Electrophysiological evidence of discontinuities in the propagation of lexical decision processes across the motor hierarchy

Michele Scaltritti [a,*], Elena Greatti [a,1], Simone Sulpizio [b,c,**]

[a] Dipartimento di Psicologia e Scienze Cognitive, Università Degli Studi di Trento, Corso Bettini 31, 38068, Rovereto TN, Italy
[b] Dipartimento di Psicologia – Università Degli Studi di Milano-Bicocca, Piazza Dell'Ateneo Nuovo 1, 20126, Milano MI, Italy
[c] Milan Center for Neuroscience (NeuroMI) – Università Degli Studi di Milano-Bicocca, Piazza Dell'Ateneo Nuovo 1, 20126, Milano MI, Italy

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ABSTRACT

This research assessed the propagation of decisional effects across multiple electrophysiological indexes related to motor-response implementation within a lexical decision task, a paradigmatic case of a 2-alternative choice task on linguistic stimuli. By co-registering electroencephalographic and electromyographic data, we focused on the lexicality effect (i.e., the difference between responses to words and nonwords), and we tracked its influence across indexes of motor-response planning (indexed by effector-selective lateralization of beta-frequency desynchronizations), programming (indexed by the lateralized readiness potential) and execution (indexed by the chronometric durations of muscular responses). In addition, we explored corticomuscular coherence as the potential physiological underpinning of a continuous mapping of information between stimulus evaluation and response channels. The results revealed lexicality effects only on indexes of motor planning and execution, with no reliable involvement of the other measures. This pattern is discussed with reference to the hypothesis of multiple decisional components exerting different influences across the motor-hierarchy.

Credit author statement

Michele Scaltritti: conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; software; supervision; visualization; writing - original draft; writing - review and editing. Elena Greatti: data curation; formal analysis; investigation; writing - review and editing. Simone Sulpizio: conceptualization; formal analysis; funding acquisition; methodology; project administration; supervision; visualization; writing - original draft; writing - review and editing.

1. Introduction

The evaluation of the surrounding environment until reaching a deliberation concerning how to act lies at the core of many human behaviors. In line with a tradition of mathematical models envisaging decisional processes as evidence accumulating towards a response boundary (e.g., Schall, 2003; Ratcliff et al., 2016), neurophysiological investigations on decision-making in humans have highlighted different signals that capture the dynamic evolution of putative decision variables accumulating evidence onto response alternatives (e.g., Donner et al., 2009; Kelly and O'Connell, 2013; O'Connell and Kelly, 2021; O'Connell et al., 2012; Twomey et al., 2015, 2016).

Accumulator-like dynamics have been highlighted for motor-related electrophysiological signatures at the level of effector-selective asymmetries of the oscillatory activity in the beta range (13–30 Hz). A decrease in oscillatory power (desynchronization) within the beta-band is reliably observed before response onset and continues during motor-response execution, usually followed by a post-movement rebound (e. g., Kilavik et al., 2013). The movement-related desynchronization is bilateral, yet it is enhanced over sites contralateral to the response effector (e.g., over right channels for a left-hand movement; Doyle et al., 2005) and the difference between contra and ipsilateral activity (i.e., the beta-band lateralization) has been exploited as a marker of effector-selective motor preparation in its unfolding. Albeit this index displays evidence-dependent modulations capturing decisional

processes (e.g., Pape and Siegel, 2016; de Lange et al., 2013; Donner et al., 2009; but see Steinemann et al., 2018; Twomey et al., 2016), its motor nature is apparently at odds with the widespread assumption that motor responses are not part of the decision. In fact, despite remarkable differences in terms of processing dynamics, parameters, and architectures, several implementations of evidence-accumulation models share the assumption that the moment at which evidence reaches the action-triggering boundary marks the termination of decision-related processes and the beginning of motor-response execution, in a serial architecture featuring separate and discrete decisional vs motor stages (e.g., Brown and Heathcote, 2005, 2008; Donkin et al., 2011; Ratcliff et al., 2004, 2016; Usher and McClelland, 2001; for different perspectives, see Calderon et al., 2018; Lepora and Pezzulo, 2015; Thura et al., 2022).

The functional segregation between decisional and motor processes has been further questioned by surface electromyographic (EMG) data and reaction time (RT) fractioning (Botwinick and Thompson, 1966), which allows single-trial measurements of response duration even in the context of fast, discrete manual responses, such as the simple button-presses typically used in psychological and neuroscientific experiments. Specifically, via the EMG traces of the muscle responsible for the button-press, one can distinguish, within each RT, two different components: (a) a premotor time (PMT), reflecting the time elapsing from stimulus onset until the onset of the muscular activity and capturing a purely "cognitive time" with no signs of motor activity, and (b) a motor time (MT), consisting in the interval between the onset of the EMG burst and the final button press, and representing a measure of motor-response duration. Recent evidence from both sensory (Servant et al., 2021; Weindel et al., 2021) and conceptual (Scaltritti et al., 2023) decision-making tasks suggests that at least some decisional components are still at play during motor-response execution.

In a series of previous experiments, we focused on a paradigmatic conceptual decision-making task, i.e., lexical decision, in which participants are presented with strings of letters and must categorize them as words or nonwords. We reported effects of decisional components both at the level of the lateralization of the beta-band desynchronization (Scaltritti et al., 2020) and at the level of MTs (Scaltritti et al., 2023). Lexical decision is an interesting test-case for decision-making theories, as decisions are based on information and evidence sampled from memory, rather than from the sensory input, thus eschewing dedicated sensorimotor pathways (Cisek, 2007; Gordon et al., 2011; Pezzulo and Cisek, 2016; Siegel et al., 2011). In this context, we observed that (a) the unfolding of effector-selective beta lateralization is modulated by word frequency (Scaltritti et al., 2020), and (b) that MTs, exactly as PMTs, are modulated by stimulus lexicality (i.e., the difference between words and nonwords; Scaltritti et al., 2023). These findings suggest that at least part of the decisional processes may still be active during actual motor-response implementation and modulate peripheral indexes of muscular activity.

Effector selective beta lateralization and MTs can be respectively considered the first and the last steps in the chain of processes unfolding across a motor-hierarchy underpinning action performance. The current research aims to track the potentially continuous transition from decision to response execution across the different stages of the motor control hierarchy, including intermediate ones. We focused on the lexicality effect in a classic lexical decision task, and, by co-registering EEG and EMG signals, we assessed the differences between words and nonwords across multiple electrophysiological indexes putatively mapping onto different levels of the motor control hierarchy. Our working hypothesis included three major processing stages: motor planning, motor programming, and motor-response execution. Motor planning represents the highest level of the hierarchy, consisting of internal models focused on the general goal of the actions (e.g., Jeannerod, 1995; Van Der Merwe, 2020; Parrell et al., 2019). At the middle level, motor plans are translated into (smaller) motor-programs, entailing spatial and temporal specifications of muscular activity (Brooks, 1986; Jeannerod,

1995; Van Der Merwe, 2020). Finally, programs are forwarded to the effectors, for motor-response execution.

