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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 2-alternative forced-choices on linguistic stimuli, words and pseudo-words. 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 towards 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, etc. This intuitive description points to a functional distinction between deliberation and action, in keeping with a widespread view in cognitive neuroscience.

As a paradigmatic case, consider the standard 2-alternatives 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, Mith, 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, and Verguts, 2018) and, in particular, from experiments showing that electroencephalographic (EEG) components such as the P300 and the centroparietal positivity (CPP) 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 (Kelly & O'Connell, 2013; O'Connell, Dockree, & Kelly, 2012; Twomey, Murphy, Kelly, & O'Connell, 2015; Twomey et al., 2016). 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; Coles, 1989) is an event-related potential 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 (Cohen, Servan-Schreiber, & McClelland, 1992; Spencer & Coles, 1999; 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 (Kivalik, 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., de Lange, Rahnev, Donner, & Lau, 2013; Donner, Siegel, Fires, & Engel, 2008; Kubanek, Snyder, Brunton, Brody & Schalk, 2013; Pape & Siegel, 2018; but see Twomey, et al., 2016; Steinemann, O'Connell, & Kelly, 2018). Further, recent developments in computational modelling 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 2-alternative forced-choice task coupled to specific effectors, in which participants have to respond on the basis of the lexical status (words vs. pseudoword) of visually presented letter strings, typically by pressing one of two buttons with their left vs right hand. Computational models of lexical decision rely on the dynamic accumulation of abstract evidence until an action-triggering threshold is reached (e.g., Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001; Dufau, Grainger, & Ziegler, 2012; Ratcliff et al., 2004; Wagenmakers, Ratcliff, Gomez, & McKoon, 2008), thus postulating, once again, a strong distinction between language-driven decisions and motor response activation.

The current research investigated the discrete vs. 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- vs. 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 towards pre-existing 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 Balota & Chumbely, 1984; Besner & Risko, 2016) 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 towards 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 supra-modal hubs (Patterson, Nestor, & Rogers, 2007; Lambon Ralph, Jefferies, Patterson, & Rogers, 2017) 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., Boulenger, Roy, Paulignan, Deprez, Jeannerod, & Nazir, 2006; Klepp, Niccolai, Buccino, Schnitzler, Biermann-Ruben, 2015).

In the present study, multiple neural indexes of motor-response activation were considered. In the time-domain we focused on the LRP and, additionally, 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., Burle, Vidal, Tandonnet, & Hasbroucq, 2004; Vidal, Burle, & Hasbroucq, 2018; Vidal, Burle, Spieser, Carbonnell, Meckler, Casini, & Hasbroucq, 2015). 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 contra- vs ipsilateral to the responding hand (e.g., De Jong, Gladwin, & t'Hart, 2006; Donner et al., 2008; Doyle et al., 2005; Poljac & Yeung, 2014; Twomey, et al., 2016). 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 (De Jong, et al., 2006; Poljac & Yeung, 2014). 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). Also, 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 due to 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, Riggio, Melli, Binkofski, Gallese, & Rizzolatti, 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 semantics 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.

In order 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 electromyographic signal recorded from the muscle responsible of the motor response.

Method

Two lexical decision experiments were devised and conducted with Italian materials and Italian native speakers. The first experiment used high (e.g., the Italian translations of *month*, *church*) and low frequency nouns (e.g., the Italian translations of *breeze*, *cork*) 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 states verbs (e.g., *to think*, *to ignore*) in their Italian infinitive form (e.g., *accarezzare*, *applaudire*, *pensare*, *ignorare*) as stimuli in order to ascertain the presence of action-related semantic effects on motor-response preparation. In addition, each experiment included pseudo-words that resembled the word stimuli. Further details are as follows.

Participants

Thirty right-handed, Italian native-speakers were recruited (18 females, $M_{age} = 24.47$, $SD_{age} = 4.95$). 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 with 10€. All the procedures received approval from the Ethical Committee of The University of Trento and participants signed an informed consent document prior to the experiment. The data from two participants were discarded: in one case because of poor signal quality, in the other because of an excessive alpha-wave activity. Data and scripts for the analyses are stored at <https://osf.io/mdw3e/> and can be accessed by submitting a request at the same webpage.

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 pre-tested in order to ensure that they differed on them being (or not being) associated to hand-actions. Twenty participants (not purposely all females, $M_{age} = 25.80$, $SD_{age} = 3.72$; 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 them think about an action performed with the hands. Hand-action and mental state verbs were significantly different for these scores. One-hundred and eight legal filler pseudowords were created for this experiment. Care was taken in order 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.

TABLE 1 ABOUT HERE

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 exact 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 personal computer. Participants sat in an armchair in front of the computer screen at a distance of about 40 cm, holding a joystick 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 the left hand on the joystick trigger. Each experiment was divided in 2 blocks. The mapping between stimulus type (word vs pseudowords) and response hand (left vs right) was reversed across the two blocks, in order 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 8 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 minutes, excluding the time for installation of EEG cap and EMG electrodes.

Stimuli were presented in uppercase 14-point Courier New, in white against a black background. Each trial began with a fixation cross (+) for 800 ms, followed by the target string which remained on screen for 1500 ms or until a response was made. Immediately after, a screen

displaying a blink stimulus ((--)) was shown for 2500 ms; participants were instructed, whenever possible, to blink only during this interval. Trials were separated by a blank screen lasting 300 ms.

