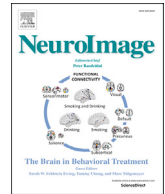




Contents lists available at ScienceDirect

NeuroImage

journal homepage: [www.elsevier.com/locate/neuroimage](http://www.elsevier.com/locate/neuroimage)

## How meaning unfolds in neural time: Embodied reactivations can precede multimodal semantic effects during language processing

Adolfo M. García<sup>a,b,c,\*,1</sup>, Sebastian Moguilner<sup>a,d,e,1</sup>, Kathya Torquati<sup>a</sup>, Enrique García-Marco<sup>f,g</sup>, Eduar Herrera<sup>h</sup>, Edinson Muñoz<sup>i</sup>, Eduardo M. Castillo<sup>j</sup>, Tara Kleineschay<sup>j</sup>, Lucas Sedeño<sup>a,b</sup>, Agustín Ibáñez<sup>a,b,k,l,m</sup>

<sup>a</sup> Laboratory of Experimental Psychology and Neuroscience (LPEN), Institute of Cognitive and Translational Neuroscience (INCYT), INECO Foundation, Favaloro University, Pacheco de Melo 1860, C1126AAB, Buenos Aires, Argentina

<sup>b</sup> National Scientific and Technical Research Council (CONICET), Godoy Cruz 2290, C1425FQB, Buenos Aires, Argentina

<sup>c</sup> Faculty of Education, National University of Cuyo (UNCuyo), Sobremonte 74, M5500, Mendoza, Argentina

<sup>d</sup> Fundación Escuela de Medicina Nuclear (FUESMEN) and Comisión Nacional de Energía Atómica (CNEA), Garibaldi 405, M5500, Mendoza, Argentina

<sup>e</sup> Instituto Balseiro and Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Cuyo (UNCuyo), Padre Jorge Contreras 1300, M5502 JMA, Mendoza, Argentina

<sup>f</sup> Instituto Universitario de Neurociencia, Universidad de La Laguna, Pabellón de Gobierno, C/ Padre Herrera s/n, 38200, San Cristóbal de La Laguna, Santa Cruz de Tenerife, Spain

<sup>g</sup> Universidad Nacional de Educación a Distancia (UNED), Paseo Senda del Rey 7, 28040, Madrid, Spain

<sup>h</sup> Universidad Icesi, Departamento de Estudios Psicológicos, Cali, Colombia

<sup>i</sup> Departamento de Lingüística y Literatura, Facultad de Humanidades, Universidad de Santiago de Chile, Av. Alameda Libertador Bernardo O'Higgins 3363, 9170022, Estación Central, Santiago, Chile

<sup>j</sup> Magnetoencephalography Laboratory, Florida Hospital for Children, 601 E Rollins St, FL 32803, Orlando, FL, United States

<sup>k</sup> Centre of Excellence in Cognition and its Disorders, Australian Research Council (ARC), NSW, Sydney, Australia

<sup>l</sup> Center for Social and Cognitive Neuroscience (CSCN), School of Psychology, Universidad Adolfo Ibáñez, Diagonal Las Torres 2640, 9170022, Peñalolén, Región Metropolitana, Santiago, Chile

<sup>m</sup> Universidad Autónoma del Caribe, Calle 90 #46-112, 080020, Barranquilla, Colombia

### ARTICLE INFO

#### Keywords:

Embodied cognition  
Multimodal semantics  
Action verbs  
Magnetoencephalography  
Machine learning

### ABSTRACT

Research on how the brain construes meaning during language use has prompted two conflicting accounts. According to the ‘grounded view’, word understanding involves quick reactivations of sensorimotor (embodied) experiences evoked by the stimuli, with simultaneous or later engagement of multimodal (conceptual) systems integrating information from various sensory streams. Contrariwise, for the ‘symbolic view’, this capacity depends crucially on multimodal operations, with embodied systems playing epiphenomenal roles after comprehension. To test these contradictory hypotheses, the present magnetoencephalography study assessed implicit semantic access to grammatically constrained action and non-action verbs ( $n = 100$  per category) while measuring spatiotemporally precise signals from the primary motor cortex (M1, a core region subserving bodily movements) and the anterior temporal lobe (ATL, a putative multimodal semantic hub). Convergent evidence from sensor- and source-level analyses revealed that increased modulations for action verbs occurred earlier in M1 (~130–190 ms) than in specific ATL hubs (~250–410 ms). Moreover, machine-learning decoding showed that trial-by-trial classification peaks emerged faster in M1 (~100–175 ms) than in the ATL (~345–500 ms), with over 71% accuracy in both cases. Considering their latencies, these results challenge the ‘symbolic view’ and its implication that sensorimotor mechanisms play only secondary roles in semantic processing. Instead, our findings support the ‘grounded view’, showing that early semantic effects are critically driven by embodied reactivations and that these cannot be reduced to post-comprehension epiphenomena, even when words are individually classified. Briefly, our study offers non-trivial insights to constrain fine-grained models of language and understand how meaning unfolds in neural time.

**Abbreviations:** M1, primary motor cortex; ATL, anterior temporal lobe; AVs, action verbs; nAVs, non-action verbs.

\* Corresponding author. Institute of Cognitive and Translational Neuroscience and CONICET, Pacheco de Melo 1860, C1126AAB, Buenos Aires, Argentina.

E-mail address: [adolfo.garcia@gmail.com](mailto:adolfo.garcia@gmail.com) (A.M. García).

<sup>1</sup> First authors.

<https://doi.org/10.1016/j.neuroimage.2019.05.002>

Received 7 November 2018; Received in revised form 8 March 2019; Accepted 2 May 2019

Available online 3 May 2019

1053-8119/© 2019 Elsevier Inc. All rights reserved.