We used EMG traces to perform RTs fractioning, thus focusing on the peripheral endpoint of the motor-hierarchy (motor-response execution) where we expected to replicate the propagation of the response slow-down for word-like nonwords (i.e., pseudowords) on MTs (Scaltritti et al., 2023). At the level of EEG data, we investigated the effector-selective asymmetries both in the time-frequency and in the time domain, by considering, respectively, the lateralization of the beta desynchronization and the lateralized readiness potential (LRP; Coles, 1989). The two measures have been interpreted as indexing different levels of the motor hierarchy. Beta desynchronizations – the starting point of the motor-hierarchy, i.e., the planning stage – would capture more general and abstract motor goals and, from a physiological perspective, have been hypothesized to play a context-setting function by opening the physiological channels and enabling the unfolding of a discrete cortical potential (Wheaton et al., 2005). The LRP would then translate these abstract motor goals into a motor program (de Jong et al., 2006; see also Poljac and Yeung, 2014; Gladwin et al., 2006). With respect to the LRP, we additionally explored the underlying pattern of lateralized event-related potentials (ERPs), consisting in a negative-going deflection unfolding over electrodes contralateral to the response hand, and a positive deflection over ipsilateral sites. The two ERPs capture, respectively, the activation of the correct response hand and the inhibition of the incorrect one (Burle et al., 2004; Vidal et al., 2003). The difference between words and pseudowords was expected to surface at the level of motor-related asymmetries in the EEG signal, possibly with enhanced lateralization reflecting a higher rate of evidence accumulation (for words compared to pseudowords, e.g., Ratcliff et al., 2004; see also Gomez and Perea, 2014; Yap et al., 2015) propagated onto multiple levels of the motor hierarchy.

Finally, we investigated long-range physiological interaction between cortical and muscular activity by resorting to corticomuscular coherence, a measure of synchronization between the cortical activity and alpha motoneurons (Schoffelen et al., 2005, 2011). We hypothesized that corticomuscular coherence could represent the physiological channel that progressively translates the decision-informed motor planning (indexed by effector-selective beta lateralization) and/or programming (indexed by the LRP and the underlying lateralized potentials) into an overt motor component (MT) that still carries informational and decision-related contents. Previous research has in fact highlighted the role of beta-frequency corticomuscular coherence in biasing response competition, being associated with the suppression of the incorrect response via an increased coherence over sites ipsilateral to the effector (van Wijk et al., 2009). More generally, we speculated that such physiological coordination may mirror long-range interactions between decisional and motor stages, thus highlighting at the level of neural coordination the continuous mapping of stimulus evaluation into the response channels.

2. Methods

2.1. Participants

Forty Italian native speakers participated to the experiment (31 females; M_{age} = 22.7; SD_{age} = 3.05). All participants had normal or corrected-to-normal visual acuity and no history of neurological problems or learning disabilities. Using the Edinburgh Handedness Inventory (Oldfield, 1971), we classified 37 participants as right-handed (M = 86.9, SD = 14.25) and 2 as mixed right-handers (with handedness scores corresponding to 41.2 and 40). Data from 1 mixed left-hander (handedness score = −29.4) were not included in the analyses. Data from 2 other participants were discarded from the analyses due to noisy data from a faulty EEG cap. The final sample thus included 37 participants.

Participation was compensated with €25. The Ethical Committee for Research of the University of Trento approved all the procedures

(protocol number 2020-028). A signed informed consent document was obtained for each participant before the experiment.

2.2. Stimuli

Experimental stimuli consisted of 250 words drawn from the PhonItalia database version 1.10 (Goslin et al., 2014) and 250 pseudowords created with the Wuggy software (Keuleers and Brysbaert, 2010). Words and pseudowords were comparable across the psycholinguistic variables listed in Table 1.

Both categories of stimuli were divided into two subsets of 125 items for counterbalancing purposes. Items were comparable within and across subsets for the variables in Table 1. One word (*bronco* – bronchus) was erroneously included among the pseudowords and removed from all the analyses.

2.3. Apparatus and procedure

Participants completed a questionnaire collecting demographic and health-related information. Then, after the installation of the EEG cap and the electrodes for the recording of the EMG signal, the experiment began. The experimental procedure and the acquisition of behavioral data were controlled by the E-Prime 2 software (Version 2.0.10.356, Psychology Software Tools) running on a laptop. Participants sat at a distance of about 40 cm in front of the computer screen, holding a joypad in their hands with their thumbs on the upper triggers. They were instructed to categorize letter strings as words or pseudowords via button presses performed using their thumbs. Response speed and accuracy were equally emphasized.

The experiment was divided into two main blocks, with the stimulus (word vs pseudoword) - response (right vs left hand) mapping being reversed across blocks, to ensure the same number of left- and right-hand responses for each category of stimuli. The order of the response mappings was counterbalanced across participants, and the assignment of the two subsets of items to either the first or the second block was counterbalanced as well. Before each block, 20 practice trials were administered to familiarize with the response configuration. Within each block, participants could take self-terminated breaks every 50 trials. The whole experimental session (including the installation of the EEG cap and the EMG electrodes) lasted about 150 min.

Table 1
Psycholinguistic variables of the stimuli used in the experiment.

Variables	Words	Pseudowords	t-value
Frequency (log)	4.65	–	–
Familiarity	7.13	–	–
Imageability	7.46	–	–
Concreteness	6.88	–	–
Valence	6.02	–	–
Arousal	5.38	–	–
N. of Letters	6.65	6.64	−0.03
N. of Syllables	2.80	2.82	0.25
Orthographic N	4.46	4.93	0.94
OLD20	1.94	1.96	0.50
Bigr. Freq. Sum	659,914	644,205	−0.58
Bigr. Freq. Mean	114,827	111,066	−1.18

Note. N. of Letters = number of letters; N. of Syllables = number of syllables; Orthographic N = number of orthographic neighbors; OLD20 = orthographic Levenshtein distance (Yarkoni et al., 2008); Bigr. Freq. Sum = summed bigram frequency; Bigr. Freq. Mean = mean bigram frequency. For words, surface variables were extracted from the PhonItalia database (Goslin et al., 2014). Familiarity, concreteness, imageability, valence, and arousal scores were taken from the Italian adaptation (Montefinese et al., 2014) of the Affective Norms for English Words database (Bradley and Lang, 1999). For pseudowords, the number of orthographic neighbors and OLD20 were computed on the PhonItalia database using the *vwr* package (Keuleers, 2013) in R. Bigram frequency variables were drawn from the same database using a custom-made script. *t*-values result from independent sample two-tailed *t*-tests.

Stimuli were written in 25-point Courier New font, in black against a grey background (RGB: 180, 180, 180). Each trial started with a fixation cross (+) presented for 1500 ms, followed by the target letter-string. The stimulus was terminated upon the button-press response, or after 1500 ms in case no response was given. A blank screen was then presented for 1800 ms, followed by a screen displaying a blinking symbol for 1800 ms. Participants were instructed to blink, if possible, during this latter interval. A final blank screen was displayed for 200 ms and served as an inter-trial interval.

2.4. EEG and EMG recording and processing

EEG and EMG data were acquired via an eego sports system (ANT Neuro) at a sampling rate of 1000 Hz. EEG data were recorded from 64 Ag–AgCl electrodes placed according to the 10–10 system, with CPz serving as the online reference. One additional electrode was placed below the left eye as an EOG. Impedance at each electrode site was kept below 20 kΩ. The EMG signal was acquired through two pairs of bipolar electrodes placed ~1.5 cm apart on the thenar eminences of both hands, in correspondence to the *flexor pollicis brevis* muscle.