EEG/EMG recording and processing

EEG data were acquired via an eego sports system (ANT Neuro, Enschede, The Netherlands), from 64 Ag/AgCl electrodes placed according to the International 10-10 System referenced online to CPz at a sampling rate of 1,000 Hz (filters: DC to 260 Hz, third order sinc filter). An additional electrode was placed below the left-eye to serve as an electro-oculogram. Impedance at each electrode site was kept below 20 K Ω .

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 ms) 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, Oostneveld, & Fries, 2011) and smoothing them using a centered moving-average procedure with a window of 50 ms. 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 pre-processing. EEG data were band-pass (0.1 to 70 Hz; order 2 Butterworth filters) and notch (50 Hz) filtered. Epochs going from 800 ms before target onset until 1850 ms 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 re-referenced 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). Afterwards, ICA was computed (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. Further, 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 pre-stimulus baseline (-200 to 0 ms before target onset) was then applied by subtraction. Finally, response locked epochs (-1000 to 350 ms centered on EMG onset) were extracted.

All analyses were conducted on Laplacian-transformed data in order 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 in the time-frequency domains (e.g.,

Twomey et al., 2016). 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}).

ERPs 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 vs. 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 were averaged with those recorded from right-electrodes during right-hand responses (Burle, van den Wildenberg, Spieser, & Ridderinkhoff, 2016). The LRPs were calculated by subtracting ipsilateral activity from the contralateral one. Following previous research, analyses in the time-domain were limited to activities recorded from electrodes C3 and C4 (e.g., Burle, van den Wildenberg, Spieser, & Ridderinkhof, 2016; Gratton et al., 1988; Tadonnet, Burle, Vidal, & Hasbroucq, 2003; 2006; Vidal et al., 2015).

Time-frequency analyses. To compute the single trial time-frequency representations, a 500 ms Hanning window was applied in frequency steps of 2 Hz (from 2 Hz to 34 Hz) and at time steps of 10 ms. Epochs were 0-padded to the length of 4s 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. In order 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 the time-frequency domain 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 Hz and 34 Hz (in order 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 ms 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 vs contralateral to the responding hand (e.g., Pape & Siegel, 2015; Twomey et al., 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, Maechler, Bolker, & Walker, 2015) in R (R Core Team, 2015). EMG-onset and RTs analyses included only the correct responses on which the algorithm of onset detection succeeded (see the section EMG processing above). Accuracy analyses (correct vs error) included all the responses, irrespective of their neurophysiological features. All the models included by-participants 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 effect structure.

Analyses of EEG signals were performed via cluster-based permutation tests. In the time-domain, the amplitude 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 before to 100 ms 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, 2008). 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 the frequency dimension. 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, i.e. 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 \sim Word Frequency + (1|Subject) + (1|Item)) significantly increased the goodness-of-fit ($\chi^2[1] = 33.47, p < .001$) compared to a null model including only random effects (EMG Onset \sim (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 \sim 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 \sim (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 ms on average (SD = 47) before the actual button press. Accuracy analyses revealed a significant contribution ($\chi^2[1] = 13.56, p < .001$) of the

Running Head: Motor-response activation in lexical decisions

model including the factor Word Frequency (Accuracy \sim Word Frequency + (1|Subject) + (1|Item), family = 'binomial'), compared to the null model (Accuracy \sim (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 \sim Action Semantics + (1|Subject) + (1|Item), family = 'binomial') in comparison with the corresponding null model (Accuracy \sim (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.

FIGURE 1 ABOUT HERE

EEG data

EMG-locked LRPs. LRPs for the different conditions are reported in Figure 2 (first column). None of the comparisons (Hand-Action vs 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 for the positive one unfolding ipsilaterally (signaling inhibition of the hand not involved in the response) there were no difference 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 ABOUT HERE

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 ms around the EMG onset, and (c) across alpha- and beta-frequency bands (10 to 24 Hz). In these frequency, spatial, and temporal coordinates, electrodes contra-lateral to the responding hand showed reduced oscillatory power compared to ipsi-lateral ones. These differences are summarized in Figure 3.

FIGURE 3 ABOUT HERE

Inferential claims on frequency and spatiotemporal features of the clusters are unwarranted (e.g., Groppe et al., 2011; Maris, 2012; Sassenhagen & Draschkow, 2019). Instead that 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 Hz to 32 Hz (thus encompassing both alpha and beta frequency bands) within a time-window going from -200 to 100 ms 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 power lateralization can be found at the onset of EMG response (roughly, from -80 ms 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 pre-response decreases in oscillatory beta power unfolds similarly across contra- and ipsilateral electrodes (i.e., bilaterally; see Figure 4B)

FIGURE 4 ABOUT HERE

General 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 towards 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 nor 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 display 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 Galdwin, Lindsen, & de Jong, 2006; Poljac & Yeung, 2014). Hence, in that context, beta-lateralization was related to general motor goals and intentions, whereas the LRPs was thought to reflect the processing necessary to translate these higher-level goals into specific motor-programs. As originally noted by de Jong and colleagues (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 vs Laplacian-transformed data, or on a restricted set of central electrodes vs the whole scalp. The effect thus does not represent a by-product of stimulus-locked language-related beta modulations (e.g., Bastiaansen, Magyari, & Hagoort, 2010; Luo, Zhang, Geng, & Zhou, 2010; Piai, Roelofs, & Maris, 2014; Piai, Roelofs, Rommers, & Maris, 2015; 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., Donkin, Heathcote, Brown, & Andrews, 2009; Gomez & Perea, 2014), however, suggested that part of the lexical frequency effect may be reflected on another parameter (i.e., *Ter*), which jointly captures putatively non-decision 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 modelled (e.g., Turner, Forstman, 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 (see Footnote 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 may reflect evidence-dependent inhibition of the incorrect responses. Thus, high-frequency words, in providing more evidence for a “word”