## 1. Introduction

How does the human brain progressively construe meaning during language processing? This hot topic of contemporary neuroscience (Pulvermüller, 2018; Lambon Ralph et al., 2017; Jackson et al., 2015; Shtyrov et al., 2014) has proven both challenging and controversial, prompting two opposite accounts (Lambon Ralph et al., 2017; Pulvermüller, 2005; Seghier, 2013; Zwaan, 2014). The ‘grounded view’ posits that words quickly reactivate the dominant sensorimotor (embodied) experiences they denote, with concomitant firing of multimodal (conceptual) hubs integrating information from various sensory streams (Pulvermüller, 2005, 2013, 2018). Conversely, according to the ‘symbolic view’, semantic processing is primarily afforded by multimodal mechanisms, with embodied systems acting epiphenomenally after word understanding (Bedny and Caramazza, 2011; Lotto et al., 2009; Hickok, 2015). Beyond theoretical factors, this disagreement largely reflects empirical shortcomings in the literature, as few studies have employed spatiotemporally precise techniques, and none has applied robust trial-by-trial decoding methods over large stimulus sets. To overcome such limitations, the present magnetoencephalography (MEG) study combines inferential and machine-learning analyses to examine when action verbs (AVs) and non-action verbs (nAVs) are processed and individually classified in embodied and multimodal semantic networks.

The systematic role of embodied circuits in word processing has been mainly established through studies on AVs. These verbs, which denote bodily motions, become selectively affected following motor-network atrophy (Birba et al., 2017; García et al., 2018), increase activation levels in the primary motor cortex (M1) (Hauk et al., 2004; Tomasino et al., 2007, 2008) and other (gross and effector-congruent) motor regions (Hauk et al., 2004; Aziz-Zadeh et al., 2006; Carota et al., 2012; Pulvermüller et al., 2009; Raposo et al., 2009; Tettamanti et al., 2005), manifest distinctive facilitation or interference effects following non-invasive stimulation of movement-related hubs (Gerfo et al., 2008; Liuzzi et al., 2010; Pulvermüller et al., 2005; Repetto et al., 2013; Willems et al., 2011), and predictably affect the early stages of overt actions (García and Ibáñez, 2016). Yet, comprehension of AVs and other word types also relies on multimodal regions, crucially including the bilateral anterior temporal lobe (ATL) (Lambon Ralph et al., 2017; Patterson et al., 2007). This area is critically engaged by verbal stimuli evoking general and specific concepts (Binney et al., 2010; Visser et al., 2012; Humphreys et al., 2015; Shimotake et al., 2015; Abel et al., 2015) –with greater modulations for AVs than other lexical classes (Liljestrom et al., 2008)–, and its disruption due to pathological damage (Lambon Ralph et al., 2007, 2012; Jefferies et al., 2009) or transient inhibition (Pobric et al., 2010a, 2010b) consistently triggers deficits across multiple semantic categories. In brief, the meanings evoked by AVs are widely agreed to hinge on both sensorimotor and heteromodal conceptual systems (Pulvermüller, 2018; Lambon Ralph et al., 2017).

Contrarily, the *temporal coordination* of such systems during AV processing remains disputed. As reported in MEG research, these words (Shtyrov et al., 2014; Mollo et al., 2016; Klepp et al., 2014; Pulvermüller et al., 2005), as well as their non-literal paraphrases (Boulenger et al., 2012), elicit both widespread and partially somatotopic effects over the motor cortex in early (80–200 ms) windows. Likewise, electroencephalographic and intracranial studies show that different AV types can elicit fast (150–250 ms) effects over sensorimotor locations (Shtyrov et al., 2004; Hauk and Pulvermüller, 2004) and even modulate the motor potential *within* M1 and other movement-related regions in a window of –75 to 35 ms locked to congruent action onset (Ibáñez et al., 2013). Yet, AVs have also been claimed to trigger early (~150 ms) semantic effects in multimodal temporal regions (Mollo et al., 2016; Pulvermüller et al., 2005). In this sense, intracranial, neurostimulation, and MEG studies on other word classes (mainly nouns) indicate that ATL activity before 250 ms may reflect coarse category-type distinctions, but that detailed semantic discrimination typically occurs after that time point (Jackson et al., 2015; Shimotake et al., 2015; Chen et al., 2016; Clarke et al., 2013;

Mollo et al., 2017). Of note, despite this specification, some such results have led to the explicit claim that embodied systems cannot be accessed before conceptual processes subserved by the ATL (Mollo et al., 2017).

However, the latter claim might not be necessarily true for AVs. First, it stems from a comparison between two sets of nouns (Mollo et al., 2017), both of which are mainly subserved by temporal (rather than motor) regions (Vigliocco et al., 2011; Capitani et al., 2003). Second, whereas AVs have been systematically linked to motor-system modulations before 200 ms post-stimulus onset (Pulvermüller, 2013, 2018), most works indicate that semantic processes recruit the ATL *after* the 250-ms mark (Jackson et al., 2015; Shimotake et al., 2015; Chen et al., 2016; Mollo et al., 2017). Third, the few reports of earlier multimodal activations during AV processing (Mollo et al., 2016; Pulvermüller et al., 2005) are undermined by stimulus-related confounds, such as the presentation of isolated words which could be interpreted as nouns, or the use of only one stimulus per condition. Therefore, the semantic processes evoked by AVs can be reasonably expected to engage motor regions before the ATL as a key multimodal hub. Crucially, evidence in this direction would cast major doubts on the pertinence of the ‘symbolic view’, as embodied reactivations could then hardly be reduced to post-comprehension phenomena.