Off-line signal processing was performed using EEGLAB (version 14_1_2b; Delorme and Makeig, 2004), ERPLAB (Lopez-Calderon and Luck, 2014) and FieldTrip functions (version 20190203; Oostenveld et al., 2011) in MATLAB (version 2018b, MathWorks Inc.), as well as custom-made scripts.

2.4.1. EMG processing

A 5 Hz high-pass filter (order 2 Butterworth) and a 50 Hz notch filter were applied offline to the EMG data. The continuous signal was then segmented into epochs from −1500 to 3300 ms centered on stimulus onset. For each epoch, the onset of the EMG activity was determined using the integrated profile method devised by Liu and Liu (2016). In detail, the cumulative sum of the absolute values of the EMG trace was subtracted from the line joining the first and the last data-points (representing the cumulative sum of a uniform distribution; Liu and Liu, 2016; Weindel et al., 2021). The EMG onset corresponded to the sample where the difference reached its minimum.

A second algorithm (devised following Servant et al., 2021) was then applied to support artifact rejection. The algorithm identified, within each epoch, windows of EMG activity by tracking those samples in which the activity exceeded the 3.5 SDs from the average value in a pre-stimulus baseline period (−500 to 0 ms). Consecutive windows separated by less than 25 ms were merged. For the resulting windows, those shorter than 50 ms or beginning after the epoch's RT were discarded. Epochs still displaying more than one window of activity were marked. All epochs were then visually inspected and only retained when the EMG onset corresponded to the last window of activity before response onset (to discard onsets corresponding to sudden noise bursts, drifts, or separate EMG bursts). On average, 3.96% of the epochs were rejected.

The same two algorithms were also applied to the signal of the hand not involved in the final button-press, to detect partial errors (i.e., trials in which a correct response was finally delivered, but after a covert activation of the incorrect response hand) and partial correct responses (i.e., trials with an incorrect response, but featuring a covert activation of the correct response hand). Epochs displaying windows of activity were marked and classified as containing true partial errors or partial-correct responses when a visually clear EMG activation was present, and the timing of its onset was accurately marked. Partial errors occurred in 12.22% of the trials, whereas partial correct responses were few (0.52%). Epochs containing partial errors or partial-correct responses were dropped from the analyses as the covert activation of motor system in these trials (other than indexing a possibly different decisional stage compared to a full-correct response) may blur effector-selective asymmetries and lateralized EEG measures.

2.4.2. EEG preprocessing

Electrodes corresponding to the mastoids were excluded. For the remaining EEG data, we first applied a high-pass (0.1 Hz), and then a low-pass filter (200 Hz; order 2 Butterworth for both). Finally, data were notch filtered (50 Hz). Epochs were segmented from 1500 ms before stimulus onset until 3300 ms afterwards. Spherical interpolation was applied to noisy channels ($M = 2.03$), and EEG data were then re-referenced to the average activity of all the electrodes. A first artifact rejection was conducted via visual inspection to discard epochs contaminated by excessive noise ($M = 2.58\%$). An Independent Component Analysis (ICA) was performed using the AMICA algorithm (Palmer et al., 2008), and the components corresponding to blinks or saccades ($M = 1.65$) were removed from the signal. To avoid issues of rank-deficiency, care was taken to compute a number of independent components that took into account the number of interpolated channels, as well as the use of the average reference. A second artifact rejection based on visual inspection was applied to remove the remaining noisy epochs ($M = 5.33\%$). From the remaining epochs, incorrect responses (4.46%) were removed, in addition to the epochs dropped from the EMG processing pipeline. On average, 73% of the epochs were retained in the analyses, with an average of 189 epochs for word and 175 epochs for pseudoword trials. Epochs time-locked to the EMG onset (-1000 to 1800 ms) were finally extracted and a 30 Hz low-pass filter (order 2 Butterworth) was applied only for ERP analyses. All analyses were performed on Laplacian-transformed EEG data to increase spatial resolution (Babiloni et al., 2001; Cohen, 2014, 2015) and to obtain a better spatiotemporal differentiation for motor-related indexes in the time (Vidal et al., 2015) as well as in the time–frequency domain (e.g., Twomey et al., 2016). The surface Laplacian was computed using the spline interpolation method (Perrin et al., 1989) as implemented by Cohen (2014) (order of splines = 4, maximal degree of Legendre polynomial = 10, lambda parameter = 10^{-5}).

2.4.3. Time-frequency analyses

For both EEG and EMG data, the time-frequency representations (power- and cross-spectra) were computed using the multitaper method (Mitra and Pesaran, 1999). Epochs (0 padded to the length of 4 s) were segmented in windows of 400 ms at time-steps of 10 ms, and each segment was tapered using Slepian tapers. For frequencies below and equal to 30 Hz (from 2 to 30 Hz, at steps of 2 Hz), we used three tapers, resulting in a spectral smoothing of 5 Hz. As noted by Schoffelen and colleagues (2005, 2011), the physiological bandwidth of the beta-frequencies corresponds to ~10 Hz, and thus a spectral concentration of 5 Hz seems particularly suited for this specific frequency band. For the analyses of oscillatory power, data were normalized to the average power of the whole EMG-locked epoch.

For corticomuscular coherence, we took the absolute values of the Hilbert-transform of the raw EMG signal (Schoffelen et al., 2005, 2011). Corticomuscular coherence was computed by calculating the summed cross-spectral density between the EMG signal of the responding hand and all the EEG electrodes and normalizing it by their respective power (using the function *ft_connectivity*, method = 'coh', in FieldTrip), resulting in values between 0 (no coherence) and 1 (perfect coherence).

2.5. Measures

2.5.1. Chronometric measures

Other than the traditional measures of response latency and accuracy, the EMG signals were used to partition single trial RTs into a premotor time (PMT) – corresponding to the interval elapsing from stimulus onset until the beginning of the EMG burst – and a motor time (MT) – corresponding to the time from EMG onset until the button press response.

2.5.2. Beta lateralization

The contrast between epochs time-locked to the EMG onset for left-vs

right-hand responses (collapsed across words and pseudowords) was used as a functional localizer to isolate the spatial, temporal, and frequency coordinates of effector-selective beta power modulations (see also Donner et al., 2009; Scaltritti et al., 2020; Twomey et al., 2016). The contrast was conducted using a cluster-based permutation test including frequencies between 6 and 34 Hz (to encompass the whole alpha/mu and beta bands, while leaving 2 additional Hz to accommodate smearing in frequency estimation), all the electrodes, and a time window going from 800 ms before EMG onset until 1600 ms afterwards. Beta-lateralization was then computed on the resulting functionally identified time-frequency and spatial coordinates, reflecting motor-related asymmetries of oscillatory activities orthogonal to the experimental manipulation. Specifically, we separately averaged oscillatory power within channels ipsilateral versus contralateral to the responding hand (e.g., Pape and Siegel, 2016; Scaltritti et al., 2020; Twomey et al., 2016) and beta-lateralization was computed, within each participant and condition, by subtracting ipsilateral activity from the contralateral one.