response, would more strongly inhibit the non-involved 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 contra and ipsilateral peri-movement beta suppression with cortical activation and pointing towards the involvement of both even in case of unimanual motor responses (Rau, Plewnia, Hummel, & Gerloff, 2003). The functional characterization of contra vs ipsilateral beta suppressions remains debated (for examples and further discussions, see Kivalik et al., 2013; Leocani, Zhuang, Gerloff & Hallett, 2001; Pastötter, Hanslmayr, & Bäuml, 2008; van Wijk Beek, & Daffertshofer, 2012; van Wijk, Daffertshofer, Roach, & Praamstra, 2009) 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., Klepp et al., 2015; Pavlova, Butorina, Nikolaeva, Prokofyev, Ulanov, Bondarev, & Stroganova, 2019). For example, within semantic tasks requiring the classification of word stimuli as abstract vs 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). Further, 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.

References

- Babiloni, F., Cincotti, F., Carducci, F., Rossini, P. M., & Babiloni, C. (2001). Spatial enhancement of EEG data by surface Laplacian estimation: The use of magnetic resonance imaging-based head models. *Clinical Neurophysiology*, *112*, 724–727.
- Bai, O., Mari, Z., Vorbach, S., & Hallett, M. (2005). Asymmetric spatiotemporal patterns of event-related desynchronization preceding voluntary sequential finger movements: a high-resolution EEG study. *Clinical Neurophysiology*, *116*(5), 1213-1221.
- Balota, D. A., & Chumbley, J. I. (1984). Are lexical decisions a good measure of lexical access? The role of word frequency in the neglected decision stage. *Journal of Experimental Psychology: Human perception and performance*, *10*(3), 340.
- Bastiaansen, M., Magyari, L., & Hagoort, P. (2010). Syntactic unification operations are reflected in oscillatory dynamics during on-line sentence comprehension. *Journal of Cognitive Neuroscience*, *22*(7), 1333–1347.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1-48.
- Besner, D., & Risko, E. F. (2016). Thinking outside the box when reading aloud: Between (localist) module connection strength as a source of word frequency effects. *Psychological Review*, *123*(5), 592.
- Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences*, *15*(11), 527-536.
- Boulenger, V., Roy, A. C., Paulignan, Y., Deprez, V., Jeannerod, M., & Nazir, T. A. (2006). Cross-talk between language processes and overt motor behavior in the first 200 msec of processing. *Journal of Cognitive Neuroscience*, *18*(10), 1607-1615.

- Bradley, M. M., & Lang, P. J. (1999). *Affective norms for English words (ANEW): Instruction manual and affective ratings* (Vol. 30, No. 1, pp. 25-36). Technical report C-1, the center for research in psychophysiology, University of Florida.
- Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., & Rizzolatti, G. (2005). Listening to action-related sentences modulates the activity of the motor system: a combined TMS and behavioral study. *Cognitive Brain Research*, *24*(3), 355-363.
- Burle, B., Vidal, F., Tandonnet, C., & Hasbroucq, T. (2004). Physiological evidence for response inhibition in choice reaction time tasks. *Brain and cognition*, *56*(2), 153-164.
- Burle, B., Van den Wildenberg, W. P., Spieser, L., & Ridderinkhof, K. R. (2016). Preventing (impulsive) errors: Electrophysiological evidence for online inhibitory control over incorrect responses. *Psychophysiology*, *53*(7), 1008-1019.
- Calderon, C. B., Gevers, W., & Verguts, T. (2018). The unfolding action model of initiation times, movement times, and movement paths. *Psychological review*, *125*(5), 785.
- Cheyne, D. O., Ferrari, P., & Cheyne, J. A. (2012). Intended actions and unexpected outcomes: automatic and controlled processing in a rapid motor task. *Frontiers in human neuroscience*, *6*, 237.
- Cohen, M. X. (2014). *Analyzing neural time series data: Theory and practice*. Cambridge, MA: MIT Press.
- Cohen, M. X. (2015). Comparison of different spatial transformations applied to EEG data: A case study of error processing. *International Journal of Psychophysiology*, *97*(3), 245-257.
- Cohen, J. D., Servan-Schreiber, D., & McClelland, J. L. (1992). A parallel distributed processing approach to automaticity. *American Journal of Psychology*, *105*, 239–269.

- Coles, M. G. H (1989). Modern mind-brain reading: Psychophysiology, physiology, and cognition. *Psychophysiology*, *26*, 251-269.
- Coltheart, M., Rastle, K., Perry, C., Langdon, R., & Ziegler, J. (2001). DRC: a dual route cascaded model of visual word recognition and reading aloud. *Psychological review*, *108*(1), 204.
- Crepaldi, D., Keuleers, E., Mandera, P., & Brysbaert, M. (2013). SUBTLEX-IT. Retrieved from <http://crr.ugent.be/subtlex-it/>
- de Jong, R., Gladwin, T. E., & M't Hart, B. (2006). Movement-related EEG indices of preparation in task switching and motor control. *Brain Research*, *1105*(1), 73-82.
- de Lange, F. P., Rahnev, D. A., Donner, T. H., & Lau, H. (2013). Prestimulus oscillatory activity over motor cortex reflects perceptual expectations. *Journal of Neuroscience*, *33*(4), 1400-1410.
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*(1), 9–21.
- Donkin, C., Heathcote, A., Brown, S., & Andrews, S. (2009). Non-decision time effects in the lexical decision task. In *Proceedings of the 31st annual conference of the cognitive science society*. Austin, TX: Cognitive Science Society.
- Donner, T. H., Siegel, M., Fries, P., & Engel, A. K. (2009). Buildup of choice-predictive activity in human motor cortex during perceptual decision making. *Current Biology*, *19*(18), 1581-1585.