Against this background, the present MEG study aimed to establish whether M1, relative to the ATL, can afford maximal discrimination and classification of AVs relative to nAVs in early windows. Participants performed a lexical decision task involving 100 items from each of those categories as well as 60 pseudoverbs, and were asked to press a key when they saw a real word and a different key when the stimulus was not a real word. Importantly, all items were presented in a grammatical context that forced their interpretation as verbs (e.g., *I am walking*). We analyzed amplitude differences and calculated trial-by-trial classification accuracy through time in six regions of interest (ROIs), namely: left, right, and bilateral M1 (as defined through a localizer task); and left, right, and bilateral ATL. To test for cross-methodological consistency, our approach combined inferential statistics and support vector machine (SVM) analyses of both sensor- and source-level information. Based on the above reasoning, we hypothesized that AVs and nAVs would be maximally discriminated and individually decoded in embodied (M1) circuits before putative multimodal (ATL) regions, which would lend strong support to the ‘grounded view’. In short, this work aims to contribute a robust approximation for understanding how meaning unfolds in neural time.

## 2. Methods

### 2.1. Participants

The study comprised 16 right-handed, English-speaking volunteers. However, one of them was removed due to major artifacts in the recordings, resulting a final sample of 15 subjects (nine women) with a mean age of 25.06 ( $SD = 9.24$ ) and an average of 14 ( $SD = 2.42$ ) years of education. The participants were healthy, possessed normal vision, and had no family history of neurological or psychiatric disease. All of them provided written informed consent according to the Declaration of Helsinki and in line with the Institutional Review Board for the Protection of Human Research Participants at Florida Hospital (Orlando, USA).

### 2.2. Behavioral tasks

All participants completed a lexical decision task and a localizer task, with stimuli presented on a screen placed at 1.5 m from their faces. Words in the former task were written in white lowercase Courier font (size 48) on a black background. Stimuli in the localizer task were also presented in white and in central position against a black background, with a size similar to that of verbal stimuli. As in previous studies (Mollo et al., 2016), the visual angle of each stimulus did not exceed 4°. Stimulus presentation and response collection were conducted on E-Prime (Schneider et al., 2002). In each task, instructions were first provided

orally and then recapped on screen. Of note, both tasks had the same timeline and involved similar decisional processes, which warranted their similarity in terms of motoric, executive, and otherwise cognitive demands.

2.2.1. Lexical decision task

The lexical decision task comprised 260 trials. Two-hundred of them featured a real verb and the remaining 60 ended with a pseudoverb—the latter were not included in the analyses, but they served to ensure task compliance and attentional engagement by forcing linguistic decisional processes item after item. Half of the real-word trials ( $n = 100$ ) involved AVs (verbs denoting bodily movements) and the other half ( $n = 100$ ) involved nAVs (verbs denoting perceptual, cognitive or affective processes which require no physical action). Unpaired  $t$ -tests, based on normative data derived from the N-Watch software (Davis, 2005) and age-of-acquisition norms (Kuperman and Stadthagen-Gonzalez, 2012), showed that both real-verb lists were similar in orthographic length [ $t(198) = 0.8456, p = .39$ ], phonemic length [ $t(198) = 1.6702, p = .10$ ], syllabic length [ $t(198) = 1.1267, p = .26$ ], frequency [ $t(198) = 0.0673, p = .95$ ], familiarity [ $t(198) = 0.5129, p = .61$ ], number of orthographic neighbors [ $t(198) = 0.4689, p = .64$ ], and age of acquisition [ $t(198) = 1.6376, p = .10$ ]—see Table 1 for descriptive statistics. The pseudoverbs were created by choosing 30 real words from each list and replacing only one letter, such that the resulting letter string, though phonotactically and graphotactically legal, did not represent an English word. The 260 trials were pseudorandomized so that no more than three target stimuli from the same category appeared in succession, and so that any two real verbs which could be related in meaning or form were separated by at least three trials.

Importantly, given that isolated English words may be interpreted as different parts of speech (e.g., *walk* could represent a noun, as in *Let's take a walk*, or a verb, as in *I walk rather fast*), target items were presented in a grammatical context which forced their interpretation as verbs.

Table 1

Lexical features of the action and non-action verbs.

Block	Orthographic length <sup>a</sup>	Phonemic length <sup>a</sup>	Syllabic length <sup>a</sup>	Frequency <sup>a,b</sup>	Familiarity <sup>a,c</sup>	Orthographic neighbors <sup>a</sup>	Age of acquisition <sup>d</sup>
Action verbs	8.65 (1.21)	6.87 (1.24)	2.71 (0.59)	22.51 (40.76)	508.77 (49.21)	1.71 (2.32)	7.78 (2.36)
Non-action verbs	8.79 (1.13)	7.17 (1.30)	2.81 (0.66)	22.76 (31.51)	512.21 (45.74)	1.9 (3.32)	8.29 (2.03)

All data corresponds to the verbs' base forms—except for orthographic length, which was calculated considering the number of letters of each verb its present participle form. Values expressed as mean (SD).

<sup>a</sup> Data obtained through N-Watch (Davis, 2005).

<sup>b</sup> Data averaged from the CELEX (total), the British National Corpus Word Frequency, and the Sydney Morning Herald Word Frequency databases.

<sup>c</sup> Data from the MRC database.

<sup>d</sup> Data from Kuperman and Stadthagen-Gonzalez (2012).

Specifically, all stimuli consisted in present continuous sentences starting with the first-person singular pronoun and finishing with a verb or pseudoverb in present participle form (e.g., *I am walking*). Participants had to decide, as fast and accurately as possible, whether the sentence-final item constituted a real English 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 point shown for 800 ms at the center of the screen. This was followed by the words *I am*, which remained visible for a random period between 300 and 500 ms. Immediately afterwards, the sentence-final target item (verb or pseudoverb) was shown for a maximum of 1400 ms (Fig. 1). Such an item disappeared upon the participant's button press, which triggered the following trial. The use of a random period for the *I am* phrase minimized the chances of target-item responses being driven by rhythmic motor habituation, with no biases for AVs or nAVs. Ten practice trials not used in the actual experiment were included at the beginning for familiarization purposes. Overall, the task lasted roughly 25 min.

