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**The neural blending of words and movement: ERP signatures
of semantic and action processes during motor-language coupling**

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Abstract

Behavioral embodied research shows that words evoking limb-specific meanings can affect responses performed with the corresponding body part. However, no study has explored this phenomenon's neural dynamics under implicit processing conditions, let alone by disentangling its conceptual and motoric stages. Here we examined whether the blending of hand actions and manual action verbs (MaVs), relative to non-manual action verbs and non-action verbs, modulates electrophysiological markers of semantic integration (N400) and motor-related cortical potentials (MRCPs) during a lexical decision task. Relative to both other categories, MaVs involved reduced posterior N400 amplitude and greater modulations of frontal MRCPs. Such effects overlapped in a window of ~380-440 ms after word presentation and ~180 ms before response execution, revealing the possible time-span in which both semantic and action-related stages reach maximal convergence. These results allow refining current models of motor-language coupling while affording new insights on embodied dynamics at large.

Keywords: embodied cognition, motor-language coupling, N400, motor-related cortical potentials.

1. Introduction

One leading contribution of the embodied cognition framework (Barsalou, 2008; de Vega, Moreno, & Castillo, 2013; Glenberg & Gallese, 2012; Moguilner et al., 2021; Pulvermüller, 2013a, 2018) is the demonstration that language can variously affect overt behavior (de Vega et al., 2013; García & Ibáñez, 2016a; Glenberg & Gallese, 2012; Kogan, Muñoz, Ibáñez, & García, 2020). In particular, motor-language coupling paradigms show that action verbs can modulate movement-related mechanisms in an effector-specific fashion (García & Ibáñez, 2016b; Kogan et al., 2020). For example, in tasks requiring explicit semantic access, processing of manual action verbs (MaVs), compared to non-manual action verbs (nMaVs) and non-action verbs (nAVs), can facilitate or delay diverse hand actions, such as keyboard typing (García & Ibáñez, 2016b) and object reaching (Dalla Volta, Gianelli, Campione, & Gentilucci, 2009). Yet, little is known about the neural dynamics underlying such limb-selective interactions and no study has explored their emergence under implicit processing conditions –let alone by considering time-locked signatures of its conceptual and motoric sub-processes. To bridge this gap, we assessed whether the blending of hand actions and MaVs, relative to nMaVs and nAVs, can modulate electrophysiological markers of semantic integration and motor preparation in a shallow processing task, while examining the temporal overlap of both sub-processes.

Motor-language coupling is a bidirectional phenomenon whereby action-language processes affect motor dynamics, and vice versa (Afonso et al., 2019; Aravena et al., 2010; Ibáñez et al., 2013; Melloni et al., 2015). Behavioral experiments show that MaVs can increase grip-force in both unimanual and bimanual tasks (Da Silva, Labrecque, Caromano, Higgins, & Frak, 2018; Frak, Nazir, Goyette, Cohen, & Jeannerod, 2010; Nazir et al., 2017), while neuroimaging studies show that these verbs differentially increase activation along partly somatotopic (hand-specific) cortical motor regions (Pulvermüller, 2013a, 2018). Yet, only limited research has examined the neurofunctional unfolding of motor-language coupling, mainly using overtly semantic tasks. In particular, manual responses to MaVs have been linked to early engagement of

motor and premotor regions (Klepp, Niccolai, Buccino, Schnitzler, & Biermann-Ruben, 2015; Mollo, Pulvermüller, & Hauk, 2016; Pulvermüller, Härle, & Hummel, 2001), fast modulation of motor evoked potentials (Buccino et al., 2005; Gianelli & Dalla Volta, 2015; Papeo, Vallesi, Isaja, & Rumiati, 2009), and reduced synchronization of movement-sensitive beta oscillations (Klepp et al., 2015). Moreover, during explicit semantic access, this functional synergy is typified by canonical neural signatures of both semantic integration (Aravena et al., 2010; Ibáñez et al., 2013) and action initiation (Aravena et al., 2010; Ibáñez et al., 2013; Melloni et al., 2015), irrespective of task accomplishment (Dalla Volta, Avanzini, De Marco, Gentilucci, & Fabbri-Destro, 2018). Thus, the dynamic neural signatures of motor-language coupling are fairly well-established for tasks that *overtly* direct attention to word meanings.

However, this empirical corpus faces two critical shortcomings. First, none of these studies examined whether such effects also emerge under shallow-processing conditions, thus overlooking a key requisite to reveal primary embodied effects (García et al., 2019; Hauk, Johnsrude, & Pulvermüller, 2004; Kiefer, Sim, Herrnberger, Grothe, & Hoenig, 2008; Mollo et al., 2016). Second, relevant EEG research (Aravena et al., 2010; Dalla Volta et al., 2018; Ibáñez et al., 2013; Melloni et al., 2015) has failed to assess whether canonical markers of semantic integration and action planning during effector-specific (e.g., manual) movements are differentially sensitive to effector-congruent meanings (e.g., by contrasting MaVs with nMaVs). Promisingly, these shortcomings can be overcome by comparing how *implicit* semantic processing of different action-verb types during motor-language coupling modulates functionally critical ERPs, such as the N400 and motor-related cortical potentials (MRCPs).

The N400 is a negative deflection peaking at approximately 400 ms after word presentation, with a centro-parietal scalp distribution (Lau, Phillips, & Poeppel, 2008). N400 modulations are a gold-standard signature of conceptual integration demands during processing of sentences, paired words, or even single words (Kutas & Federmeier, 2000, 2011; Lau et al., 2008). For their part, MRCPs comprise two primary (pre-movement) components (Castro, Díaz, & van Boxtel, 2005; Deecke, Scheid, & Kornhuber, 1969; Kutas & Donchin, 1980) which are typically maximal in central/fronto-central sites (Nguyen, Breakspear, & Cunningham, 2014; Smith & Staines, 2006) with sources in sensorimotor regions (Shibasaki & Hallett, 2006; Toma et al., 2002; Yazawa et al., 2000), namely: the readiness potential (RP), a slow-rising negativity that precedes movement onset by 100-400 ms in forced-choice tasks (Haggard, 2008; Kutas & Donchin, 1980; Travers, Khalighinejad, Schurger, & Haggard, 2020); and the motor potential (MP), a subsequent sharply negative peak occurring immediately before (-100 to -10 ms) the response (Deecke et al., 1969; Shibasaki & Hallett, 2006). Both these components are canonical indexes of increased sensorimotor cortical excitability during motor preparation (Deecke et al., 1969; Shibasaki & Hallett, 2006; Toma et al., 2002; Yazawa et al., 2000). Importantly, reduced N400 amplitude (Aravena et al., 2010; Ibáñez et al., 2013) and increased MRCP modulations (Aravena et al., 2010; Ibáñez et al., 2013; Melloni et al., 2015) have been shown to index compatibility between MaVs and (compatible) manual responses during explicit semantic tasks. Therefore, these ERPs emerge as suitable candidates to track movement-related and conceptual dimensions of *implicit* motor-language coupling.