- Doyle, L. M., Yarrow, K., & Brown, P. (2005). Lateralization of event-related beta desynchronization in the EEG during pre-cued reaction time tasks. *Clinical Neurophysiology, 116*(8), 1879-1888.
- Dufau, S., Grainger, J., & Ziegler, J. C. (2012). How to say “no” to a nonword: A leaky competing accumulator model of lexical decision. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 38*(4), 1117.
- E-Prime (Version 2.0.10.356) [Computer software]. Pittsburgh, PA: Psychology Software Tools.
- Gladwin, T. E., Lindsen, J. P., & de Jong, R. (2006). Pre-stimulus EEG effects related to response speed, task switching and upcoming response hand. *Biological Psychology, 72*(1), 15-34.
- Gomez, P., & Perea, M. (2014). Decomposing encoding and decisional components in visual-word recognition: A diffusion model analysis. *The Quarterly Journal of Experimental Psychology, 67*(12), 2455-2466.
- Gratton, G., Coles, M. G. H., Sirevaag, E. J., Eriksen, C. W., & Donchin, E. (1988). Pre- and post-stimulus activation of response channels: A psychophysiological analysis. *Journal of Experimental Psychology: Human Perception and Performance, 14*, 331–344.
- Groppe, D. M., Urbach, T. P., & Kutas, M. (2011). Mass univariate analysis of event-related brain potentials/fields I: A critical tutorial review. *Psychophysiology, 48*(12), 1711-1725.
- Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron, 41*(2), 301-307.
- Jurkiewicz, M. T., Gaetz, W. C., Bostan, A. C., & Cheyne, D. (2006). Post-movement beta rebound is generated in motor cortex: evidence from neuromagnetic recordings. *Neuroimage, 32*(3), 1281-1289.

- Kelly, S. P., & O'Connell, R. G. (2013). Internal and external influences on the rate of sensory evidence accumulation in the human brain. *Journal of Neuroscience*, *33*(50), 19434-19441.
- Kiefer, M., Sim, E. J., Herrnberger, B., Grothe, J., & Hoenig, K. (2008). The sound of concepts: four markers for a link between auditory and conceptual brain systems. *Journal of Neuroscience*, *28*(47), 12224-12230.
- Kilavik, B. E., Zaepffel, M., Brovelli, A., MacKay, W. A., & Riehle, A. (2013). The ups and downs of beta oscillations in sensorimotor cortex. *Experimental Neurology*, *245*, 15-26.
- Klepp, A., Nicolai, V., Buccino, G., Schnitzler, A., & Biermann-Ruben, K. (2015). Language-motor interference reflected in MEG beta oscillations. *NeuroImage*, *109*, 438-448.
- Kubaneck, J., Snyder, L. H., Brunton, B. W., Brody, C. D., & Schalk, G. (2013). A low-frequency oscillatory neural signal in humans encodes a developing decision variable. *Neuroimage*, *83*, 795-808.
- Lambon-Ralph, M. A., Jefferies, E., Patterson, K., & Rogers, T. T. (2017). The neural and computational bases of semantic cognition. *Nature Reviews Neuroscience*, *18*(1), 42.
- Leocani, L., Toro, C., Zhuang, P., Gerloff, C., & Hallett, M. (2001). Event-related desynchronization in reaction time paradigms: a comparison with event-related potentials and corticospinal excitability. *Clinical Neurophysiology*, *112*(5), 923-930.
- Lopez-Calderon, J., & Luck, S. J. (2014). ERPLAB: An open-source toolbox for the analysis of event-related potentials. *Frontiers in Human Neuroscience*, *8*, 213.
- Luo, Y., Zhang, Y., Feng, X., & Zhou, X. (2010). Electroencephalogram oscillations differentiate semantic and prosodic processes during sentence reading. *Neuroscience*, *169*(2), 654-664.

- Maris, E. (2012). Statistical testing in electrophysiological studies. *Psychophysiology*, *49*(4), 549-565.
- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, *164*, 177–190.
- Montefinese, M., Ambrosini, E., Fairfield, B., & Mammarella, N. (2014). The adaptation of the affective norms for English words (ANEW) for Italian. *Behavior Research Methods*, *46*(3), 887-903.
- O'Connell, R. G., Dockree, P. M., & Kelly, S. P. (2012). A supramodal accumulation-to-bound signal that determines perceptual decisions in humans. *Nature neuroscience*, *15*(12), 1729.
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, 156869. doi: 10.1155/2011/156869
- Palmer, J. A., Makeig, S., Kreutz-Delgado, K., & Rao, B. D. (2008). Newton method for the ICA mixture model. In *Proceedings of the 33rd IEEE international conference on acoustics and signal processing (ICASSP 2008)*, (pp. 1805–1808). Las Vegas, NV
- Pape, A. A., & Siegel, M. (2016). Motor cortex activity predicts response alternation during sensorimotor decisions. *Nature communications*, *7*, 13098.
- Pastötter, B., Hanslmayr, S., & Bäuml, K. H. (2008). Inhibition of return arises from inhibition of response processes: an analysis of oscillatory beta activity. *Journal of Cognitive Neuroscience*, *20*(1), 65-75.

- Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience*, 8(12), 976.
- Pavlova, A. A., Butorina, A. V., Nikolaeva, A. Y., Prokofyev, A. O., Ulanov, M. A., Bondarev, D. P., & Stroganova, T. A. (2019). Effortful verb retrieval from semantic memory drives beta suppression in mesial frontal regions involved in action initiation. *Human Brain Mapping*, 40(12), 3669-3681.
- Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp potential and current density mapping. *Electroencephalography and Clinical Neurophysiology*, 72, 184–187.
- Piai, V., Roelofs, A., & Maris, E. (2014). Oscillatory brain responses in spoken word production reflect lexical frequency and sentential constraint. *Neuropsychologia*, 53, 146–156.
- Piai, V., Roelofs, A., Rommers, J., & Maris, E. (2015). Beta oscillations reflect memory and motor aspects of spoken word production. *Human Brain Mapping*, 36, 2767–2780.
- Poljac, E., & Yeung, N. (2014). Dissociable neural correlates of intention and action preparation in voluntary task switching. *Cerebral Cortex*, 24(2), 465-478.
- Pulvermüller, F. (2005). Brain mechanisms linking language and action. *Nature Reviews Neuroscience*, 6(7), 576-582.
- R Core Team (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org/>
- Ratcliff, R., Gomez, P., & McKoon, G. (2004). A diffusion model account of the lexical decision task. *Psychological review*, 111(1), 159.

Ratcliff, R., Smith, P. L., Brown, S. D., & McKoon, G. (2016). Diffusion decision model:

Current issues and history. *Trends in cognitive sciences*, 20(4), 260-281.

Rau, C., Plewnia, C., Hummel, F., & Gerloff, C. (2003). Event-related desynchronization and excitability of the ipsilateral motor cortex during simple self-paced finger movements.

Clinical Neurophysiology, 114, 1819-1826.

Sassenhagen, J., & Draschkow, D. (2019). Cluster-based permutation tests of MEG/EEG data do not establish significance of effect latency or location. *Psychophysiology*, 56(6), e13335.

Schoffelen, J. M., Poort, J., Oostenveld, R., & Fries, P. (2011). Selective movement preparation is subserved by selective increases in corticomuscular gamma-band coherence. *Journal of Neuroscience*, 31(18), 6750-6758.

Servant, M., White, C., Montagnini, A., & Burle, B. (2015). Using covert response activation to test latent assumptions of formal decision-making models in humans. *Journal of Neuroscience*, 35(28), 10371-10385.

Servant, M., White, C., Montagnini, A., & Burle, B. (2016). Linking theoretical decision-making mechanisms in the Simon task with electrophysiological data: A model-based neuroscience study in humans. *Journal of Cognitive Neuroscience*, 28(10), 1501-1521.

Spencer, K. M., & Coles, M. G. (1999). The lateralized readiness potential: Relationship between human data and response activation in a connectionist model. *Psychophysiology*, 36(3), 364-370.

Steinemann, N. A., O'Connell, R. G., & Kelly, S. P. (2018). Decisions are expedited through multiple neural adjustments spanning the sensorimotor hierarchy. *Nature communications*, 9(1), 3627.

- Tandonnet, C., Burle, B., Vidal, F., & Hasbroucq, T. (2003). The influence of time preparation on motor processes assessed by surface Laplacian estimation. *Clinical Neurophysiology*, *114*(12), 2376-2384.
- Tandonnet, C., Burle, B., Vidal, F., & Hasbroucq, T. (2006). Knowing when to respond and the efficiency of the cortical motor command: A Laplacian ERP study. *Brain Research*, *1109*(1), 158-163.
- Turner, B. M., Forstmann, B. U., Love, B. C., Palmeri, T. J., & Van Maanen, L. (2017). Approaches to analysis in model-based cognitive neuroscience. *Journal of Mathematical Psychology*, *76*, 65–79.
- Twomey, D. M., Kelly, S. P., & O'Connell, R. G. (2016). Abstract and effector-selective decision signals exhibit qualitatively distinct dynamics before delayed perceptual reports. *Journal of Neuroscience*, *36*(28), 7346-7352.
- Twomey, D. M., Murphy, P. R., Kelly, S. P., & O'Connell, R. G. (2015). The classic P300 encodes a build-up to a threshold decision variable. *European Journal of Neuroscience*, *42*(1), 1636-1643.
- Tzagarakis, C., Ince, N. F., Leuthold, A. C., & Pellizzer, G. (2010). Beta-band activity during motor planning reflects response uncertainty. *Journal of Neuroscience*, *30*(34), 11270-11277.
- van Elk, M., van Schie, H. T., Zwaan, R. A., & Bekkering, H. (2010). The functional role of motor activation in language processing: motor cortical oscillations support lexical-semantic retrieval. *Neuroimage*, *50*(2), 665-677.
- van Wijk, B.C.M., Beek, P.J., & Daffertshofer, A. (2012). Neural synchrony within the motor system: what have we learned so far? *Frontiers in Human Neuroscience*, *6*, 252.

