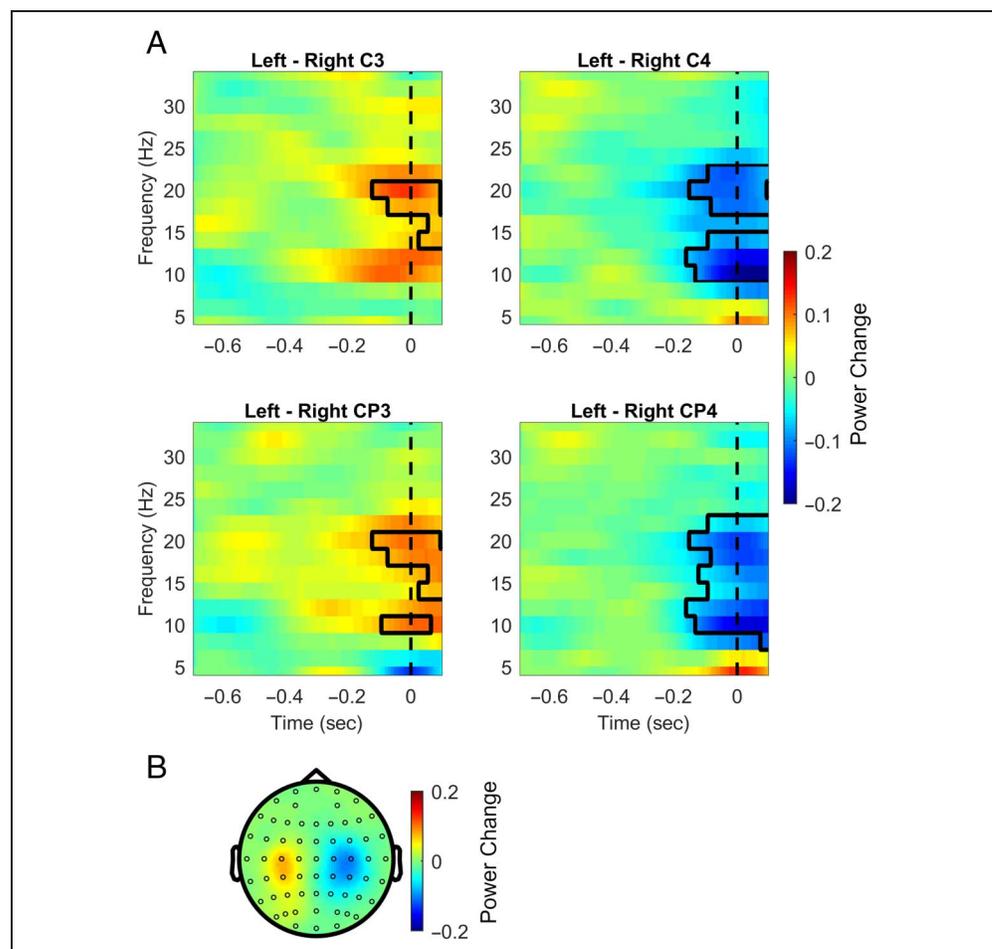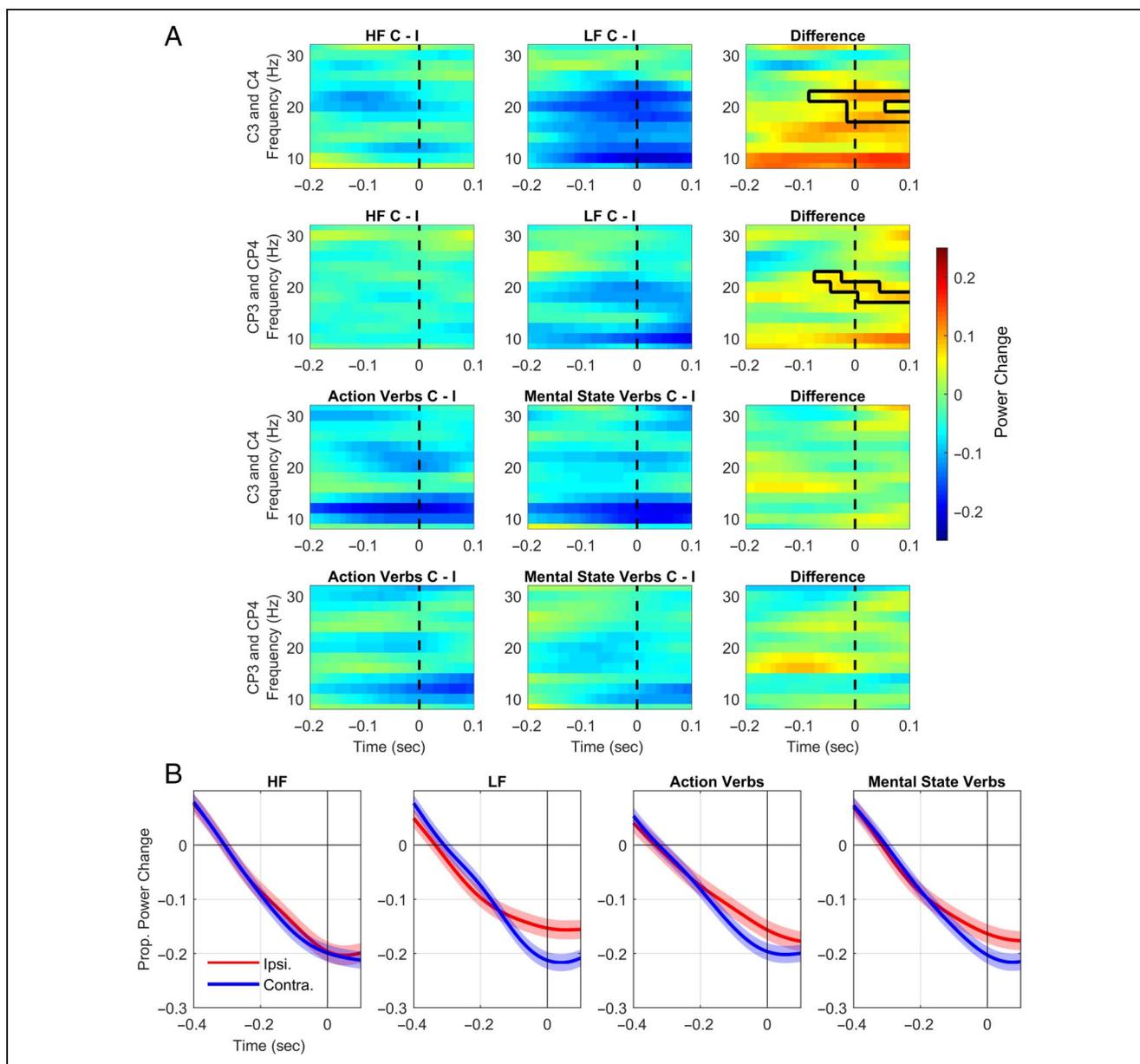
Figure 4. Beta-band lateralization is modulated by the lexical frequency of the words, not by their action semantics. (A) Lateralization was computed by subtracting the oscillatory activity recorded over sites ipsilateral to the responding hand from the one recorded over homologous contralateral electrodes and then normalizing by their sum. Contoured areas represent the samples identified in the cluster with $p < .025$. The dashed vertical lines mark the time of EMG onset. Lateralization indexes calculated from both C3/C4 and CP3/CP4 channels are reported (Rows 1 and 3 and Rows 2 and 4, respectively). C − I = contralateral − ipsilateral; HF = high frequency; LF = low frequency. (B) Time-varying power changes averaged over the entire beta-frequency range (12–30 Hz) and selected electrodes (C3/C4 and CP3/CP4) for activity recorded ipsilaterally to the responding hand (red) and contralaterally (blue) with respect to the average activity of the whole EMG-locked epoch (−700 to 100 msec). Shaded areas represent *SEM*. Prop. = proportion (of).