2.5.3. Lateralized readiness potential and lateralized ERPs

Event-related potentials were obtained by averaging, within each participant and condition, EMG-locked epochs over sites contralateral vs. ipsilateral to the response hand, collapsing across left- and right-hand responses (e.g., contralateral ERPs were computed by averaging together activity from right-channels for left-hand responses and from homologous left-channels for right-hand responses). LRPs were then computed by subtracting ERPs ipsilateral to the response hand from the homologous contralateral ones. For the analysis of the lateralized ERPs, we separately considered the contralateral and ipsilateral EPRs. These analyses only involved the classic C3 and C4 electrodes (e.g., Gratton et al., 1988; Burle et al., 2004).

2.5.4. Corticomuscular coherence

The contrast between left-vs right-hand responses (collapsed across experimental conditions) was again used to isolate coherence phenomena related to effector selection and activation. This comparison included all channels and all the frequency bins between 6 and 32 Hz. The time-window was restricted to a time-window going from 200 ms before EMG onset until 400 ms afterwards. In fact, the median duration of MTs – capturing EMG activity from its onset until button press – was 189 ms, which was rounded to 200 ms. An additional 200 ms was added to the time-window of interest to accommodate for the temporal smearing of the cross-spectra estimation, which was performed on tapered windows of 400 ms (see the Time-Frequency Analysis section). Within the resulting coordinates, we separately analyzed contralateral and ipsilateral (with respect to the responding hand) coherence, without computing any index of lateralization.

2.6. Statistical analyses

The analyses of chronometric measures were performed using linear mixed effect models, whereas generalized linear mixed effects models were used for response accuracy due to the binomial nature of the dependent variable. For both classes of measures, analyses were conducted using the *lme4* library (version 1.1.27.1; Bates et al., 2015) and the *afex* package (version 28.1; Singman et al., 2021) in R (version 4.2.1; R Core Team, 2022). Figures were made via the *ggplot2* package (version 3.3.6; Wickham, 2016).

Fitted models included the fixed effect of lexicality and, for random effects, the structure of maximal complexity (Barr et al., 2013), i.e., including random intercepts for participants and items, the random slopes of the fixed effect, and their correlations with the by-participants intercepts. In case of non-converging models (reflecting an over-parameterization; e.g., Bates et al., 2018; Matuschek et al., 2017), the random-effect structure was progressively simplified by first removing correlations among random terms (i.e., fitting zero-correlation

models), then by removing random slopes (or intercepts) featuring the smallest amount of variance. Fixed effects were considered as significant when their corresponding *t*-value was larger than |2|.

Analyses of EEG signals were performed via cluster-based permutation tests, in which the dependent variables were compared across conditions of interest by a series of *t*-tests conducted within each channel, at each sample, and in each frequency bin. The *t* statistics exceeding a predefined threshold ($p < .05$) were aggregated into clusters as a function of their temporal and/or spatial proximity. Cluster statistics were then obtained by summing all the *t* values included within the clusters. Cluster *p* values were finally calculated based on a null distribution of *t* values obtained via permutations (n = 1000) in which observations were randomly shuffled across conditions. The cluster *p* value corresponded to the proportion of permutations displaying a test statistic larger than the observed one (Groppe et al., 2011; Maris and Oostenveld, 2007). Statistical significance was assessed by setting the alpha level to .025, due to the two-tailed nature of the underlying hypothesis. All the cases in which the temporal, spatial, or frequency coordinates on which the tests were conducted have been restricted to specific samples, channels, or frequency bins are explicitly noted in the text of the Results section.

3. Results

3.1. Chronometric measures

Trials with errors (5.79% of the total), partial errors (12.75%), or an inaccurate detection of the EMG onset (4.12%) were excluded from the analyses. Results are presented in Fig. 1. There was a significant effect of lexicality (pseudowords vs words) for RTs, PMTs, and MTs. In the final models, the random effect structure of maximal complexity was retained for models of RTs and PMTs. By-items random intercepts were dropped for the model on MTs, as the estimated variance component was equal to 0. Parameters of the models are reported in Table 2. Words were faster than pseudowords for all three measures.[2]

The lexicality effect was significant also in terms of response accuracy, with higher likelihood of a correct response for words (*M* = .96, *SD* = .03) compared to pseudowords (*M* = .92, *SD* = .08), *b* = 0.49, *SE* = .15, *z* = 3.19 (see also Supplementary Materials 1).

3.2. Beta lateralization

The contrast serving as a functional localizer, i.e., the comparison between activities for left- and right-hand responses (collapsed across experimental conditions), revealed significant differences captured by two positive (both *ps* < .001) and two negative clusters (*p* < .001; *p* = .002). To isolate effector-selective asymmetries, we just focused on the earliest positive and negative clusters, surfacing before EMG onset (the later ones appeared to be linked to the post-movement beta rebound; Fig. 2A). For each of these two clusters, we identified (considering all electrodes) the first (positive = −800 ms; negative = −540 ms) and the final sample (positive = 660 ms; negative = 810 ms) and isolated the time-window of interest by separately averaging the time of the first vs last samples involved in the positive and negative clusters. Within the resulting time-window (−670 to 730 ms time-locked to EMG onset), for each electrode we averaged the power of beta-frequency bins (14–30 Hz) at each sample, and we identified those samples in which beta activity for a given electrode was different from 0. Finally, we restricted

the channels to those showing beta activity for more than 70% of the samples included within the above-defined time window. The topography of the beta asymmetries and involved channels are provided in Fig. 2B.

Beta lateralization was computed only on those channels showing the involvement of homologous sites over the other hemisphere (i.e., FC3, FC1, FC2, FC4, C3, C1, C2, C4). The analysis was further restricted to frequencies between 14 and 30 Hz, and within the time-window identified with the functional localizer (−670 to 730 ms, EMG locked). There was no averaging of the data over any of the dimensions (i.e., time, channels, frequency). The results revealed a significant difference in beta lateralization across words and pseudowords captured by a significant negative cluster (*p* = .022). As visible in Fig. 2C, effector-selective lateralization of beta power was enhanced for words compared to pseudowords within a time-window roughly corresponding to −440 to 250 ms centered on EMG onset. The pattern is brought by an enhanced differentiation between contra and ipsilateral activity for words compared to pseudowords around the time of EMG onset (Fig. 2D).

3.3. Lateralized readiness potential

The EMG-locked LRPs and the underlying lateralized ERPs triggered by words and pseudowords were remarkably similar in terms of both amplitude and timing (Fig. 3). No analyses were performed to assess potential differences, given the indistinguishable results.

3.4. Corticomuscular coherence

Overall inspection of the coherence spectra revealed an unexpected lack of coherence for the beta-frequency range (14–30 Hz). Differently, coherence in our task configuration was found within lower bands, including alpha/mu (8–12 Hz) and possibly theta (Fig. 4A). For the latter frequency band, no additional analysis was performed, as the 5 Hz high-pass filter applied to the EMG signal prevents any consideration.

The functional localizer contrast between left- and right-hand response revealed the presence of significant difference captured by one positive and one negative cluster (both *ps* < .001). As for measures of oscillatory power, for each of these two clusters we identified (considering all electrodes) the first (positive = −110 ms; negative = −540 ms) and the final samples (positive = 400 ms; negative = 300 ms) and isolated the time-window of interest by separately averaging the time of the first vs last samples involved in the positive and negative cluster. Within the resulting time-window (from −110 to 350 ms time-locked to EMG onset), we computed, at each sample within each electrode, the average coherence across alpha/mu frequency bins (8–12 Hz) and identified the samples in which alpha/mu coherence for a given electrode was different from 0. We finally identified the channels showing alpha/mu coherence for more than 70% of the samples included within the above defined time window. The topography of alpha/mu coherence and surviving electrodes are plotted in Fig. 4B.