Against this background, we employed high-density electroencephalography (HD-EEG) to identify core neural signatures of semantic and motoric dynamics during motor-language coupling under implicit semantic processing conditions. We designed a lexical decision task requiring manual responses to MaVs, nMaVs, and nAVs. Building on previous findings (Aravena et al., 2010; Ibáñez et al., 2013), we predicted that MaVs would involve reduced N400 modulations relative to response-incongruent verb types (nMaVs and nAVs). Moreover, considering relevant evidence (Aravena et al., 2010; Ibáñez et al., 2013; Melloni et al., 2015), we predicted that MaVs would enhance the amplitude of MRCPs during manual response preparation. Also, to ascertain the period of maximal semantic-motoric integration, we aimed to identify the temporal overlap between effector-specific modulations in both ERPs. Additionally, based on emergent results in the motor-language coupling literature (Klepp et al., 2015), we performed an exploratory analysis of stimulus- and response-locked time-frequency modulations over the beta band. Briefly, with this novel approach, the present work seeks to illuminate the functional underpinnings of semantic and action dimensions in implicit motor-language coupling.

2. Methods

2.1. Participants

The study comprised 22 participants (13 female), a sample size that reaches a power of .93 (Supplementary data A). All subjects were adult native Spanish speakers who were enrolled in or had completed higher education programs. The sample had a mean age of 25.9 ($SD = 4.7$) and an average of 17.1 years of education ($SD = 3.5$). All but two participants were exclusively right-handed. None of the subjects reported a history of neuropsychiatric diseases or substance abuse and all had normal or corrected-to-normal vision. Each participant read and signed an informed consent form before entering the study. All experiments and procedures were performed in accordance with relevant guidelines and regulations of the Declaration of Helsinki. The study's protocols were approved by the institutional ethics committee.

2.2. Stimuli

This study used 75 verbal stimuli belonging to four categories. Sixty items were real Spanish words, including 20 MaVs, denoting actions performed with the hands (e.g., *cut* [*cortar*]); 20 nMaVs, denoting actions performed with body parts other than the hands (e.g., *walk* [*caminar*]); and 20 nAVs, denoting cognitive or affective processes which do not involve bodily motion (e.g., *improve* [*mejorar*]). All these items appeared in infinitive form (most of them ending in *-ar*), which forced their interpretation as verbs. Finally, the task included 15 pseudoverbs (PsVs). These were created by choosing five real words from each list and replacing only one letter such that the resulting letter string, though phonotactically and graphotactically legal, did not represent a Spanish word (e.g., *coltar*, *capinar*, *meborar*).

Psycholinguistic data for all stimuli were extracted from B-Pal (Davis & Perea, 2005), except for age-of-acquisition data, which were taken from a survey used in previous motor-language coupling research (García & Ibáñez, 2016b; Kogan et al., 2020). One-

way ANOVA tests showed that all categories were similar in log frequency [$F(2, 57) = .39, p = .68$], familiarity [$F(2, 57) = .21, p = .82$], orthographic length [$F(2, 57) = .58, p = .56$], imageability [$F(2, 57) = 1.2823, p = .28$], and age of acquisition [$F(2, 57) = 1.01, p = .37$]. As in previous motor-language coupling experiments, all items had four to eight letters; this guaranteed that all of them could be visualized in a single fixation, so that the time needed for their recognition would remain constant across categories (Lavidor & Ellis, 2002; Weekes, 1997). As expected, an additional test revealed significant differences in concreteness [$F(2, 57) = 18.974, p < .001$] among categories. A post hoc analysis (Tukey's HSD test, $MSe = .30156, df = 57$) corroborated that nAVs were less concrete than both MaVs ($p < .001$) and nMaVs ($p < .001$), as expected; crucially, however, no significant differences were observed between the latter two categories ($p = .36$). For the full stimulus list (including approximate English translations), see Supplementary data B.

2.3. Procedure

Participants were tested individually in a dimly illuminated room. They sat comfortably at a desk, facing a laptop equipped with a 15.6 16:9 HD (1366 x 768) LED backlight. As the HD-EEG electrodes were being placed on their scalps, they received oral instructions on the lexical decision task (instructions were then recapped on-screen before the start of the experiment).

The task comprised three blocks of 75 trials. Each trial consisted in the presentation of a single stimulus belonging to one of the four categories (MaVs, nMaVs, nAVs or PsVs). As in previous studies (García et al., 2019), PsVs were irrelevant for brain-signal analyses but they served to ensure task compliance and attentional engagement by forcing linguistic decisional processes item after item. Each block included the same stimuli but in different pseudorandomized sequences (no more than three stimuli from the same category appeared in succession, and real words linked by meaning or form were separated by at least three trials). As in previous research (García et al., 2020), this allowed maximizing signal-to-noise ratio while retaining a strict control of psycholinguistic variables across conditions. Participants had to decide, as fast and accurately as possible, whether the string constituted a real Spanish word or not by pressing the left arrow with the index finger or the right arrow with the middle finger of their right hand, respectively.

Each trial began with a fixation cross shown for a random period between 700 and 1000 ms at the center of the screen. Immediately afterwards, the target item (verb or pseudoverb) was shown until response and for a maximum of 2300 ms, with responses being allowed after the first 300 ms. A new trial was triggered upon the participant's button press or if the trial's overall duration elapsed without a response (Figure 1A). The use of a random period for the fixation cross minimized the chances of responses being driven by rhythmic motor habituation, with no biases for any lexical category. The fixation cross and the targets (font: Microsoft Sans Serif; color: white; size: 48; style: regular) were presented at the center of the screen against a black background. A custom-made script written in Matlab's Psychtoolbox was used to run the task and record behavioral responses (see below for details about simultaneous HD-EEG data acquisition). Before the actual task, ten practice trials were presented with stimuli not

included in the experimental blocks. The complete session for each participant lasted roughly 30 min.

2.4. Behavioral data analysis

Accuracy and response time (RT) data were analyzed via a linear mixed model, with ‘category’ as a fixed factor and ‘subject’ as a random factor. As in previous EEG studies on action-verb processing (Mollo et al., 2016; Pulvermüller et al., 2001), trials with RTs falling 2 *SDs* away from each subject’s mean were considered outliers and removed from analysis. All analyses were performed on Matlab (R2015a) software.