power lateralization can be found at the onset of EMG response (roughly from −80 msec until the end of the epoch) for frequencies in the beta range (18–22 Hz). Differently, no significant difference was found when comparing action verbs with mental-state ones (all clusters' ps > .2). A rather clear lateralization seems to surface for all the categories of stimuli across the two experiments, except for high-frequency words, where preresponse decreases in oscillatory beta power unfold

similarly across contralateral and ipsilateral electrodes (i.e., bilaterally; see Figure 4B).

DISCUSSION

This research explored the influence of linguistic variables on EEG indexes of motor-response activation. Lexical processing, indexed by word frequency, modulated the lateralization of response-locked attenuation

of beta-frequency oscillatory power. This result points toward a continuity in the processing stream from the accumulation of lexical evidence onto the implementation of response-related motor goals. In contrast, conceptual processing of action semantics showed no influence on the measured EEG indexes of effector-selective motor activation.

The word-frequency manipulation replicated the classic behavioral effects on response latency and accuracy, with faster and more accurate responses to high- than low-frequency words (e.g., Balota, Cortese, Sergent-Marshall, Spieler, & Yap, 2004). More importantly, lexical frequency modulated motor-response activation. Specifically, whereas EEG indexes of motor-response preparation in the time domain were immune to lexical frequency (i.e., no difference in the LRP or in each hemisphere's ERP), a lexical frequency effect surfaced in terms of effector-selective lateralization of beta-frequency power. This dissociation between LRPs and beta lateralization provides a chance to better define the functional locus of the frequency effect.

Previous evidence and its interpretation suggest that the two neurophysiological measures used here capture motor-response activation at different levels of abstraction. In task-switching paradigms where task switches correspond to a switch in the effector in charge of the response, motor-related reduction of beta oscillatory power displays an anticipatory reversal of the lateralization during the preparatory period preceding a switch trial, whereas the LRP displays a similar reversal only after stimulus onset (de Jong et al., 2006; see also Poljac & Yeung, 2014; Gladwin, Lindsen, & de Jong, 2006). Hence, in that context, beta lateralization was related to general motor goals and intentions, whereas the LRPs were thought to reflect the processing necessary to translate these higher-level goals into specific motor programs. As originally noted by de Jong et al. (2006), such distinctions between beta lateralization and LRP are consistent with a more general view of the hierarchy of processes related to motor-response preparation. Desynchronizations of cortical oscillations linked with movement preparation would exert a context-setting function in opening physiological channels to enable the subsequent processing of information reflected within discrete cortical motor potentials (Wheaton, Shibasaki, & Hallett, 2005). In the context of our experiments, this suggests that lexical evidence may affect the settling of higher-order effector-selective motor goals (indexed by motor-related beta activity), whereas subsequent motor programs indexed by cortical potentials remain unaffected, possibly because the system has committed to a specific response as determined by upstream motor goals.

The beta-related lexical frequency effect detected in the experiment seems to be genuinely motor in nature. A notable feature of our observations was indeed the selectivity of the word frequency effect on beta-band

lateralization. Additional post hoc analyses (not reported herein) revealed no evidence of beta-power modulations as a function of stimulus type within stimulus-locked epochs. This remained true whether the analyses were conducted on standard versus Laplacian-transformed data or on a restricted set of central electrodes versus the whole scalp. The effect thus does not represent a by-product of stimulus-locked language-related beta modulations (e.g., Piai, Roelofs, Rommers, & Maris, 2015; Piai, Roelofs, & Maris, 2014; Bastiaansen, Magyari, & Hagoort, 2010; Luo, Zhang, Feng, & Zhou, 2010; van Elk, van Schie, Zwaan, & Bekkering, 2010) but rather a direct influence on the setting of abstract motor goals.

This latter point may become relevant when considering that, in the framework of drift-diffusion models, the word-frequency effect has been traditionally linked to the rate of evidence accumulation captured by the drift rate parameter (Ratcliff et al., 2004). More recent work (e.g., Gomez & Perea, 2014; Donkin, Heathcote, Brown, & Andrews, 2009), however, suggested that part of the lexical frequency effect may be reflected on another parameter (i.e., Ter), which jointly captures putatively nondecision processes related to visual encoding and motor implementation. Our result thus suggests that the part of the word-frequency effect not directly mapping onto the drift rate may actually involve motor-response implementation. A more thorough investigation, probably one in which the chronometric and electrophysiological data are jointly modeled (e.g., Turner, Forstmann, Love, Palmeri, & Van Maanen, 2017), would be required to consolidate such parameter-based interpretation.

It is important to acknowledge some limitations with respect to the effect of lexical frequency on response-related beta-frequency lateralization. In a framework in which lexical evidence accumulation continuously maps onto motor-response activation, we expected—if anything—a stronger lateralization for high- compared to low-frequency words, reflecting the steeper rate of evidence accumulation characterizing the former class of stimuli. The actual data show, however, the opposite pattern. High-frequency words, in fact, displayed a more bilateral beta suppression, which seems to be driven by an increased ipsilateral beta suppression compared to all the other categories of stimuli (Figure 4B). To corroborate this observation, we ran a post hoc analysis in which we assessed the direct relationship between word lexical frequency and single-trial beta power. The analysis was conducted using data from both experiments and showed that ipsilateral (but not contralateral) beta power decreases as lexical frequency increases.[1]