Further analyses were restricted to the above defined time window (−110 to 350, time-locked to EMG onset), and to the coherence averaged over alpha/mu frequency bins separately within those channels showing the involvement of homologous sites over the other hemisphere (i.e., F3, F1, F2, F4, FC3, FC1, FC2, FC4, C5, C3, C4, C6, CP5, CP3, CP1, CP2, CP4, CP6, P4, P2, P1, P3). The comparison between words and pseudowords revealed no significant difference, either in contralateral or ipsilateral sites (no clusters found for both comparisons; Fig. 4C). Corticomuscular coherence in the alpha band was clearly enhanced over sites contralateral to the responding hand. However, it was very much comparable across experimental conditions (Fig. 4D).

4. General discussion

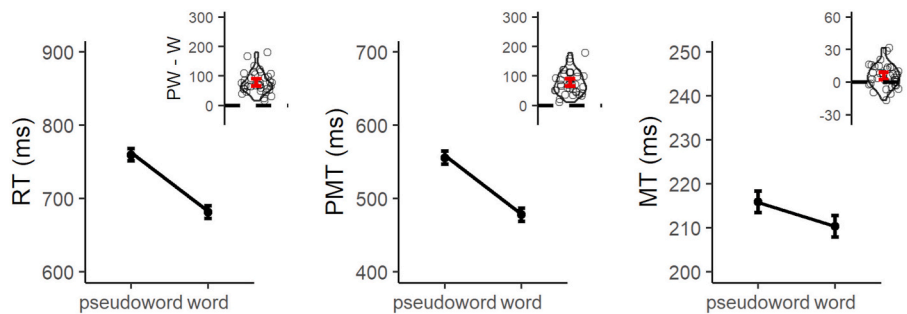The present research tracked the lexicality effect across

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[2] All the analyses on chronometric measures were replicated (a) after trimming for particularly fast RTs, possibly related to guessing mechanisms (Weindel et al., 2021; Supplementary Materials 2), and (b) after log-transforming the dependent variables (Supplementary Materials 3). The results, in terms of significance and direction of the coefficients, were fully consistent with those reported here.

Fig. 1. Results of chronometric measures
Note. Points represent empirical means (with error bars reflecting 95% confidence intervals), lines represent means predicted by the statistical model. For inset plots, points represent individual difference-scores between pseudowords and words, with the violin-plot reflecting the corresponding distribution. Red error-bars convey 95% confidence-intervals of the mean effect for the whole sample. All confidence intervals were adjusted for within-participants variables following Morey (2008).

Table 2
Parameters of the models for chronometric measures.

Random Effects	Variance	SD	Correlation
RTs			
Participants	11,101	105.36	
Lexicality (word)	1103	33.22	−0.26
Items	1746	41.78	
Residual	18,643	136.54	
PMTs			
Participants	9195	95.89	
Lexicality (word)	1392	37.30	−0.60
Items	1750	41.83	
Residual	13,450	115.97	
MTs			
Participants	2208.3	46.99	
Lexicality (word)	50.7	7.12	0.01
Residual	4727.1	68.75	
Fixed Effects	b	Std. Error	t value
RTs			
Intercept	762.71	17.60	43.33
Lexicality (word)	−80.09	7.01	−11.43
PMTs			
Intercept	559.09	16.05	34.84
Lexicality (word)	−79.95	7.45	−10.73
MTs			
Intercept	215.82	7.77	27.78
Lexicality (word)	−5.40	1.64	−3.29

Note. Std. Error = standard error; RTs = reaction times; PMTs = premotor times; MTs = motor times.

electrophysiological correlates of motor-response planning, programming, and execution to capture the transition from decision onto action over the multiple levels of the motor-hierarchy underlying overt behavioral responses.

The higher level of this hierarchy, i.e., the settling of abstract motor-goals during response planning, was indexed via the effector-selective lateralization of beta-frequency desynchronizations time-locked to EMG onsets (de Jong et al., 2006; Wheaton et al., 2005). Interestingly, beta lateralization was enhanced for word- compared to pseudoword-responses. This result extends to conceptual decisions the previous findings from perceptual decision-making, in which the lateralization of the beta-band desynchronization has been reported to scale with the amount of evidence provided by the stimulus (Pape and Siegel, 2016; de Lange et al., 2013; Donner et al., 2009; but see Steinemann et al., 2018; Twomey et al., 2016), thus mimicking the rate at which the evidence accumulates. This interpretation would also be consistent with the fitting of behavioral data via mathematical models of decision-making, where words are associated with a higher rate of evidence accumulation compared to nonwords (Ratcliff et al., 2004; see also Gomez and Perea, 2014; Yap et al., 2015), at least when these are highly word-like (i.e., pseudowords). However, as discussed below, the picture is more complex.

We also replicated the lexicality effect on chronometric indexes of motor-response execution, with reliably longer MTs for pseudowords

compared to words (Scaltritti et al., 2023).[3] Having observed a propagation of the lexicality effect at what can be considered the start- and the endpoint of the motor-hierarchy, it is thus tempting to map these findings onto the buildup of a decisional variable that progressively and continuously translates cognitive deliberations into an overt behavioral response across action planning, programming, and execution. However, this interpretation is not supported by the other results from the current experiment. First, the LRP, which may translate the more abstract motor goals settled by the lateralization of beta desynchronizations into a motor program (de Jong et al., 2006), was not affected by the lexicality of the stimulus. This sort of differentiation between beta-lateralization and LRP is not new and is taken as evidence of the different functional characterization of motor-related EEG asymmetries in the time-frequency vs in the time domain (e.g., de Jong et al., 2006; Poljac and Yeung, 2014). In the present context, this might further suggest that the propagation of the decisional variable onto motor response implementation seems halted at the higher levels of the motor-hierarchy (see also Scaltritti et al., 2020, discussed below). Caution is however warranted in interpreting the null finding on LRPs. Considering the inflated signal-to-noise ratio introduced by the subtraction of activities from different channels, the temporal smearing induced by averaging procedures, and difficulties in estimating precise temporal features for the LRPs (e.g., Ulrich and Miller, 2001), the likelihood of Type II errors is not negligible. This concern might be mitigated by the results on the lateralized ERPs, as both the contralateral negative potential (signaling activation of the response hand) and the ipsilateral positive one (signaling inhibition of the incorrect response) were both seemingly unaffected by lexicality effects. Also, null lexicality effects on the LRPs and on the lateralized ERPs were replicated when using epochs time-locked to the actual button-press (Supplementary Materials 4), an event that eschews potential distortions caused by noisy estimates of the onset of EMG activity.