2.5. HD-EEG data acquisition and processing

HD-EEG data were acquired with a Biosemi Active-two 128-channel system at 2048 Hz, resampled offline at 256 Hz. The EEG-Lab (13.4.4b) toolbox (Delorme & Makeig, 2004) was used for offline processing and analysis. Three participants were excluded from analysis due to data acquisition problems. For all remaining subjects, data were band-pass filtered during recording (0.1-100 Hz) and offline (0.5-40 Hz) to remove undesired frequency components. The latter cutoff (40 Hz) was based on gold-standard recommendations to maximize data quality and temporal precision (Cohen, 2014), and to favor comparability with ERP studies on motor responses (Fabi & Leuthold, 2017; Gentili et al., 2018; Kadosh et al., 2007), action-verb processing (Casado et al., 2018; Sokoliuk, Calzolari, & Cruse, 2019), and other embodied language categories (Daly et al., 2019; García et al., 2020; Gentsch, Sel, Marshall, & Schütz-Bosbach, 2019).

References for N400 and MRCP analyses were selected based on gold-standard recommendations (Luck, 2014) to maximize comparability with key studies in the field. N400 analyses were referenced to link mastoids and then re-referenced offline to the average of all electrodes, as done in previous studies on motor-language coupling (Aravena et al., 2010) and semantic effects at large (Kutas & Donchin, 1980; Lim et al., 2009). Also, given the posterior topography of canonical N400 modulations (Kutas & Federmeier, 2011) and the location of our ROIs, especially in a dense-array setting like ours, this procedure guarantees a reference-independent estimation of scalp voltage for this ERP (Nunez & Srinivasan, 2006). Instead, signals for MRCP analyses were referenced to link mastoids, a common choice across embodied cognition studies targeting MRCPs and other response-locked ERPs (Aravena et al., 2010; Falkenstein, Hoormann, & Hohnsbein, 1999; Guan, Meng, Yao, & Glenberg, 2013; Melloni et al., 2015; Santana & de Vega, 2013; Senderecka, Grabowska, Szewczyk, Gerc, & Chmylak, 2012; Smith & Staines, 2006; Wang et al., 2019), including those which also tap on N400 effects by common average reference (Aravena et al., 2010). Importantly, mastoid reference also meets other gold-standard requisites (Luck, 2014) for MRCP analyses, as they offer a low electrical activity site away from the frontal ROIs capturing maximal effects (Nguyen et al., 2014; Smith & Staines, 2006) while avoiding hemispheric bias and reducing noise (e.g., Kutas & Donchin, 1980; Nguyen & Cunnington, 2014). All subsequent processing steps were identical for both components.

In line with reported procedures (Dottori et al., 2020; Fittipaldi et al., 2020; García et al., 2020; Salamone et al., 2018; Vilas et al., 2019), eye movements or blink artifacts were corrected with independent component analysis, and remaining artifacts were

rejected offline from trials that contained voltage fluctuations exceeding $\pm 200 \mu\text{V}$. Bad channels were identified via visual inspection by two experts (SC and AP) following the exact same approach used by our team in previous EEG studies on semantic and motoric processes (Aravena et al., 2010; Dottori et al., 2017, 2020; García-Cordero et al., 2016; Ibáñez et al., 2010, 2013; Melloni et al., 2015; Vilas et al., 2019; Yoris et al., 2017). Once identified, such channels were replaced with statistically weighted spherical interpolation (based on all sensors) and then the variance of the signal across trials was calculated to guarantee stability of the averaged waveform (Courellis, Iversen, Poizner, & Cauwenberghs, 2016). **HD-EEG** data were then segmented offline into 1.5 s epochs extending from 500 ms pre-stimulus to 1000 ms post-stimulus for stimulus-locked segments in N400 analyses (where time zero corresponds to stimulus onset) and for hand response-locked segments in MRCP analyses (where time zero corresponds to motor response execution). The epochs were baseline-corrected, using a baseline of -300 ms to 0 ms for the N400 component and -600 ms to -300 ms for motor responses. Noisy epochs were rejected from the analysis using a visual inspection procedure as in previous studies (García-Cordero et al., 2016).

2.6. ERP data analysis

Analyses of N400 and MRCP modulations were performed considering only correct trials. As regards N400 analysis, upon removal of incorrect or artifactual trials, the number of remaining epochs averaged across subjects was 47.4 (78.9%) for MaVs, 47 (78.3%) for nMaVs, and 49.6 (82.6%) for nAVs [$F(2, 54) = .74, p = .48$]. Also, after removal of incorrect trials and faulty segments, the number of MRCP-related epochs, averaged across subjects, was 51.6 (86%) for MaVs, 52.3 (87.2%) for nMaVs, 53.5 (89.1%) for nAVs, and 35.5 (78.9%) for PsVs. The number of epochs analyzed did not differ significantly between categories [$F(2, 54) = 1.06, p = .35$].

N400 analyses were conducted over three canonical six-electrode ROIs, as reported in previous studies (Lim et al., 2009; Manfredi, Cohn, & Kutas, 2017; Schmidt-Snoek, Drew, Barile, & Agauas, 2015; Wu & Coulson, 2005), namely: a centro-posterior ROI (channels A2, A3, A4, A19, D16, and B2); a left posterior ROI (channels A5, A6, A7, D16, D17, and D28); and a right posterior ROI (channels A32, B3, B4, B16, B18, and B19) –Figure 2. Of note, these regions have proven sensitive to various semantic manipulations in action-language research –e.g., expectancy or congruency between words, gestures, symbols and images (Ibáñez et al., 2010; Lau et al., 2008). As regards MRCPs, given their typical markedly frontal distribution (Nguyen et al., 2014), these were examined in two symmetrical frontal regions of interest (ROIs), comprised of six electrodes each: a right frontal ROI (channels C4, C9, C10, C12, C13, and C14) and a left frontal ROI (channels D4, C25, C26, C27, C31, and C32) –Figure 3.

Point-by-point comparisons along the whole ERP signal were made via Monte Carlo permutation tests combined with bootstrapping, as done in previous works (Salamone et al., 2018; Yoris et al., 2017, 2018). This method circumvents the multiple comparisons problem and does not depend on multiple comparison corrections or Gaussian distribution assumptions (Nichols & Holmes, 2002). In addition, it avoids the selection of narrow a-priori windows for analysis, preventing circularity biases. The number of randomly simulations partitioning the data (permutations) was set to 5000. A *p*-value was thus obtained for each distance, but only those below .05 were considered

significant. Then, a minimum extension of ten consecutive points was used as the criterion to capture reliably significant effects (Mueller, Swainson, & Jackson, 2009). In line with standard practice for permutation test results in ERP research, results of significant windows are presented by reporting the limits of the corresponding time interval, the mean difference between condition, the associated p -value, and the effect size.