Interestingly, previous reports suggest that contralateral desynchronizations of beta power are related to excitatory processes, whereas homologous ipsilateral suppression would reflect inhibitory processes related to the prevention of erroneous mirror movements of the incorrect effector (e.g., Cheyne, Ferrari, & Cheyne,

2012; Jurkiewicz, Gaetz, Bostan, & Cheyne, 2006; see also Bai, Mari, Vorbach, & Hallett, 2005). Under this perspective, the stronger ipsilateral beta suppression found for high-frequency words may reflect evidence-dependent inhibition of the incorrect response. Thus, high-frequency words, in providing more evidence for a "word" response, would more strongly inhibit the noninvolved hand at the level of motor goals, yielding faster and more accurate behavioral responses. Clearly, this interpretation needs to be considered tentative, not only because of its ad hoc formulation. Other authors, in fact, suggested alternative functional interpretations linking both contralateral and ipsilateral perimovement beta suppression with cortical activation and pointing toward the involvement of both even in case of unimanual motor responses (Rau, Plewnia, Hummel, & Gerloff, 2003). The functional characterization of contralateral versus ipsilateral beta suppressions remains debated (for examples and further discussions, see Kilavik et al., 2013; van Wijk, Beek, & Daffertshofer, 2012; van Wijk, Daffertshofer, Roach, & Praamstra, 2009; Pastötter, Hanslmayr, & Bäuml, 2008; Leocani, Toro, Zhuang, Gerloff, & Hallett, 2001) and, admittedly, our data are not able to discriminate between alternative frameworks.

In contrast to the effect of lexical frequency, no effect of action semantics was detected in any of the indexes of motor-response activation. Albeit null results warrant against any strong conclusion, this pattern may be indicative of the boundary conditions for the effect of action semantics on motor-response preparation and implementation (e.g., Pavlova et al., 2019; Klepp et al., 2015). For example, within semantic tasks requiring the classification of word stimuli as abstract versus concrete, motor-related response-locked attenuation of beta oscillations is reduced for verbs referring to an action performed by the hand, the effector involved in the response (Klepp et al., 2015). Furthermore, the amplitude of motor-evoked potentials is reduced when participants are performing hand or foot responses, and the target sentence of a semantic task refers to the same effector required for the behavioral response (Buccino et al., 2005). Possibly, the reliance on semantic information is crucial for this sort of effects, and lexical decision does not emphasize such a reliance on conceptual-semantic information (Kiefer, Sim, Herrnberger, Grothe, & Hoenig, 2008), thus preventing the interplay between semantically driven and movement-related motor-response processes. If this were true, the more general interpretation would be that only the symbolic information driving the decision (here lexical status, not semantic content) percolates in the motor response. Straightforward predictions from this view should be tested in future tightly designed task comparisons.

In summary, during decisions driven by linguistic stimuli, lexical evidence indexed by a word's frequency of occurrence propagates its influence onto the implementation of high-level effector-selective motor preparation. The effect of a linguistic variable on indexes of motor-response implementation seems incompatible with a strictly thresholded flow of information, where lexical activation stemming from the frequency of written words and the settling of effector-selective motor goals would remain segregated. On the contrary, the observations seem consistent with models in which decision-related modulations flow "down" to the level of motor structures (Calderon et al., 2018), selectively affecting motor programming.

Note

1. The relationship between lexical frequency and ipsilateral beta activity was further explored via linear mixed effects analysis on single-trial data from both experiments. Lexical frequency was entered as the predictor variable. As the dependent variable, we considered the average power (expressed in terms of relative change with respect to the whole epoch) detected in the beta-frequency band (12–30 Hz) within the time window going from -100 to 100 msec (centered on EMG onset) and within the ipsilateral recording sites (C3 and CP3 for left-hand responses; C4 and CP4 for right-hand responses). The model also included by-participant random intercepts. Results showed a significant effect of lexical frequency on beta oscillatory power, $\chi^2(1) = 8.13$, $p = .004$ ($b = -0.0048$, $SE = 0.0017$, $t = -2.85$), capturing the decrease in beta activity as stimulus lexical frequency increases. Notably, contralateral beta activity failed to display any significant relationship with lexical frequency, $\chi^2(1) = 0.55$, $p = .46$ ($b = -0.0012$, $SE = 0.0017$, $t = -0.74$).

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