We also found no evidence of lexicality effects on measures of corticomuscular coherence. In our working hypothesis, the synchronization between cortical and spinal/muscular activity looked like a promising pathway to instantiate the potentially continuous mapping of stimulus evaluation onto the response channels. Physiologically, corticomuscular coherence in the beta range has been linked with the pooling of spinal motoneurons driven by the motor cortex during isometric muscle contractions (Gross et al., 2000; see also Conway et al., 1995; McAuley et al., 1997), and with the specification of motor parameters (Kilner et al., 2000). Importantly, as mentioned in the Introduction, beta-range corticomuscular coherence has been observed to play a role in response

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[3] The duration of MTs in the current experiment (as well as the one reported in Scaltritti et al., 2023) is longer compared to what observed in other works (e. g., Weindel et al., 2021; Servant et al., 2021). Two elements may possibly account for this difference. The first concerns the different response devices used in our study, i.e., a joypad, as opposed to more traditional hand-held response buttons. The second is possibly related to the difference between tasks, with lexical decision yielding longer RTs, and thus also longer MTs, compared to perceptual decision-making tasks.
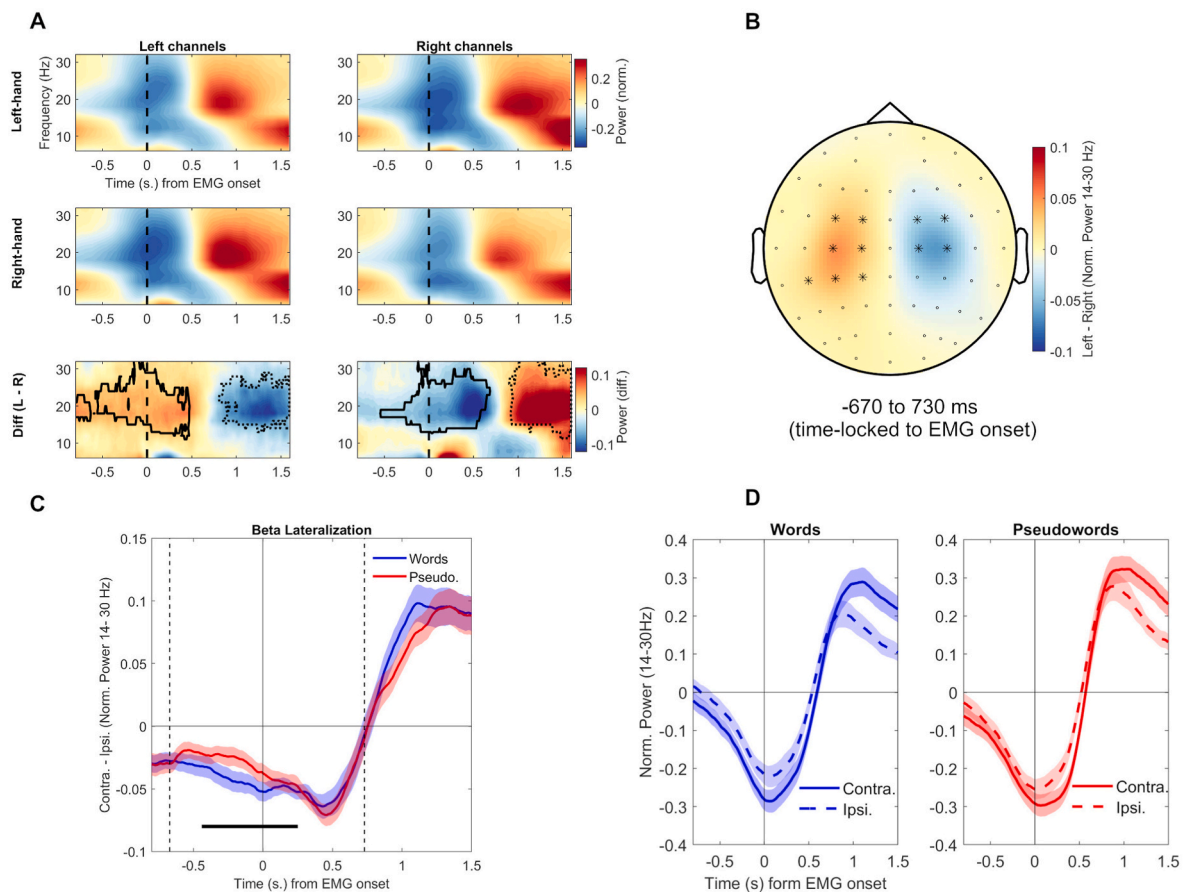
Fig. 2. Functional localizer and beta-power lateralization.

Note. Panel A: power spectra for left (FC3, FC1, C3, C1; first column) and right channels (FC2 FC4, C2, C4; second column), broken down for left-hand (first row) and right-hand (second row) responses, collapsed across lexicality. The third row reports the difference in power between left- and right-hand responses. The continuous lines represent the first positive and negative clusters, whereas dotted lines represent the second positive and negative clusters, highlighting differences at the level of post-movement beta rebound. Panel B: Topography of the first positive and negative clusters and corresponding average time-window. The electrodes marked with * were those involved for more than 70% of the time samples of the clusters (see text for details). Panel C: Time course of the beta lateralization (contralateral – ipsilateral beta power; Pseudo. = pseudoword). Shaded areas represent the standard error of the mean. Vertical dashed lines represent the time-interval included in the statistical assessment, based on information provided by the functional localizer contrast (panels A and B). The horizontal black line highlights the samples involved in the cluster found when comparing words vs pseudowords. Panel D: Lateralized beta activity for channels contralateral (Contra.; continuous lines) and ipsilateral (Ipsi.; dashed lines) to the responding hand. Shaded areas represent the standard error of the mean.
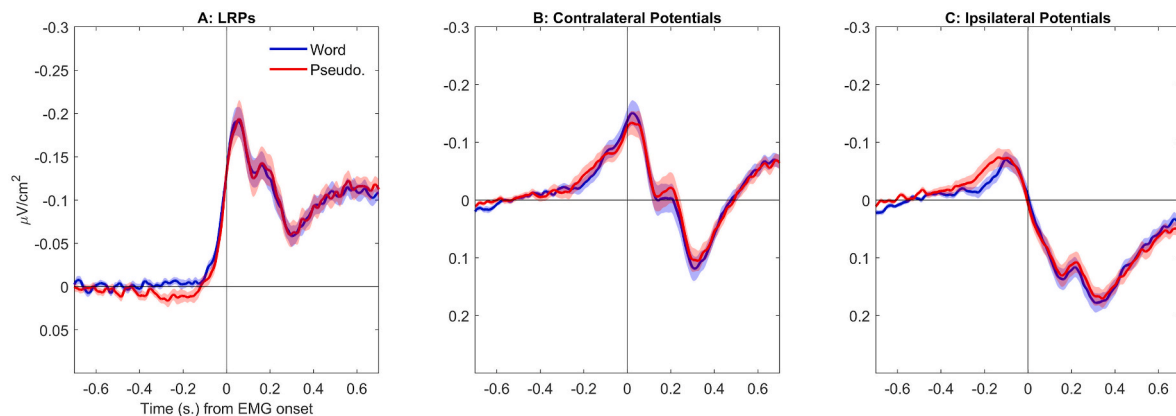

Fig. 3. Lateralized readiness potential (A), contralateral (B), and ipsilateral (C) ERPs.
Note. Shaded areas represent the standard error of the mean. Pseudo. = pseudoword.