2.7. Exploratory time-frequency analysis

In light of emerging research (Klepp et al., 2015), we explored stimulus- and response-locked oscillatory modulations in the beta band (12-30 Hz) within the same ROIs used for N400 and MRCP analyses, respectively. In line with this antecedent, we computed the time-frequency representation (TFR) on the targeted spectral power by convolving four-cycle complex Morlet wavelets with steps of 2 Hz for each single-trial epoch. Each stimulus-locked epoch ranged from -500 to 950, while response-locked epochs ranged from -600 to 950 ms. A baseline subtraction was performed in every time point, and the ensuing difference was divided by the mean power of the baseline (set to -500 to -200 for stimulus-locked analyses and -600 to -300 ms for response-locked analyses). The single-trial TFRs were averaged for each condition (MaVs, nMaVs, nAVs). The averaged TFRs were compared between each condition pair through a random pairwise permutation test across time over the same ROIs used for ERP analyses. The statistical significance threshold was set to $p = .05$.

3. Results

3.1. Behavioral results

Accuracy outcomes were high across all categories (MaVs = 96.9%, nMaVs = 97.1%, nAVs = 97.5%, PsVs = 87.3%). Statistical analysis revealed a main effect of category. PsVs ($\beta = 87.34$, $SE = 1.13$, $df = 66.39$) elicited more errors than all real-word categories (MaVs: $\beta = 9.52$, $SE = 1.34$, $df = 63$; nMaVs: $\beta = 9.74$, $SE = 1.34$, $df = 63$; nAVs: $\beta = 10.12$, $SE = 1.34$, $df = 63$; all p -values $< .001$), showing a canonical lexicality effect. However, there was no significant difference among the three categories of real verbs (all p -values $> .90$) –Figure 1B.

After removing outliers for RT analyses, the mean of remaining trials across subjects was 19.4 (96%) for MaVs, 19 (94.6%) for nMaVs, 19 (95%) for nAVs, and 14.1 (96.1%) for PsVs. No trials were lost due to recording issues. RT results also revealed a main effect of category. PsVs (mean = 760 ms, $\beta = .75$, $SE = .02$, $df = 66.39$) yielded slower responses than all real-word categories (MaVs: mean = 632 ms, $\beta = -.13$, $SE = .008$, $df = 63$; nMaVs: mean = 617 ms, $\beta = -.14$, $SE = .008$, $df = 63$; nAVs: mean = 626 ms, $\beta = -.13$, $SE = .008$, $df = 63$; all p -values $< .001$), again showing a canonical lexicality effect. However, mean RTs did not differ between the real-verb categories (all p -values $> .30$) –Figure 1C.

[INSERT FIGURE 1 HERE]

3.2. N400 results

Permutation analyses showed that N400 amplitudes were smaller for MaVs than nAVs in the right posterior ROI (from 328.1 to 410.2 ms, $M_{diff} = 0.34$, $p < .05$, $d = 2.08$) and in the centro-posterior ROI (from 347.6 to 437.5 ms, $M_{diff} = 0.39$, $p < .05$, $d = .79$). MaVs also elicited significantly smaller N400 amplitudes than nMaVs in a left posterior ROI (from 383.7 to 437.9 ms, $M_{diff} = 0.34$, $p < .05$, $d = .99$). Significant differences between nMaVs and nAVs were found only in the right posterior ROI (from 347.7 to 418 ms, $M_{diff} = 0.35$, $p < .05$, $d = 1.68$). For details, see Figure 2.

[INSERT FIGURE 2 HERE]

3.3. MRCP results

As revealed by permutation analyses, MaVs elicited significantly more negative amplitudes than nAVs over the left frontal ROI (from -232.8 to 17.2 ms, $M_{diff} = 1.18$, $p < .05$, $d = 1.10$), and over the right frontal ROI (from -248.4 to 71.9 ms, $M_{diff} = 1.23$, $p < .05$, $d = .86$). Furthermore, MaVs elicited greater negative modulations than nMaVs prior to the onset of motor action, in both the left (from -252.3 to -139.1 ms, $M_{diff} = 1.16$, $p < .05$, $d = 3.59$; and from -123.4 to -84.4 ms, $M_{diff} = .83$, $p < .05$, $d = 1.82$) and the right (from -236.7 to -135.2 ms, $M_{diff} = 1.35$, $p < .05$, $d = 5.52$; and from -123.4 to -84.4 ms, $M_{diff} = .84$, $p < .05$, $d = 1.71$) frontal ROIs. Differences between nMaVs and nAVs were solely observed over the right frontal ROI (from -84.4 to 5.5 ms, $M_{diff} = .95$, $p < .05$, $d = 5.21$; and from 25.0 to 75.8 ms, $M_{diff} = .97$, $p < .05$, $d = 1.17$). For details, see Figure 3. Of note, similar results were obtained using a more distant baseline (Supplementary data C). In addition, a complementary exploratory analysis indicated that our results were not reference-dependent (Supplementary data D).

[INSERT FIGURE 3 HERE]

3.4. Exploratory time-frequency results

Exploratory time-frequency analyses over the beta band revealed significant effects ($p < .05$) over specific time segments. For stimulus-locked analyses, significant differences between MaVs and nAVs were observed only in the left posterior ROI, from 50 to 90 ms. The contrast between MaVs and nMaVs yielded significant differences only in the centro-posterior ROI (from 680 to 770 ms). Finally, differential modulations between nMaVs and nAVs were observed in both the centro-posterior (80-750 ms) and the right posterior (120-760 ms) ROIs. For response-locked analyses, MaVs and nAVs yielded significantly different modulations over the left frontal ROI (in segments between -260 and 110 ms) and in the right frontal ROI (between -270 and 100 ms). Differences between MaVs and nMaVs reached significance over the left frontal ROI (in time segments comprised between -270 and 0 ms) and over the right frontal ROI (between -

270 and 120 ms). Finally, differences between nMaVs and nAVs reached significance in the left-frontal ROI (across successive time segments between -190 and 150 ms) and in the right frontal ROI (between -200 and 120 ms). For details, see Figures S3 and S4 and their legends in Supplementary data E.

4. Discussion

This study examined neural signatures of semantic and motoric dynamics during motor-language coupling in a shallow processing task. Relative to both nAVs and nMaVs, MaVs involved (a) reduced posterior N400 effects locked to stimulus onset and (b) greater modulations of frontal MRCPs locked to response execution. Moreover, only the former ERP discriminated between nMaVs and nAVs. Suggestively, effector-specific modulations for both components overlapped in a window of ~380-440 ms after word presentation and ~180 ms before response execution. Such results provide new insights to understand the neural co-determinations of lexical and motoric processes, as discussed below.