2.2.2. Localizer task

The localizer task was used to establish a ROI on the left M1 for source-level analyses. This region was chosen given its well-established role in the embodiment of AVs (Hauk et al., 2004; Klepp et al., 2014; Boulenger et al., 2012; Ruschemeyer et al., 2007; Papeo et al., 2009), which rendered it a logical target for classification analysis. As in previous language embodiment studies (Shtyrov et al., 2014; Klepp et al., 2015; Dreyer and Pulvermuller, 2018), hand responses used for localization purposes were made with the right limb only. The task was composed of 65 trials in which an initial stimulus (an arrow) was followed by either a rectangle ( $n = 43$ ) or a triangle ( $n = 22$ ). Participants were instructed to decide, as fast and accurately as possible, whether the final item was a rectangle or not—by pressing the left arrow with the index finger or the right arrow with the middle finger, respectively. The timeline of this task was identical to that of the lexical decision task (with

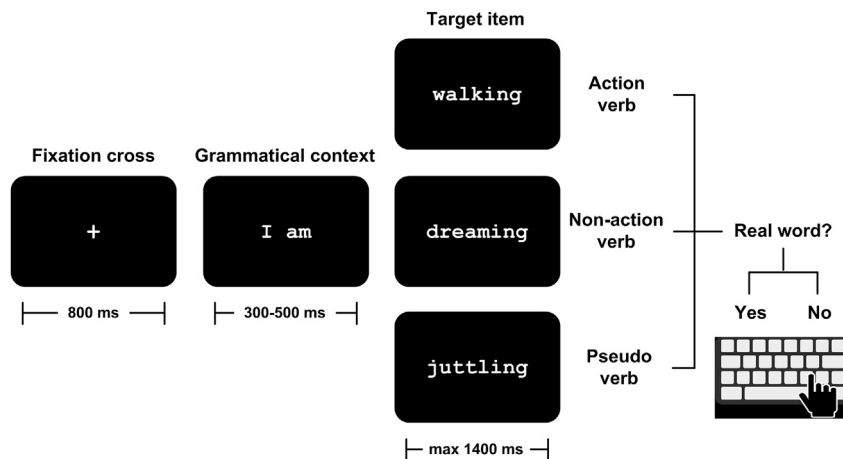


Fig. 1. Lexical decision task. Participants viewed a fixation cross, followed by the words *I am* and then the target item. The latter could be an action verb, a non-action verb, or a pseudoverb. In each trial, participants had to choose whether the target item was a real word or not.

the arrow in lieu of the *I am* phrase, and the rectangles and triangles acting as target items). Ten practice trials were included prior to the actual task, which lasted approximately 10 min.

### 2.3. MEG procedures

#### 2.3.1. MEG data acquisition

All MEG recordings were obtained in the Magnetoencephalography Laboratory at the Florida Hospital for Children, with a 306-channel Elekta Neuromag TRIUX system in a three-layer magnetically shielded room (Vacuumschmelze GmbH & Co, Germany), following recommended practices for conducting and reporting MEG research (Gross et al., 2013). The MEG system consists in an array of 204 orthogonal planar gradiometers and 102 magnetometers housed in a head-shaped helmet over 102 locations. During the recordings, participants were in supine position and their heads were covered by the MEG sensor array. Prior to MEG recordings, a 3D digitizer (Polhemus, VT, USA) was used to record the position of fiducial landmarks (i.e., nasion and preauricular points), five head-position-indicator (HPI) coils, and head shape. The individual position of each participant's head relative to the sensor helmet was determined at the beginning and at the end of the recording session, based on the five HPI coils. A closed-loop real-time noise cancellation ("MaxShield", Elekta Neuromag, Helsinki, Finland) was applied during the recordings, and data were acquired at a sampling rate of 1000 Hz with a 0.1–330 Hz band-pass filter.

#### 2.3.2. MEG data preprocessing

MEG data were spatially filtered using a temporally-extended signal space separation (tSSS) method (Taulu and Simola, 2006) to suppress noise generated by sources outside the brain. Offline analyses were carried out on Brainstorm toolbox (v 3.4) (Tadel et al., 2011). Continuously recorded MEG signals were bandpass filtered from 1 to 150 Hz. MRI co-registration, using a standard MNI brain, was successfully achieved in all 15 subjects through an MRI wrap with three fiducial points (nasion, left and right preauricular). Noisy channels and segments exhibiting movement- or sensor-related artifacts were rejected on visual inspection. Across subjects, valid trials totaled an average of 84.06 ( $SD = 14.62$ ) AVs and 85.93 ( $SD = 13.97$ ) nAVs, there being no significant difference between conditions ( $t(28) = 0.35$ ,  $p = .722$ ,  $d = 0.13$ ). No trials from the localizer task had to be discarded due to artifacts or recording issues. Physiological artifacts caused by cardiac activity and eye blinks were removed separately from the magnetometers and the gradiometers using signal space projections (Gross et al., 2013): for each artifact type, a relevant, highly affected sensor was selected for detection purposes and the number of projectors to be applied was validated by comparing signals before and after artifact correction.

Data from the lexical decision task were then segmented into AV and nAV trials, defined from –100 to 800 ms relative to word onset, and averaged for each of these conditions –baseline correction was applied from –100 to –1 ms, as in previous studies (Gross et al., 2013). Instead, data from the localizer task were subjected to a response-locked analysis, with epochs from –900 to 500 ms being extracted and baseline corrected from –900 to –800 ms, as in previous works (Moreno et al., 2013a, 2015).