competition, with the suppression of incorrect responses mediated by an enhanced coherence ipsilaterally to the effector (van Wijk et al., 2009). Therefore, it seemed reasonable to hypothesize that the long-range

neural interactions highlighted by synchronous oscillatory dynamics could represent the physiological underpinning of long-range decisional-motor interactions at the cognitive and behavioral level. This
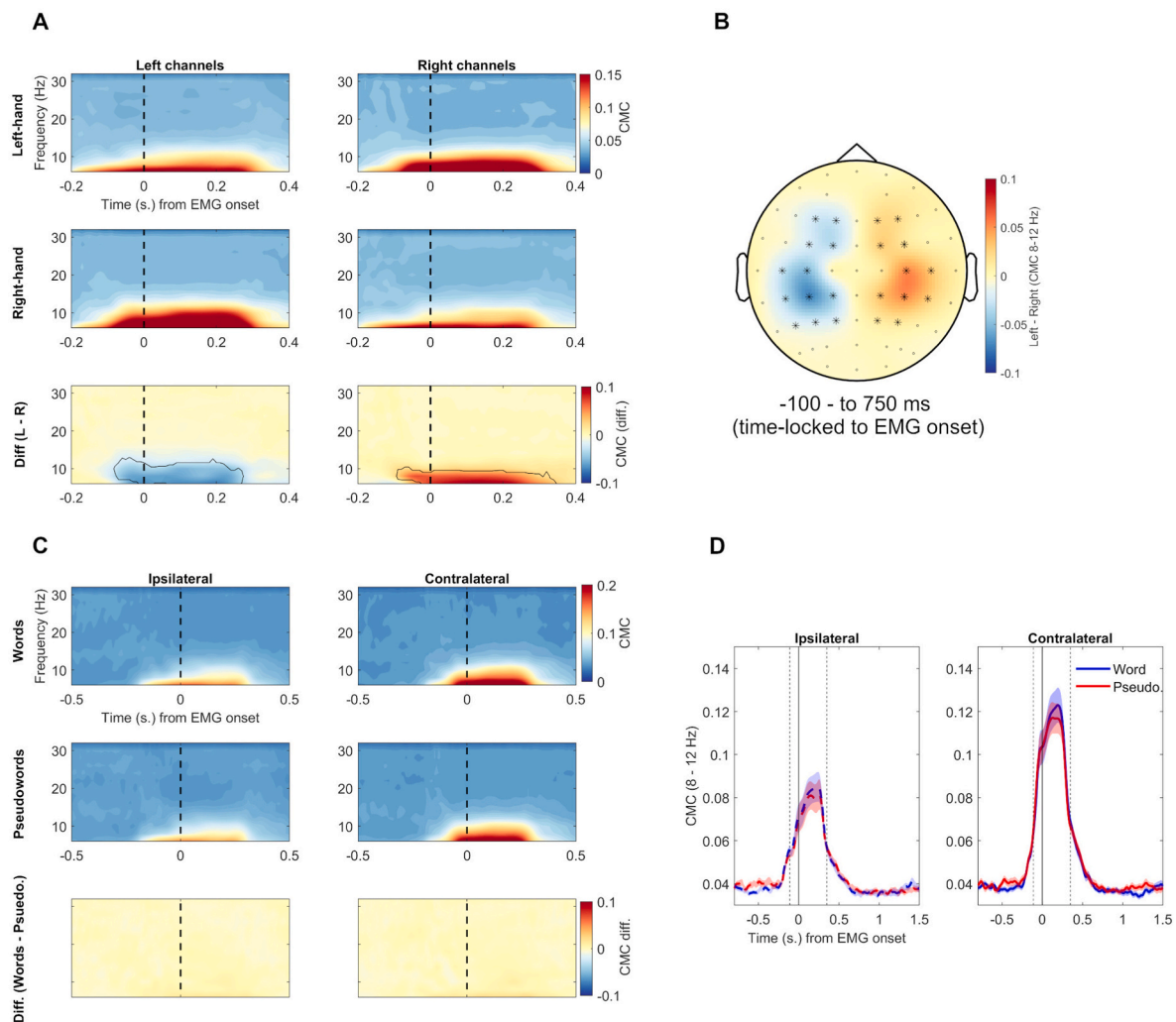
Fig. 4. Corticomuscular coherence.

Note. Panel A: coherence spectra for left (F3, F1, FC3, FC1, C5, C3, CP5, CP3, CP1, P3, P1; first column) and right channels (F2, F4, FC2, FC4, C4, C6, CP2, CP4, CP6, P2, P4; second column), broken down for left-hand (first row) and right-hand (second row) responses, collapsed across lexicality. The third row reports the difference in power between left- and right-hand responses, with the black line capturing the negative and positive clusters. Panel B: Topography of the clusters and corresponding average time-window. The electrodes marked with * were those involved for more than 70% of the time samples of the clusters (see text for details). Panel C: coherence spectra for channels ipsilateral (first column) and contralateral (second column) to the response hand, for words (first row) and pseudowords (second row). The third row reports the difference in coherence between words and pseudowords. Panel D: Time course of the corticomuscular coherence for alpha frequency bins (8–12 Hz) for channels contralateral and ipsilateral to the responding hand (Pseudo. = pseudoword). Shaded areas reflect the standard error of the mean. Vertical dashed lines represent the time-interval included in the statistical assessment, on the basis of information provided by the functional localizer contrast (panels A and B).

hypothesis, however, did not find support in our data.

Admittedly, a few factors warn against any strong interpretation of our results on measures of corticomuscular coherence. First, we are speculating about a null effect. Beyond that, and somewhat unexpectedly, corticomuscular coherence in our experimental setup (featuring fast button-press responses) was bounded within lower ranges of oscillatory frequencies – i.e., it included the alpha/mu rhythm (8–12 Hz), but not the beta range (>14 Hz). Alpha/mu corticomuscular coherence has been previously observed, but more in the context of slow finger movements based on precision (e.g., Gross et al., 2002; see also Hori et al., 2013), which are quite different from the motor responses required in the current experiment. Also, whereas corticomuscular coherence in the beta range has been previously characterized in the context of dynamics of response competition (van Wijk et al., 2009), to the best of our knowledge, such functional characterization has not been advanced for alpha/mu frequencies. It is however worth noticing that the functional localizer contrast used to isolate motor-related

coordinates of corticomuscular coherence displayed both the enhancement of coherence typically found contralaterally to the effector (e.g., Gross et al., 2002), and clear differences between left- and right-hand responses. These results are thus reassuring with respect to the genuine motor connotation of the observed alpha/mu corticomuscular coherence.

In summary, we observed reliable lexicality effects at the highest and the most peripheral levels of the motor-related chain of electrophysiological indexes, but no effects within putatively interim steps. This pattern is hard to reconcile with traditional evidence-accumulation models of decision making, but also with the hypothesis of a continuous transition from decision onto action driven by a single decisional variable percolating all the way through the different motor-steps. Concerning traditional evidence-accumulation models, our findings, together with other ones from perceptual decision-making (e.g., Servant et al., 2021; Weindel et al., 2021), seem to contradict the notion of a serial transition from decisional onto motor stages, given the decisional

effects we observed across different electrophysiological indexes of motor activity. Notably, this assumption of a "thresholded flow of information" between decision and action (Calderon et al., 2018) is shared across a wide range of exemplars within the large family of evidence-accumulation models (e.g., Brown and Heathcote, 2005, 2008; Donkin et al., 2011; Ratcliff et al., 2004, 2016; Usher and McClelland, 2001; Van Zandt et al., 2000), albeit we remain agnostic with respect to which specific instantiation, if any, might more conveniently accommodate a more continuous transition.