4.1. N400 modulations: semantic dynamics during motor-language coupling

N400 results revealed two informative patterns. First, Both MaVs and nMaVs elicited smaller N400 amplitude than nAVs. This resembles previous research (Dalla Volta, Fabbri-Destro, Gentilucci, & Avanzini, 2014) showing that ERP modulations for MaVs and nMaVs differed from those of nAVs in windows from roughly 220 to 400 ms. Given that N400 amplitude indexes semantic integration of linguistic material with active contextual signals (Lau et al., 2008), even during lexical access (Penolazzi, Hauk, & Pulvermüller, 2007), increased modulations for nAVs than for both action-verb categories probably signals the former's greater incongruity with an ongoing physical response. In fact, as amply shown by speech/co-speech gesture paradigms, N400 amplitude is greater for incongruent than congruent pairings of word meaning and manual movement (Cornejo et al., 2009; Holle & Gunter, 2007; Ibáñez et al., 2010, 2012, 2013; Kelly, Creigh, & Bartolotti, 2010; Kelly, Kravitz, & Hopkins, 2004; Kelly, Ward, Creigh, & Bartolotti, 2007; Özyürek, Willems, Kita, & Hagoort, 2007; Wu & Coulson, 2005) –for a review, see Amoruso et al. (2013).

More particularly, the N400 modulations yielded by MaVs were smaller than those of nMaVs. Comparable effects were reported in manual-response tasks showing enhanced beta suppression for MaVs relative to nMaVs (foot verbs) around 350 and 750 ms (Klepp et al., 2015) –although the effect may also occur in later time windows (Klepp, Van Dijk, Niccolai, Schnitzler, & Biermann-Ruben, 2019). Also, mismatch negativity effects around ~300 ms can be modulated over frontocentral electrodes when a preceding action sound (e.g., footsteps) is incompatible with an effector-specific action word (e.g., *kiss*) (Grisoni, Dreyer, & Pulvermüller, 2016). This suggests that, during motor-language coupling, N400 modulations are not only sensitive to general motor resonance, but also to effector-specific dynamics.

This interpretation fits with evidence that N400 modulations capture compatibility between the hand positions evoked by words and those used for ongoing actions (Aravena et al., 2010; Ibáñez et al., 2013), and with hemodynamic (Assmus, Giessing,

Weiss, & Fink, 2007; Buxbaum, Kyle, Tang, & Detre, 2006; Hamzei et al., 2003; Kemmerer, Castillo, Talavage, Patterson, & Wiley, 2008) and electromagnetic (Mollo et al., 2016; Pulvermüller, Shtyrov, & Ilmoniemi, 2005) studies showing that motor-language coupling is indexed by modulation changes in different hubs of core semantic networks (e.g., posterior superior temporal cortex). In line with these antecedents, our results suggest that semantic components of motor-language coupling are sensitive to fine-grained (limb-specific) features, and not just to coarse (limb-neutral) integrations of movement and meaning (Pulvermüller, 2013a, 2013b).

4.2. MRCP modulations: action dynamics during motor-language coupling

MRCP results also revealed two key patterns. First, compared to nAVs, MaVs yielded greater frontal modulations since 250 ms before until 75 ms after response execution, with nMaVs yielding similar effects in the latter part of that segment (from -85 until 75 ms). This extended pattern encompasses two critical ERPs, namely: the RP and the MP (Haggard, 2008; H. Shibasaki, Barrett, Halliday, & Halliday, 1980) –even extending onto post-movement MRCPs (Deecke et al., 1969; Shibasaki & Hallett, 2006). Crucially, modulation of these components indexes heightened motor-system recruitment not only during action preparation and execution (Siemionow, Yue, Ranganathan, Liu, & Sahgal, 2000) respectively, but also during relevant higher-order processes, such as action imagery (Moran, Campbell, Holmes, & MacIntyre, 2012; Niazi et al., 2011; Sharma, Pomeroy, & Baron, 2006) and observation (Bozzacchi, Spinelli, Pitzalis, Giusti, & Di Russo, 2015). More particularly, RP amplitude discriminates between nAVs and diverse (mouth-, leg, and hand-related) action verbs, with additional modulations for each category around the MP window (Dalla Volta et al., 2018). In line with this evidence, our results suggest that verbs which evoke bodily motion, relative to those that do not, prime successive action-related cortical mechanisms.

Yet, when compared with nMaVs, MaVs elicited a greater negative deflection only between -250 and -85 ms, thus being mainly restricted to the canonical window of the RP (Haggard, 2008; Libet, Wright, & Gleason, 1993). Interestingly, previous motor-language coupling studies assessing response-locked activity (Aravena et al., 2010; Ibáñez et al., 2013; Melloni et al., 2015) reported MP effects without RP modulations. However, since these studies compared different subtypes of MaVs (denoting open and closed manual actions) following congruent hand shapes (i.e., open or closed), they were blind to the integration of same- and different-effector information. Accordingly, our findings suggest that RP modulations during motor-language coupling are particularly sensitive to *effector-specific effects*. In other words, this ERP seems to index the match between the limb implied by a verb and the one set in motion –a synergy that is also captured in hemodynamic (Assmus et al., 2007; Buxbaum et al., 2006; Hamzei et al., 2003; Kemmerer et al., 2008) and electromagnetic (Mollo et al., 2016; Pulvermüller et al., 2005) dimensions.

It is worth noting that such effector specificity was traced by the RP, as opposed to the MP. Unfortunately, the only previous EEG study on response-locked modulations during processing of mouth-, leg-, and hand-related action verbs did not compare among these categories, as it exclusively contrasted them with nAVs (Dalla Volta et al., 2018). Still, this dissociation between MRCPs does echo previous findings. Indeed, the

RP has proven sensitive to action dynamics that escape the MP and other MRCs, such as the contrast between executed and non-executed movements (Castro et al., 2005). Compatibly, then, our results indicate that MRCs would have a graded sensitivity in the unfolding of motor-language coupling, with the RP capturing both coarse-grained (general motor resonance) and fine-grained (effector-specific) embodied dynamics, and the MP tracking only the former effects. Note, incidentally, that this pattern was corroborated even when considering a much longer window (see Supplementary data C).

4.3. Theoretical implications

The results above have a number of theoretical implications. First, they indicate that both the semantic and action dimensions of motor-language coupling are typified by effector-sensitive neural modulations. In other words, both the conceptual integration and movement-related stages of the phenomenon are influenced by fine-grained (limb-specific) features of the word's meaning and the to-be-executed action. Note that previous studies have reached similar conclusions by comparing different categories action verbs relative to nAVs (but not with each other) in manual-response tasks (Dalla Volta et al., 2018) or by examining compatibility effects between subsets of MaVs and different hand responses (Aravena et al., 2010; Ibáñez et al., 2013; Melloni et al., 2015). Therefore, all this previous evidence proves blind to limb-specific effects. Conversely, in line with recent works (Klepp et al., 2015; Klepp et al., 2019), our study indicates that motor-language coupling is characterized not only by gross motor resonance and effector-position effects, but also to the overlap between the body part denoted by the verbal material and the one used to perform an action.