#### 2.3.3. Definition of ROIs for sensor-level analysis

Sensor-level ROIs were defined by reference to anatomical labels provided by the Brainstorm software (Tadel et al., 2011). We created six sensor-level ROIs (Tan et al., 2016), comprised of three electrodes each, over the left, right, and bilateral M1 region –overlapping with ROIs of previous MEG embodiment studies (Klepp et al., 2014)–, and left, right, and bilateral ATL (defined by Brainstorm's channel grouping). This resulted in a left (MEG 0711, 0712, 0713), a right (MEG 0721, 0722, 0733), and a bilateral central ROI; and a left (MEG 0131, 0132, 0133), a right (MEG 1441, 1442, 1443), and a bilateral temporal ROI. Each channel group was averaged to obtain one signal per sensor-level ROI.

Note that, in line with numerous MEG and EEG embodiment experiments (e.g., (Klepp et al., 2014; Urrutia et al., 2012; Moreno et al., 2013b; Santana and de Vega, 2013)), the use of identical criteria (same number of and proximity among electrodes) for establishing sensor-level ROIs rules out potential biases by maximizing comparability of topographical coverage and signal-to-noise ratio among them. Also, given the vast topographical extension comprised by the ATL, we replicated these analyses over a set of more anterior ventral sensor-level ROIs, as defined by Brainstorm's channel grouping. These ROIs overlapped with the ATL electrodes considered in previous sensor-level analyses of semantic effects (Del Prato and Pykkänen, 2014) and corresponded to canonical anterior ventral ATL sites (Lambon Ralph et al., 2017) –see Supplemental Information A.

#### 2.3.4. Definition of ROIs for source-level analysis

Functional data analyses were also run on the Brainstorm toolbox (v 3.4). Source estimates were computed for each subject and each condition using a depth-weighted minimum L2 norm estimator with dSPM normalization and source orientation constrained to be normal to the cortex (Hamalainen and Ilmoniemi, 1984; Lin et al., 2006; Gramfort et al., 2014). Analyses were performed on two sets of source-level ROIs, namely: M1, involved in modality-preferential activity during AV processing (Pulvermuller, 2005, 2013, 2018); and the ATL, implicated in multimodal semantic processing (Pulvermuller, 2013, 2018; Lambon Ralph et al., 2017). Note that the two regions contain tangential sources of cortical activity (namely, the type of modulation that can be captured by MEG) and both can be assumed to be similarly sensitive to MEG-derived modulations (Mollo et al., 2016; Pulvermuller et al., 2005; Boulenger et al., 2012).

**2.3.4.1. Definition of the source-level M1 ROI.** The source-level M1 ROIs were established on the basis of the localizer task. First, the left M1 source-level ROI was defined in each subject from motor-evoked activations elicited by the key press. The left M1 source, assumed to represent activity directly related to motor commands, was derived from the motor field peaking around movement onset (Cheyne and Weinberg, 1989; Kristeva-Feige et al., 1994). The source map was displayed on the 3D cortex and the amplitude threshold was increased to reveal focal activity. A source-level ROI was then seeded on the left M1, centered in the vertex of the cortical surface showing maximum activity. The source-level ROI was then expanded to 2 cm<sup>2</sup>, with the software option "constrained" selected in order to include only the vertices with supra-threshold source values (Farahibozorg et al., 2017). As done in previous research (White et al., 1997), the right M1 source-level ROI was defined symmetrically on the opposite hemisphere and then it was expanded to 2 cm<sup>2</sup> adding the closest vertices. The M1 ROI was successfully located for each participant in the primary motor cortex (average MNI coordinates: left = –35, –21, 55; right = 32, –20, 52), in line with previous reports on sensorimotor activity (Hauk et al., 2004; Kristeva-Feige et al., 1994).

**2.3.4.2. Definition of the source-level ATL ROI.** The source-level ATL ROIs were defined by reference to anatomical labels provided by the Brainstorm software, as done in previous MEG research on AV processing (Klepp et al., 2014). Then, through visual inspection of source-estimation results, source-level ROIs in each hemisphere were centered on the peaks of sustained activity observed across subjects in the average between the two verb conditions. This approach has been recommended in the absence of localizers for the ATL, especially considering that using reported fMRI coordinates could lead to ambiguous analysis due to the limited spatial resolution and accuracy of head positioning estimations in EEG/MEG data (Tadel et al., 2011).

Source estimation maps obtained for all correct items (collapsing both conditions) showed clear activity in the temporal lobe across participants, focused on two left-hemisphere and two right-hemisphere areas.

Each of these areas revealed two close spots showing similar activity in time, and they were thus taken together as part of the same activated area. Indeed, as MEG is sensitive only to the tangential component of a current source in a spherical volume conductor, and since we used a stringent and constrained localization method, extended activity in a gyrus or sulcus would produce two separate spots in the map (Ahlfors et al., 2010). Therefore, the two spots of each activated area were summed in a 2-cm<sup>2</sup> source-level ROI. Anatomical labels from Brainstorm indicated that the two areas belonged within dorsal and posterior portions of the ATL (Dors-ATL and Post-ATL, respectively). Note that the latter was detected at the boundary of the mid/posterior portion of the dorsal ATL and the anterior superior temporal cortex, overlapping with semantic-sensitive hubs in previous ATL research (Lau et al., 2013). MNI coordinates averaged across subjects for these regions are the following: (−50, −5, −15) and (−53, −6, −17) for the left Dors-ATL; (−53, −6, −17) and (56, −9, −13) for the right Dors-ATL; (−52, −17, −10) and (−57, −20, −10) for the left Post-ATL; and (51, −23, −3) and (56, −23, −4) for the right Post-ATL. In addition, considering the anatomical expansion of the ATL, we replicated our analyses in more anterior ventral ATL ROIs. These were based on coordinates which were explicitly reported in previous semantic studies (Binney et al., 2010; Molloy et al., 2017) and they were comprised within semantically-sensitive hubs in meta-analytic (Binder et al., 2009) and theoretical (Lambon Ralph et al., 2017) works –see Supplemental Information A.