For example, recent extension to the classic drift diffusion model (Servant et al., 2021), posit a continuation of evidence accumulation dynamics beyond EMG onset, nicely capturing phenomena such as partial errors and modulations of MTs from decisional dynamics, that are difficult to accommodate within the classic instantiation of the model. Nonetheless, the notion of a single decisional variable continuously accumulating all the way from decisional stages to motor-response execution is problematic as well. If this were the case, the lexicality effect would have been reliably reflected across all the electrophysiological indexes we investigated. This would have supported the idea of a continuous flow of a single decisional component across stages of motor processing, with a reverberation across all the stages of any decisional effect surfacing at the starting point of the motor hierarchy. A more complex pattern is instead suggested not only by the current data, but also when placing the present results in the context of some of our previous findings.

Concerning peripheral measures of motor-response execution, we have previously observed that whereas lexicality effects propagate to the motor component of response latency, this is not the case for word frequency, i.e., the contrast between high-vs low-frequency words (e.g., *house* and *sapphire*), which remains confined within PMTs (Scaltritti et al., 2023). The differentiation between lexicality and word frequency effects on MTs may point towards specific decisional components, related to late control/verification mechanisms (see also Weindel et al., 2021), that are uniquely recruited by pseudowords, i.e., for responses to items with no representation in long-term memory.

This hypothesis is supported by two ancillary phenomena revealed by measures of response accuracy. Pseudowords are in fact more prone to both fast, impulsive errors as well as partial errors (i.e., the covert activation of the incorrect response hand before the correct response is delivered; see Supplementary Materials 1; see also Fernández-López et al., 2022; Scaltritti et al., 2021, 2023). Impulsive errors may trigger the recruitment of additional monitoring and/or control processes (e.g., Ridderinkhof, 2002; van den Wildenberg et al., 2010), and – indeed – the increased likelihood of partial errors for pseudowords points to those same online correction mechanisms working at the level of motor-response execution (Burle et al., 2002) that have been linked to prolonged MTs (e.g., Allain et al., 2004; Weindel et al., 2021). Possibly, these monitoring mechanisms may be linked with second-order decision variables concerned with performance monitoring (Desender et al., 2021). Also, although decision-making models often assume a single decisional process for words and pseudowords alike (e.g., Ratcliff et al., 2004), psycholinguistic research has highlighted the specificities related to pseudoword decisions, that is, concerning the fact that a given stimulus is not part of the repertoire of existing representations (Dufau et al., 2012). Experimental evidence (e.g., Perea et al., 2005) suggests that specific verification processes would perform an additional check for items that fail to activate a representation in long-term memory stores.

The notion of a single decisional variable reverberating on motor processing is also complicated by the results on the index of effector-selective lateralization of beta desynchronizations. In fact, although both lexicality (current experiment) and word frequency (Scaltritti et al., 2020) modulate beta lateralization, they do so in fundamentally different ways. Lexicality, as observed in the current experiment, yields an enhanced lateralization for stimuli allowing for a steeper accumulation of evidence, i.e., for words (Ratcliff et al., 2004). Quite differently, in our previous work (Scaltritti et al., 2020) we observed a *reduced* beta

lateralization for high-compared to low-frequency words, that is, a reduction of effector-selective beta asymmetries for the condition associated with a steeper buildup of the decisional variable (Ratcliff et al., 2004). In Scaltritti et al. (2020), the reduction of beta-lateralization for high-frequency words was driven by an increased ipsilateral beta suppression compared to low-frequency words, and – in line with other authors (e.g., Cheyne et al., 2012; Jurkiewicz et al., 2006) – we tentatively linked this enhanced ipsilateral beta suppression with an inhibitory process preventing erroneous movements of the incorrect effector, which would be magnified for very familiar words. Assuming this interpretation is tenable, it clearly does not drive the lexicality effect.

Possibly, the different manifestations of the lexicality effect across the stages of the motor-hierarchy highlighted in the current work, paired with the differences between lexicality and word frequency effects, both point towards multiple decisional components that modulate different stages of the chain of processes driving the implementation of a decision into an overt behavioral response. Even within the same motor stage, different manipulations may yield different modulations, pointing to further differentiations triggered by unique specificities of the stimuli (words vs pseudowords; high-vs low-frequency words) and of the decisional configuration (lexical decision). It is noteworthy that, in contrast with perceptual decision-making, lexical decision hinges on evidence drawn from memory and provides two fundamentally different response alternatives: words, for which we can retrieve corresponding representations in the lexicon(s), and nonwords, with no pre-existing representations. Decision concerning the latter items, as mentioned above, may rely on additional and specific decisional components that could exert a different and specific impact across layers of the motor-hierarchy, as well as within the same layer. Differences between lexicality and word-frequency effects may thus underlie the difference in terms of the decisional components recruited to respond to the two classes of stimuli.

It must be acknowledged that a better functional specification of the decisional content of motor responses requires a significant amount of additional experimental work. For example, the use of random consonant strings instead of the word-like nonwords (i.e., pseudowords) used here, may actually provide new insights into the decisional dynamics (and their motor components) triggered when stimuli provide more direct and "positive" evidence of their nonword status. This type of stimuli would be expected to eschew the additional verification process that we hypothesize to affect motor-response execution. Further, in lexical decision stimulus lexicality is necessarily associated with the response options. Variants of the semantic classification tasks (e.g., Vergara-Martínez et al., 2011) may instead break this association, for example by asking participants to respond with one hand to stimuli which are exemplars of one category (e.g., animals) and with the other hand to all the other strings (including nonwords), thus allowing a contrast of word and nonword trials within the same response option. Go/no-go variants of the task, instead, would prevent those anticipations errors (Vergara-Martínez et al., 2020; see also Gomez et al., 2007) that may also underlie the fast incorrect responses to nonwords stimuli (Supplementary Materials 1; Scaltritti et al., 2021, 2023), thus mitigating the recruitment of control processes that we putatively associate with prolonged MTs. Finally, other experimental phenomena within the lexical decision configuration (e.g., priming paradigms; see Gomez et al., 2013) may provide interesting cases for tests of selective influence (Weindel et al., 2021) by further elucidating the difference between manipulations that, within the behavioral data fitting provided by evidence accumulation models, selectively affect the decision components vs the putatively nondecision ones.

In summary, higher levels of the motor-hierarchy linked to abstract motor goals are sensitive to stimulus lexicality (current experiment), and to lexical frequency (Scaltritti et al., 2020), although the two effects stem from sharply different dynamics, possibly pointing towards specific decisional components reflected since the onset of motor planning. More peripheral levels might also be influenced by a different set of decisional components, related to response verification and control. Under this

perspective, the reflections of decisional dynamics on motor-response implementation, at least in the context of lexical decision, may highlight different decisional components that are selectively and specifically reflected over different levels of the motor-hierarchy. Thus, other than questioning the traditional functional segregation between decisional and motor stages, the current findings may also prompt a reconsideration of the notion of a single decisional variable continuously mapping stimulus evaluation into motor responses, pointing instead towards different decisional components that are differentially reflected across the stages of the motor control hierarchy. While higher levels corresponding to motor planning might more closely reflect the ongoing dynamics of evidence accumulation, the peripheral stages of motor-response execution may be related with late-occurring verification and control processes.

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Data availability

The link to the data is reported in the article. Scripts are available on request

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2023.108630.

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