Also, to our knowledge, our study is the first to dissociate specific MRCs underlying these two embodied phenomena. General motor resonance effects seem to cut across the RP (Haggard, 2008; Marta Kutas & Donchin, 1980; Travers et al., 2020) and the MP (Deecke et al., 1969; Shibasaki & Hallett, 2006), suggesting that coarse-grained embodied dynamics extend from distal stages of motor preparation until motor execution proper. Conversely, effector-specific effects were indexed only by the RP, indicating that fine-grained embodied dynamics are shorter-lived and vanish as motor execution becomes imminent. This suggests that semantic specificity might influence which motor-processing stages are engaged in motor-language coupling, opening new avenues for research.

Such findings allow extending the Hand-Action-Network Dynamic Language Embodiment (HANDLE) model (García & Ibáñez, 2016a), the most systematic account of motor-language coupling phenomena to date. Succinctly, this framework posits that ongoing manual action processes can be modulated in predictable ways if accompanied by verbal materials evoking hand-specific meanings. In particular, the model posits that the temporal lag between word onset and action execution can determine whether the latter will be facilitated (Afonso et al., 2019; Kelly et al., 2010; Lindemann, Stenneken, Van Schie, & Bekkering, 2006; Masson, Bub, & Warren, 2008; Springer & Prinz, 2010; Tucker & Ellis, 2004) or delayed (Bergen, Lau, Narayan, Stojanovic, & Wheeler, 2010; García & Ibáñez, 2016b; Mirabella, Iaconelli, Spadacenta, Federico, & Gallese, 2012; Sato, Mengarelli, Riggio, Gallese, & Buccino, 2008; Spadacenta, Gallese, Fragola, & Mirabella, 2014). However, the model is exclusively rooted in behavioral evidence, and

it fails to disentangle the time course of motoric and semantic dynamics underlying its target phenomenon. In this sense, HANDLE can be refined by incorporating core findings of our study: effector-specific motor-language coupling modulates electrophysiological signatures of *both* action-related and semantic integration processes, and these feature their own, partially overlapping, temporal and functional dynamics (Figure 4).

[INSERT FIGURE 4 HERE]

Based on present results, the diagram in Figure 4 maps the temporal span in which semantic and motoric processes coalesce during motor-language coupling. First, effector-specific N400 modulations, signaling semantic integration, were observed ~380-440 ms after stimulus onset. Second, considering that response latencies fell in the order of ~620 ms, and that response-locked MRCs yielded effector-specific effects starting ~250 ms before action execution, motoric stages of the phenomenon began almost in synchrony with semantic ones and extended for ~200 ms thereon. Accordingly, both stages seem to co-occur over a window of ~380-440 ms post-stimulus presentation. This time-span, we propose, might signal the moment of convergence between the two contributing streams shaping effector-specific motor-language coupling –a conclusion that simply cannot be derived from previous ERP studies comparing MaVs and nMaVs with nAVs, but not with each other (e.g., Dalla Volta et al., 2018). Together with research on the time course of MaV-induced muscular activity (Da Silva et al., 2018; Frak et al., 2010), such a finding further illuminates the complex embodied dynamics linking meanings and actions.

Moreover, previous motor-language coupling studies relied on explicit processing tasks, as they required participants to semantically categorize stimuli (Dalla Volta et al., 2018) or indicate when they were understood (Aravena et al., 2010; Ibáñez et al., 2013; Melloni et al., 2015). Therefore, they overlooked a key requisite to detect primary embodied effects: their emergence under implicit semantic conditions (García et al., 2019; Hauk, Shtyrov, & Pulvermüller, 2008; Kiefer et al., 2008; Mollo et al., 2016; Pulvermüller et al., 2001). Unlike those studies, our experiment was based on a lexical decision task, so that no explicit attention to meaning was required. As proposed for other embodied phenomena (García et al., 2019), this suggests that motor-language coupling dynamics are sufficiently pervasive to operate even when language is processed at a shallow level.

Finally, the observed neural patterns emerged without accompanying effects on accuracy or RT. Whereas behavioral experiments show that MaVs can induce involuntary grip force modulations shortly after presentation (Da Silva et al., 2018; Frak et al., 2010), these two variables typically yield null motor-language coupling effects in shallow-processing paradigms (García & Ibáñez, 2016a). However, several neuroscientific studies have shown that significant neural effects can be traced in embodied paradigms yielding no behavioral differences between conditions (García et al., 2020; Klepp et al., 2014; Mollo et al., 2016; Pulvermüller et al., 2001; Sato et al., 2008). As argued for other neurolinguistic phenomena (Dottori et al., 2020), this reminds us that a null effect on one dependent variable must not be taken to reflect a null effect of the independent variable at large. Indeed, as shown in the present study,

motor-language phenomena may be indexed by neural indices of motoric and semantic integration despite yielding no significant effects on overt behavior.

The same might be true of different neurophysiological dimensions. As mentioned above, previous motor-language coupling research found effector-specific beta-band effects in both stimulus- and response-locked analyses (Klepp et al., 2015). Our preliminary exploration of stimulus-locked time-frequency modulations over this band yielded late (670 to 770 ms) coarse-grained and effector-specific effects, partly overlapping with the time window (350-750 ms) capturing comparable effects in Klepp et al.'s (2015) study. This aligns with previous works showing different temporal dynamics between N400 effects and beta oscillations in linguistic tasks (Wang et al., 2012), some of which are actually tracked by only one of these measures (Dottori et al., 2020; Vilas et al., 2019). Moreover, response-locked analyses yielded effects that broadly echoed the time windows capturing our main ERP results. Reduced beta oscillations were observed for all three contrasts starting at roughly the same time as MRCP effects and covering the entirety of their duration. However, they also extended beyond the window capturing such ERP effects. This might speak to the different temporal dynamics of motor-language coupling in each analytical dimension, a possibility that should be explored in new studies designed to compare both approaches.

5. Limitations and avenues for further research

Notwithstanding its contributions, our study presents some limitations. First, our sample size was modest. Although the present number of subjects provided good statistical power (Supplementary data A) and while most previous EEG studies on motor-language coupling have employed similar or even smaller *N*s (Dalla Volta et al., 2018; Melloni et al., 2015; Mollo et al., 2016), replications with a larger group would be desirable. In addition, though recent works with comparable experimental designs (Dalla Volta et al., 2018) have used similar numbers of stimuli, it would be ideal to extend the present study with more items per category. Moreover, it would be useful to assess whether the modulations observed during our present shallow-level task manifest similarly when explicit semantic processing is required –as observed in behavioral motor-language coupling experiments (Afonso et al., 2019). Finally, even though the question addressed in this study pertained to the temporal dimension, future studies should aim to complement our approach with high-spatial-resolution methods, as done in recent magnetoencephalography (García et al., 2019; Klepp et al., 2015; Klepp et al., 2019; Klepp et al., 2014) and intracranial (García et al., 2020; Ibáñez et al., 2013) EEG experiments.