### 2.3.5. Amplitude differences across time

All analyses were conducted following the statistical analysis pipeline in Brainstorm (version 3.4) (Tadel et al., 2011), using the time-courses of the mean activity in each of the six sensor-level ROIs and the four source-level ROIs extracted from the AV and nAV averages (bandpass filtered from 0.1 to 40 Hz). To test for differences between conditions, we ran a temporal cluster-based permutation analysis (1000 permutations) (Gross et al., 2013), within a window of interest from −100 to 600 ms. This analysis overcomes the multiple comparison problem and does not depend on assumptions about normal data distribution (Gross et al., 2013). For the cluster-based analysis, temporal clusters were identified via a two-tailed *t*-test ( $p < .05$ ) with a minimum threshold of 15 significant contiguous time points (i.e., 15 ms). This temporal window resembles that of previous EEG and MEG action-language studies reporting effects with a duration between 10 and 20 ms (Shtyrov et al., 2014; Dalla Volta et al., 2014, 2018). Clusters were considered as significant against the permutation data with a  $p < .05$ . Specifically for the source-level analyses, an M1 ROI and an ATL ROI were established in each hemisphere of each participant, with each ROI covering a surface of 2 cm<sup>2</sup> (Shtyrov et al., 2014). These source-level ROIs were used for assessing amplitude differences between conditions across time, using the same parameters employed for sensor-level analyses as regards time windows and the number of permutations. Importantly, considering that our hypothesis requires testing *when each region* affords significant discrimination between AVs and nAVs, such a comparison was performed for M1 and ATL ROIs separately. In this sense, note that all analyses focused on magnetic flux density values (in fT units) and that these can correspond to either positive or negative signs because a change in orientation of the magnetic flux density in the MEG coils produces a flip in the sign of the values. Therefore, significant differences between conditions can be detected irrespective of the absolute values of their respective modulations.

### 2.3.6. Machine learning decoding across time

To determine when embodied and multimodal regions reached maximum accuracy in classifying between AVs and nAVs, both sensor- and source-level data were subjected to decoding analysis. MATLAB's linear kernel SVM classifier was executed on each time point of the trials [4]. For each sensor- and source-level ROI, the AV and nAV trials from eight subjects were used for training, while those from the remaining seven subjects were used for prediction/generalization. This process was

repeated 10 times by randomly selecting the subject groups –i.e., random subsampling validation (Hirshorn et al., 2016; Cruz-Garza et al., 2014; Estep and Christensen, 2015)–, and the mean classification accuracy was then calculated for each time point. To test for statistical significance, an empirical *p*-value was computed for each time point via a permutation test randomly shuffling the trials' AV and nAV labels, followed by a cluster-based analysis to obtain the significant classification clusters (Gaonkar and Davatzikos, 2013).

## 3. Results

### 3.1. Behavioral results

For the trials remaining after artifact rejection, mean accurate response rates in the lexical decision task were 0.94% for AVs and 0.92% for nAVs. A Shapiro-Wilk test showed that accuracy scores for both AVs (0.9825,  $p > .05$ ) and nAVs (0.9535,  $p > .05$ ) had normal distributions. Results from a paired two-sample *t*-test revealed that accuracy did not differ significantly between conditions ( $t(28) = 1.01$ ,  $p = .33$ ,  $d = 0.06$ ). For the reaction-time analysis, as done in previous neuroscientific research on AVs (Pobric et al., 2010b; Lau et al., 2013), trials more than 2 SDs away from the subject's mean were removed as outliers. Mean reaction times were 644.929 ms ( $SD = 38.72$  ms) for AVs and 655.571 ms ( $SD = 28.33$  ms) for nAVs. A Shapiro-Wilk test showed that reaction times for both AVs (0.9701,  $p > .05$ ) and nAVs (0.9729,  $p > .05$ ) had normal distributions. Results from a paired two sample *t*-test revealed no significant differences between conditions ( $t(28) = 0.82$ ,  $p = .414$ ,  $d = 0.07$ ).

Results from the localizer task indicated that mean inaccurate button response rates for the rectangular figure were 0.0016%. For the reaction-time analysis, trials more than 2 SDs away from the subject's mean were removed as outliers (0.0183% for the triangle and 0.0181% for the rectangle). Mean reaction times for the rectangular figure –responses to which were used to locate the source-level M1 ROI– were 454.493 ms ( $SD = 92.39$  ms).

### 3.2. Sensor-level results

#### 3.2.1. Amplitude differences between conditions

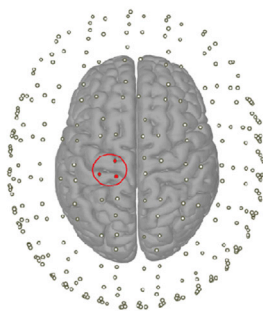
Sensor-level analyses over the left M1 ROI (Fig. 2-A1) revealed significantly higher activity for AVs than nAVs ( $t = 2.57$ ,  $p = .032$ , cluster-corrected) between 133 and 169 ms (Fig. 2-A2). Differences in the same direction ( $t = 2.74$ ,  $p = .027$ , cluster-corrected) were observed over the left ATL ROI (Fig. 2-B1) only in a later (380–405 ms) window (Fig. 1-B2) –and the same was observed over a more anterior ventral ATL ROI (see Supplemental Information B and Fig. S1). No statistically significant differences were found for either the right or the bilateral ATL and M1 ROIs ( $p > .05$ , cluster-corrected). Importantly, considering our point-by-point analysis, the temporal separation between the significant windows in each ROI indicates that their respective data distributions did not overlap.