- van Wijk, B.C. M., Daffertshofer, A., Roach, N., & Praamstra, P. (2009). A role of beta oscillatory synchrony in biasing response competition? *Cerebral Cortex*, *19*(6), 1294-1302.
- Vidal, F., Burle, B., & Hasbroucq, T. (2018). The way we do the things we do: how cognitive contexts shape the neural dynamics of motor areas in humans. *Frontiers in Psychology*, *9*, 1296.
- Vidal, F., Burle, B., Spieser, L., Carbonnell, L., Meckler, C., Casini, L., & Hasbroucq, T. (2015). Linking EEG signals, brain functions and mental operations: Advantages of the Laplacian transformation. *International Journal of Psychophysiology*, *97*(3), 221-232.
- Wagenmakers, E. J., Ratcliff, R., Gomez, P., & McKoon, G. (2008). A diffusion model account of criterion shifts in the lexical decision task. *Journal of Memory and Language*, *58*(1), 140-159.
- Wheaton, L. A., Shibasaki, H., & Hallett, M. (2005). Temporal activation pattern of parietal and premotor areas related to praxis movements. *Clinical neurophysiology*, *116*(5), 1201-1212.
- Wyart, V., Myers, N. E., & Summerfield, C. (2015). Neural mechanisms of human perceptual choice under focused and divided attention. *Journal of Neuroscience*, *35*(8), 3485-3498.

Footnote

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 and 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 and 100 ms (centered on EMG onset) and within the ipsilateral recording sites (C3 and CP3 for left-hand responses; C4 and CP4 for right-hand responses) as the dependent variable. The model also included by-participant random intercepts. Results showed a significant 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 ($\chi^2 [1] = 0.55$, $p = .46$; $b = -0.0012$, $SE = 0.0017$, $t = -0.74$).

Table 1

Psycholinguistic variables controlled across stimulus categories of the 2 experiments. For each variable, mean values are reported (SD within parentheses).

| 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) | - | - |

Note. N. of Letters = number of letters; Orth. N = orthographic neighborhood size; 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 were taken from the Italian adaptation (Montefinese, Ambrosini, Fairfield, Mammarella, 2014) of the Affective Norms for English Words database (ANEW; Bradley & Lang, 1999).

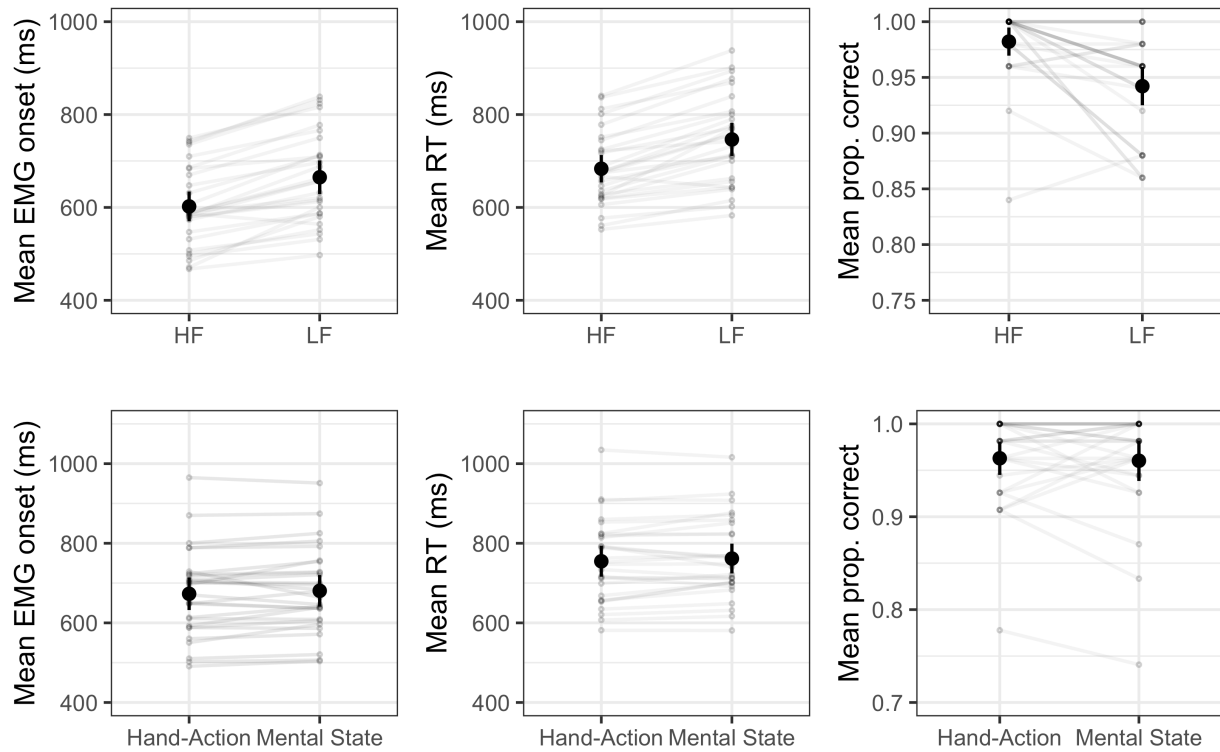


Figure 1. Behavioral results. Black points represent grand mean score and error bars indicate 95% confidence intervals across individuals. Smaller gray points represent individual means, with lines connecting observations from the same participant. HF = High Frequency; LF = Low Frequency.