6. Conclusion

This is the first ERP study assessing the semantic and action stages of motor-language coupling during a shallow-processing task. Our core finding is that the execution of a manual response after processing of MaVs (as compared with nMaVs) involves reduced N400 modulations and increased MRCP effects, signaling semantic and motoric dynamics, respectively. Such modulations overlapped in a window of ~380-440 ms after word presentation and ~180 ms before response execution, a pattern that motivates new insights on when both stages reach maximal convergence during effector-specific

motor-language coupling. Moreover, we showed that the RP is sensitive to both coarse-grained and effector-specific dynamics, while the MP only captures the former modulations, suggesting different functional roles for each ERP. Further work in this direction can hone our understanding of how language and movement coalesce in neural time.

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Conflict of interest

The authors declare no conflicts of interest.

Data and code availability statement

All experimental data and the scripts used for their collection and analysis are available online (García, 2020).

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Figure captions

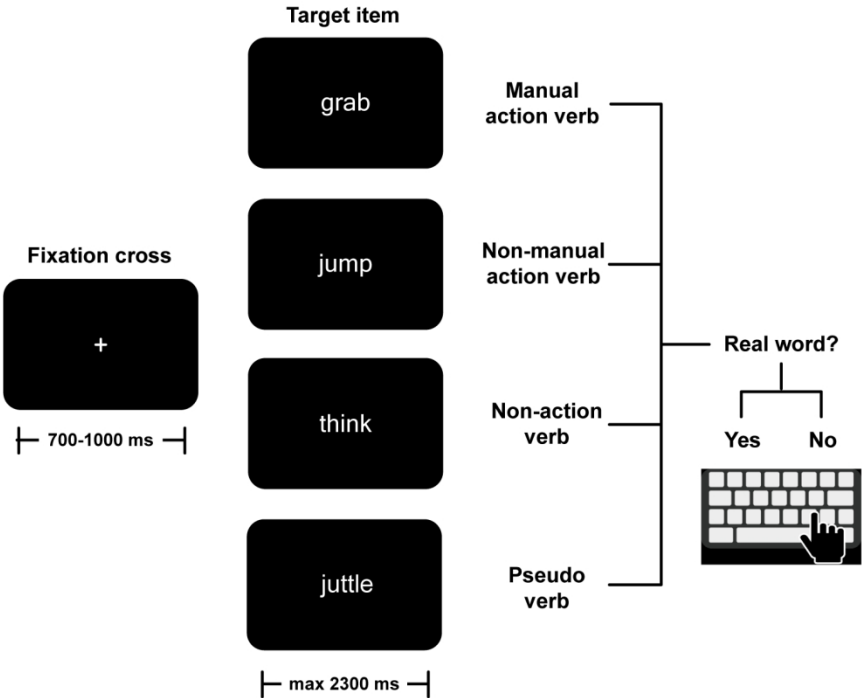
Figure 1. Lexical decision task and behavioral results. **(A)** Participants viewed a fixation cross, followed by a target item belonging to any of four categories: manual action verbs, non-manual action verbs, non-action verbs, and pseudoverbs). In each trial, participants had to decide whether the target item was a real word or not. Verbs from each category have been translated into English for illustrative purposes. **(B and C)** Accuracy and reaction time outcomes. Circles represent each subject's score per category. The large black dot represents the mean of each condition. Asterisks indicate significant differences. Subjects were significantly less accurate and slower responding to PsVs than to all real-verb categories, there being no differences among the latter. MaVs: manual action verbs; nMaVs: non-manual action verbs; nAVs: non-action verbs; PsVs: pseudoverbs.

Figure 2. Electrophysiological markers of semantic integration (N400) effects during motor-language coupling. The topoplots show average modulations, locked to stimulus onset, within a canonical 350-450 window over the left (A), medial (B), and right (C) centro-posterior regions of interest for MaVs (black line), nMaVs (red line), and nAVs (blue line). The baseline ranged from -300 ms to 0 ms before stimulus onset. Shaded bars around the lines indicate standard errors. Vertical pink bars indicate significant differences at $p < .05$ (with a threshold of at least ten contiguous points). MaVs: manual action verbs; nMaVs: non-manual action verbs; nAVs: non-action verbs.

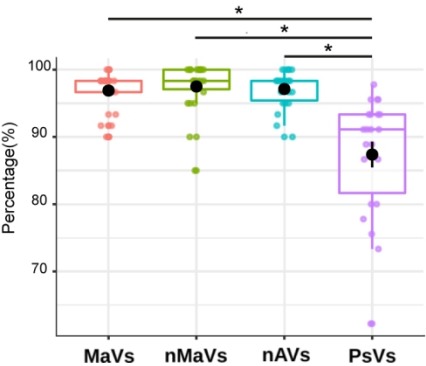
Figure 3. Electrophysiological markers of motor dynamics (MRCP) effects during motor-language coupling. The topoplots show average response-locked modulations within a canonical window (from -250 to -85 ms) over the left (A) and right (B) frontal regions of interest for MaVs (black line), nMaVs (red line), and nAVs (blue line). The baseline ranged from -600 ms to -300 ms before response execution. Shaded bars around the lines indicate standard errors. Vertical pink bars indicate significant differences at $p < .05$ (with a threshold of at least ten contiguous points). MaVs: manual action verbs; nMaVs: non-manual action verbs; nAVs: non-action verbs.

Figure 4. Schematic representation of the temporal integration of semantic and motor processes during motor-language coupling. The upper part of the figure shows N400 effects, indexing semantic integration dynamics during motor-language coupling. While limb-neutral semantic integration during MaV processing (relative to nAVs) covers a ~330-440 ms window (light yellow), effector-specific N400 effects (relative to nMaVs) extend from ~380 to ~440 ms (dark yellow). The lower part of the figure shows MRCP effects, indexing motor dynamics during motor-language coupling. Limb-neutral motor dynamics during MaV processing (relative to nAVs) extend roughly from -250 to 75 ms relative to response execution (light purple). Instead, effector-specific MRCP modulations (relative to nMaVs) extend from approximately -250 to -85 ms (dark purple). Accordingly, the overlap between both effector-specific modulations occurs in a 380-440 ms window (brown), signaling the convergence of semantic and motoric stages during hand-specific motor-language coupling. MaVs: manual action verbs; nMaVs: non-manual action verbs; nAVs: non-action verbs.