#### 3.2.2. Machine-learning decoding

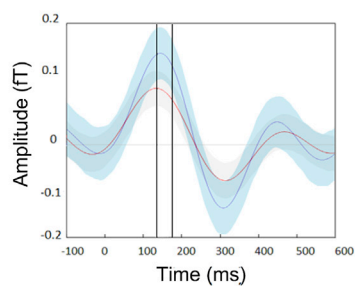
Classification between AVs and nAVs based on sensor-level activity in the left M1 ROI reached its peak (65.74% mean accuracy) in an early time segment (137–172 ms) ( $t = 2.15$ ,  $p < .05$ ), with accuracy in every other time-point cluster interval falling below 61.54% (Fig. 2-A3). As regards the ATL, maximal classification between AVs and nAVs was reached on the left sensor-level ROI (71.45% mean accuracy) in a late time segment (345–472 ms) ( $t = 2.44$ ,  $p < .05$ ), with accuracy in every other time-point cluster interval falling below 62.42% (Fig. 2-B3) –complementary results from a more anterior ventral ATL ROI replicated this pattern (see Supplemental Information B and Fig. S1). No statistically significant clusters were found for the right and bilateral M1 or ATL sensor-level ROIs.

## A. Sensor-level M1 ROI

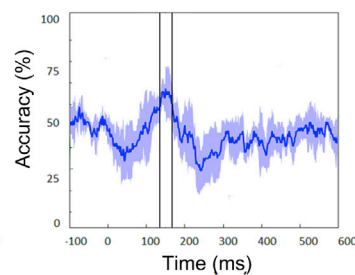
### 1. ROI location



### 2. Amplitude differences

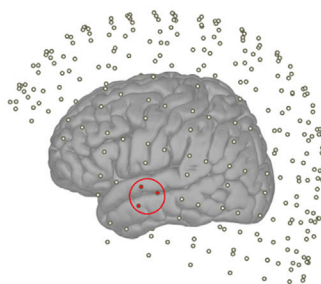


### 3. SVM classification

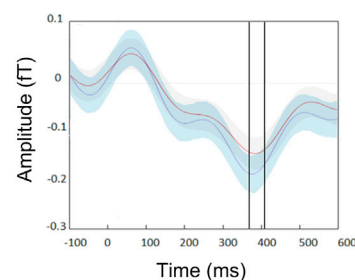


## B. Sensor-level ATL ROI

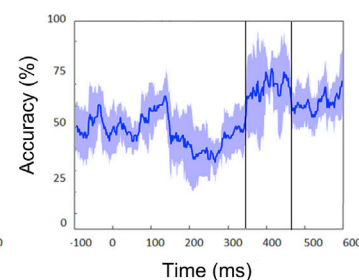
### 1. ROI location



### 2. Amplitude differences



### 3. SVM classification



**Fig. 2.** Sensor-level results. **(A1)** Location of the left sensor-level M1 ROI. **(A2)** Amplitudes and for the AV and nAV trial averages for the left M1 ROI (SEM in light blue for AVs and in light red for nAVs). **(A3)** Time-amplitude decoding via SVM. Classification accuracy in purple and SEM in light purple. The most significant classification cluster is marked within the time segment of 137–172 ms. **(B1)** Location of the left sensor-level ATL ROI. **(B2)** Amplitudes for the AV and nAV trial averages (SEM in light blue for AVs and in light red for nAVs). **(B3)** Time-amplitude decoding via SVM. Classification accuracy in purple and SEM in light purple. The most significant classification cluster is signaled within the time segment of 345–472 ms. ROI: region of interest; M1: primary motor area; ATL: anterior temporal lobe; AVs: action verbs; nAVs: non-action verbs; SEM: standard error of the mean.

## 3.3. Source-level results

### 3.3.1. Amplitude differences between conditions

Comparisons of amplitude for AVs and nAVs in source-level M1 ROIs across time (Fig. 3-A1) revealed significant differences between conditions. In the left M1 ROI, AVs yielded significantly higher activity ( $t = 3.32$ ,  $p < .05$ ) between 179 and 189 ms. The same was observed in the right M1 ROI throughout a 165–174 ms window ( $t = 2.46$ ,  $p < .05$ ). When both ROIs were taken together, amplitude increases for AVs over nAVs extended across a wider time window (157–184 ms) ( $t = 3.00$ ,  $p < .05$ , cluster-corrected). The latter result is shown in Fig. 3-A2.

Results from the ATL source-level ROIs also revealed higher activity for AVs than nAVs exclusively in later windows. In Dors-ATL (Fig. 3-B1), these differences emerged between 247 and 258 ms on the right hemisphere ( $t = 3.34$ ,  $p < .05$ , cluster-corrected), there being no significant effects for the left-hemisphere or the bilateral analyses ( $p > .05$ , cluster-corrected). In Post-ATL, whereas no significant differences were observed in the left-hemisphere analysis ( $p > .05$ , cluster-corrected), larger modulations for AVs did occur between 393 and 410 ms on the right hemisphere ( $t = 3.00$ ,  $p < .05$ , cluster-corrected), and between 399 and 409 ms in the bilateral analysis ( $t = 2.48$ ,  $p < .05$ , cluster-corrected). The former result is shown in Fig. 3-B2. Also, this pattern was replicated in a more anterior ventral ROI (see Supplemental Information B and Fig. S1). As was the case with sensor-level outcomes, the temporal separation of the significant windows in each ROI rules out the possibility of an overlap between their respective data distributions.