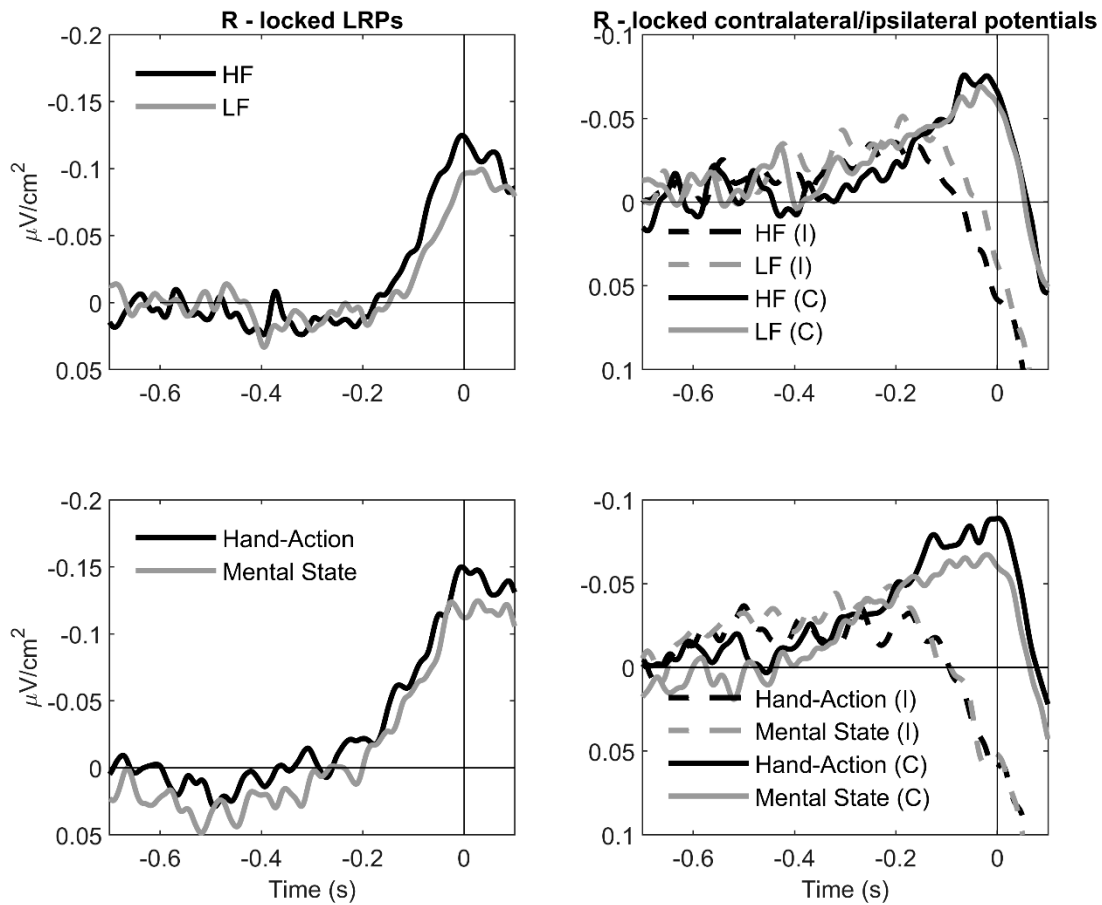


Figure 2. Response-locked ERPs computed on Laplacian-transformed data from C3/C4 electrodes. First column: Response-locked LRPs. Second column: lateralized ERPs related to motor-response preparation. I = ipsilateral to the response hand (dashed lines), C = contralateral to the response hand (solid lines). HF = High Frequency; LF = Low Frequency.