A. Task design



B. Accuracy



C. Reaction time

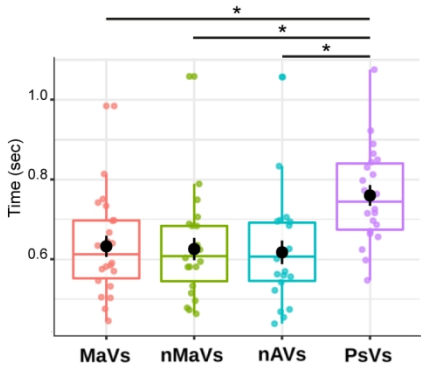


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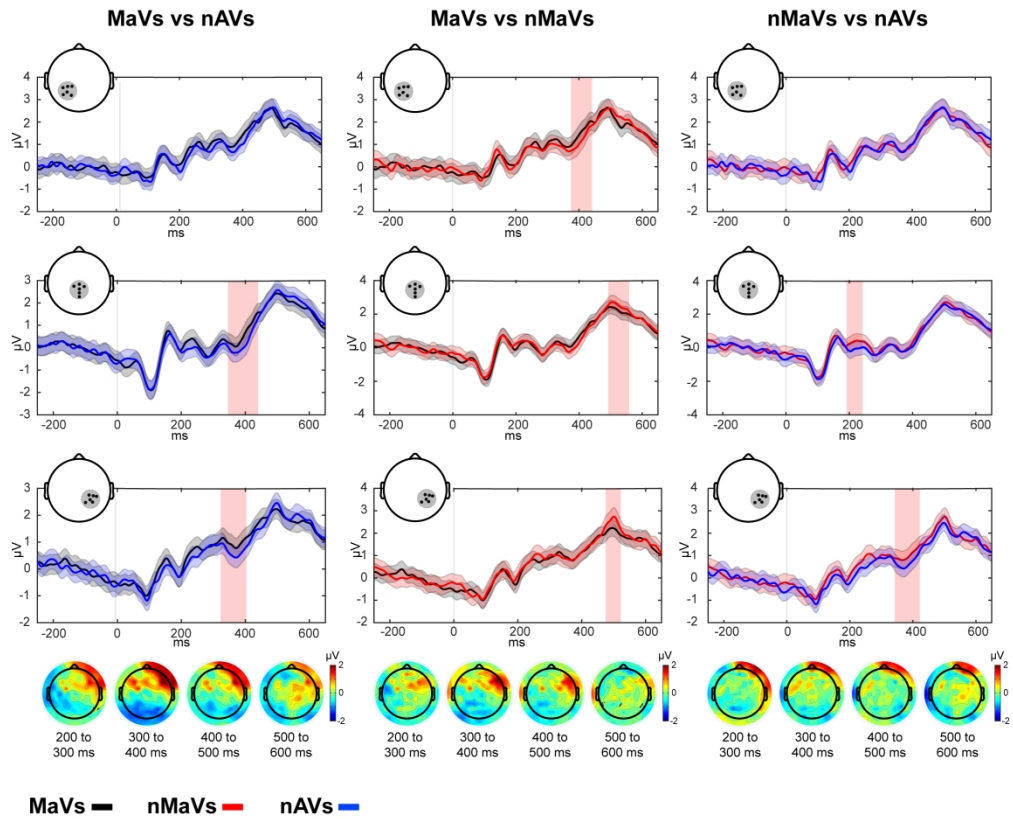


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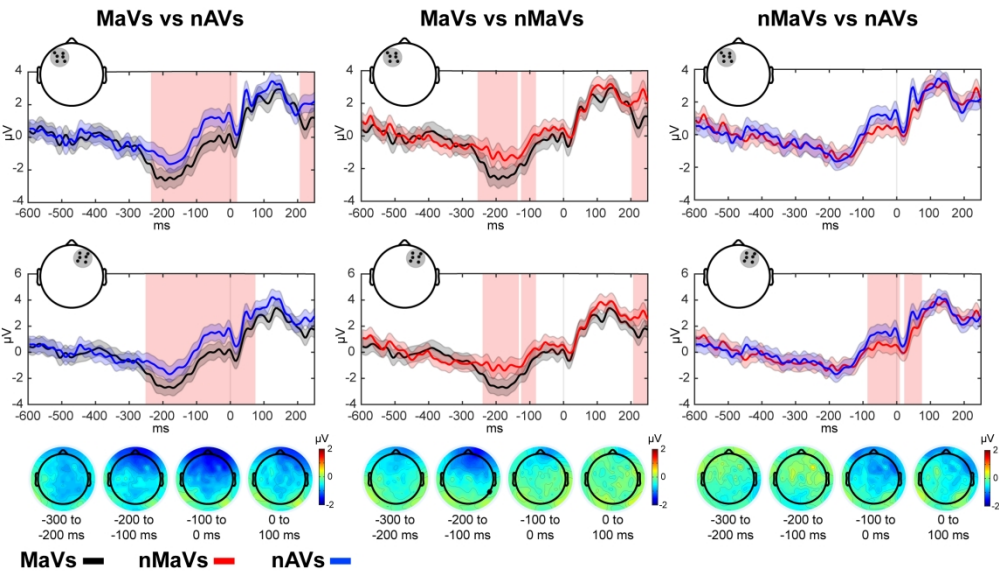


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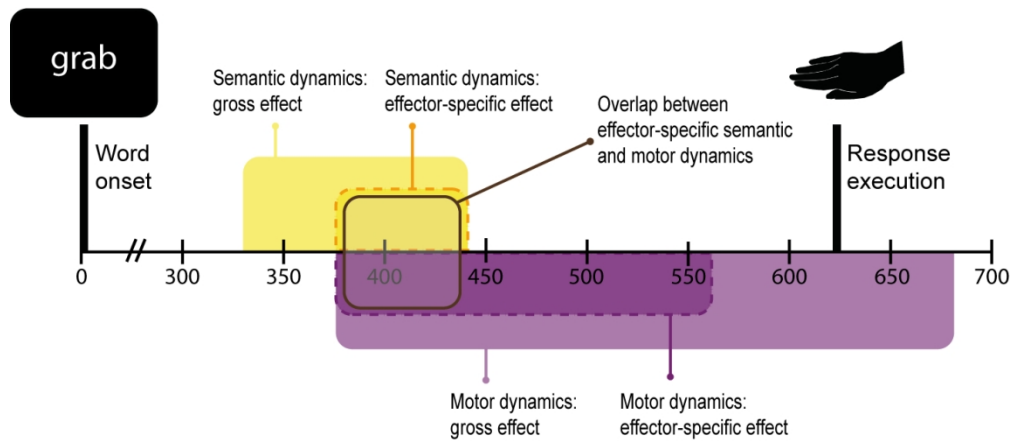


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