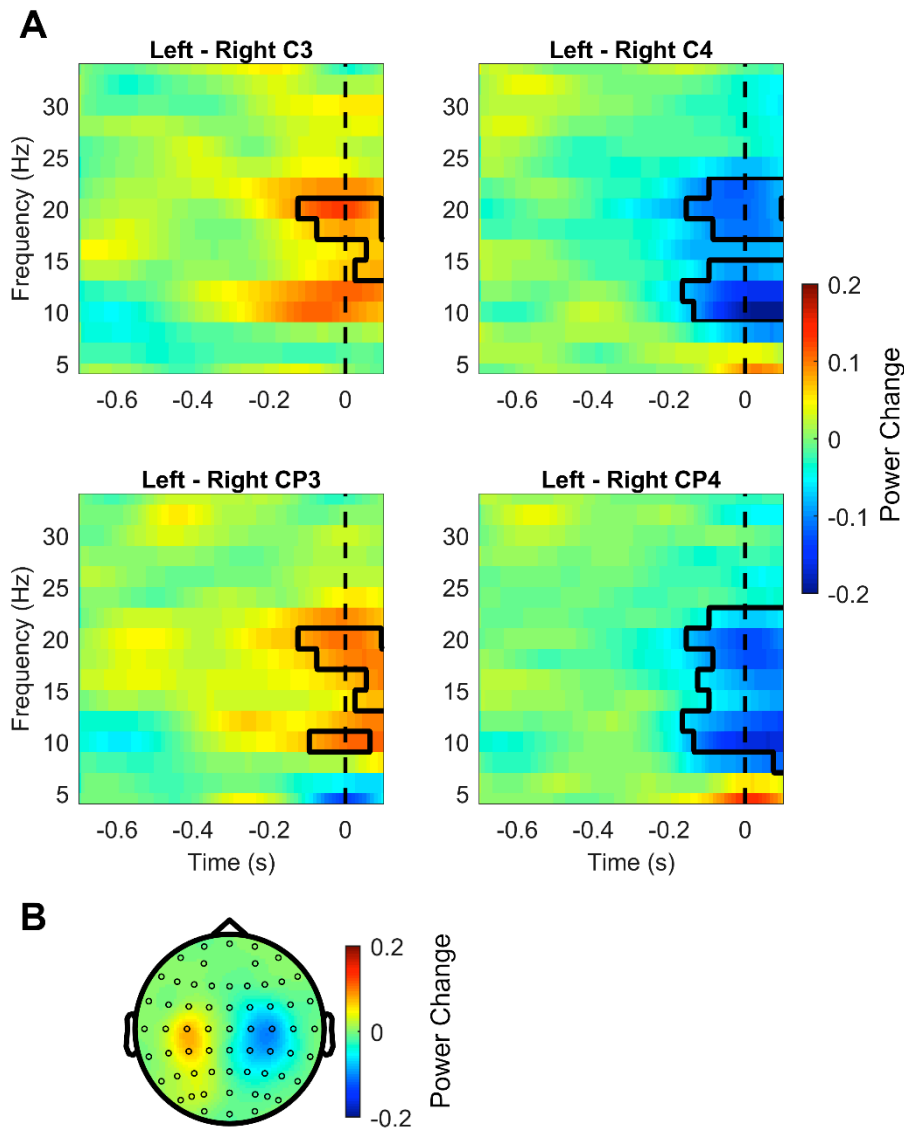


Figure 3. Results from the contrast between left- and right-hand responses, used as a functional localizer. A: Time-frequency representation (power) of the difference between Left- and Right-hand responses normalized by their sum, centered on EMG onset (0; dashed lines). Contoured areas highlight time-samples 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 ms EMG-locked time-window, for activity between 10 and 22 Hz.

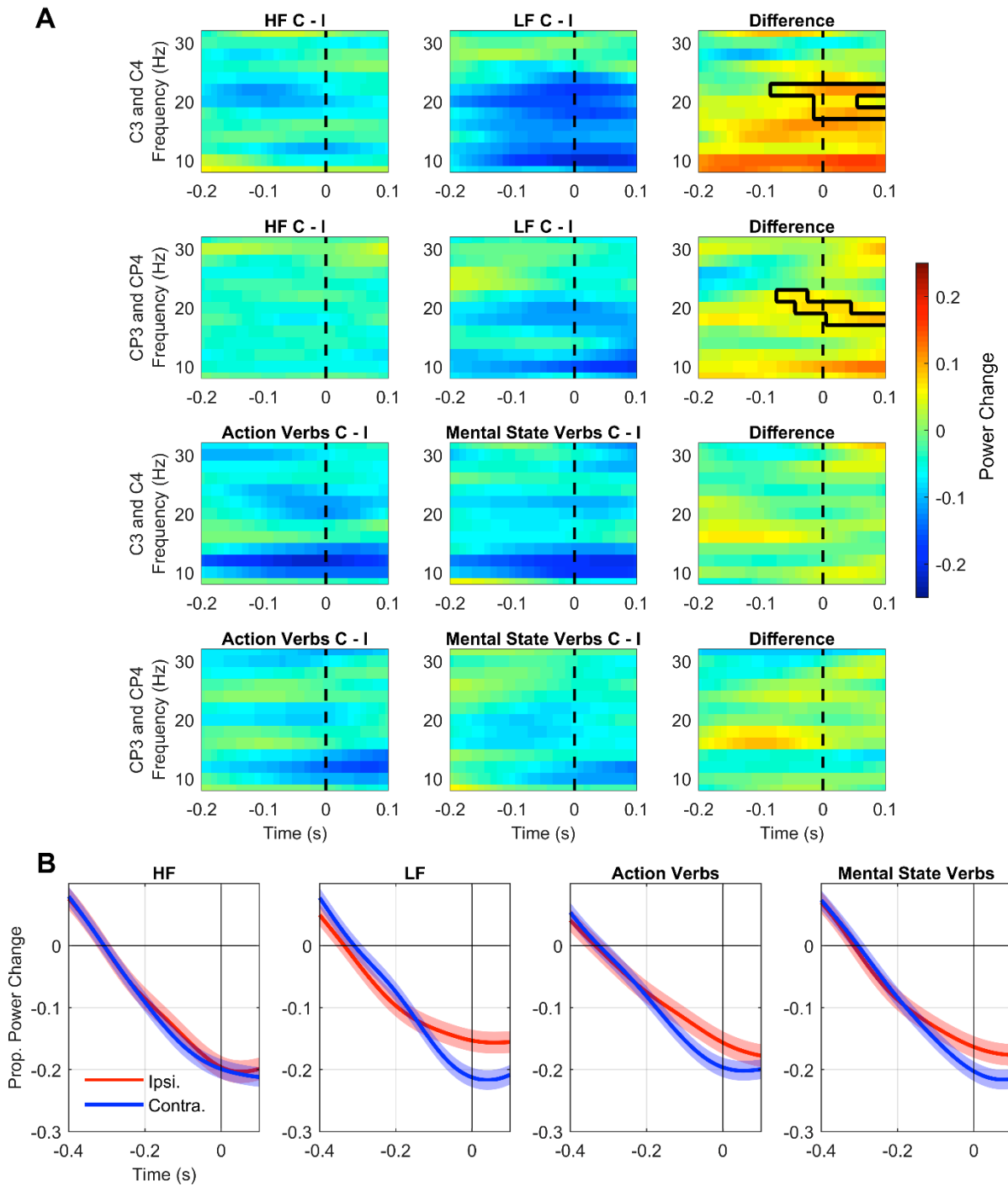


Figure 4. Beta-band lateralization is modulated by the lexical frequency of the words, not by their action semantics. A: Lateralization was computed by subtracting the oscillatory activity recorded over sites ipsilateral to the responding hand from the one recorded over homologous

contralateral electrodes, 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 C3/4 and CP3/4 channels are reported (rows 1 and 3, 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 (C3/4 and CP3/4) 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 ms). Shaded areas represent standard error of the mean.