### 3.3.2. Machine-learning decoding

Similar results were obtained for classification between conditions based on source-level signals. Classification between AVs and nAVs for the bilateral M1 ROI reached its peak (71.15% mean accuracy) in an early window (104–173 ms) ( $t = 2.23$ ,  $p < .05$ ), with accuracy in every other time-point cluster interval falling below 68.78% (Fig. 3-A3). ATL results showed maximal classification in the right source-level ROI (64.88% mean accuracy) during a late time segment (373–499 ms) ( $t = 2.05$ ,  $p < .05$ ) –classification accuracy in every other time-point cluster interval fell below 59.34%. (Fig. 3-B3). Once again, compatible results were obtained upon considering modulations in a more anterior ventral ROI (see Supplemental Information B and Fig. S1). No statistically significant clusters were found for the left or right M1 ROIs, nor for the left or bilateral ATL ROIs.

## 4. Discussion

This study aimed to track the time-course of embodied and multi-modal semantic processes through inferential and machine-learning analyses. Sensor- and source-level results consistently revealed that differential modulations for AVs and nAVs occurred earlier in M1 (<190 ms) than in particular ATL hubs (>250 ms). Likewise, trial-by-trial classification peaks emerged faster in M1 (<175 ms) than in such ATL sites (>340 ms). On the assumption that the ATL is critically implicated in processing cross-modal meanings, these findings suggest that early semantic processes are critically driven by embodied reactivations and

that these are not epiphenomenal to more abstract conceptual operations. Such results offer important theoretical constraints for neuro-linguistic models, as detailed below.

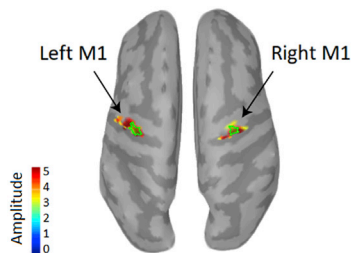
Amplitude analyses revealed consistently greater M1 modulations for AVs than nAVs in a window from ~130 to 190 ms, corroborating the critical role of motor hubs in grounding action meanings (Hauk et al., 2004; Tomasino et al., 2007, 2008). While evidence of embodied reactivations before the 100-ms mark (Shtyrov et al., 2014) proves controversial (Papeo and Caramazza, 2014; Shtyrov and Stroganova, 2015), several MEG (Mollo et al., 2016; Klepp et al., 2014; Pulvermüller et al., 2005; Boulenger et al., 2012) and EEG (Shtyrov et al., 2004; Hauk and Pulvermüller, 2004) studies point to virtually the very window we detected (120–200 ms) as the earliest period at which AVs elicit differential motor-system effects. Compatibly, initial embodied effects have been observed within a similar time span for other word classes, such as sound-evocative nouns (in auditory brain areas) (Kiefer et al., 2008) and negative markers (in inhibition-related areas) (Beltran et al., 2018). As claimed elsewhere (Pulvermüller, 2018), the latency of these modulations matches the earliest reported indexes of semantic activation, with a minimal (15–25 ms) delay from sensory access to linguistic input. Therefore, such results could hardly be interpreted as post-comprehension phenomena (Pulvermüller, 2018). By replicating these findings on both sensor- and source-level data, our study not only supports the primary nature of embodied reactivations during semantic processing, but it also highlights their cross-methodological systematicity.

Instead, data from both dimensions convergently showed that differential AV modulations in the target ATL ROIs only reached significance in a later (~250–410 ms) window. In fact, this was the case even

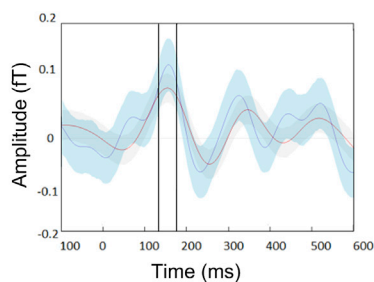
when considering a more putative ventral ATL ROI based on previously reported coordinates (as detailed in Supplemental Information B). Such a finding aligns with multiple MEG and intracranial studies (Ralph et al., 2017) indicating that detailed multimodal semantic distinctions in that region emerge after 250 (Shimotake et al., 2015; Chen et al., 2016), 300 (Abel et al., 2015; Lau et al., 2013), or even 400 (Jackson et al., 2015) ms post-stimulus presentation. Importantly, although earlier ATL effects have been reported, these typically reflect coarse-grained contrasts between particular *noun* types evoking concrete entities (Clarke et al., 2011, 2013; Mollo et al., 2017). Therefore, those findings may be markedly influenced by the general specialization of temporal areas for noun (as opposed to verb) processing (Vigliocco et al., 2011) and by the presence of specific networks for particular noun types within the ATL (Capitani et al., 2003). Indeed, the scant evidence of early (~150 ms) differences between AV types in multimodal regions (confined to posterior superior temporal sites) is objectively weak. The first study to report it (Pulvermüller et al., 2005) employed only two stimuli, thus proving statistically underpowered. The second one (Mollo et al., 2016) was undermined by its use of decontextualized base forms (like *kick* or *pick*). As it happens, in the absence of grammatical, co-lexical, or semantic constraints, such items could readily be interpreted as nouns (as used in sentences like *That was a fast kick* or *What's your pick for tonight?*). Thus, the study in question cannot guarantee that its target stimuli were actually processed as AVs. Moreover, the AV-related results captured therefrom were observed in only one out of three pre-400-ms windows, and with null effects in an ATL ROI. In this sense, by employing extended stimulus sets and ruling out word-class confounds through the use of present participle forms in a grammatically unambiguous context (e.g., *I am juggling*), our results suggest that AV-specific modulations in the ATL do not occur earlier than

## A. Source-level M1 ROI

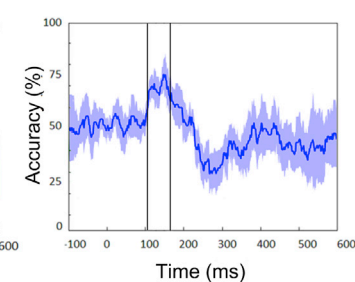
### 1. ROI location



### 2. Amplitude differences

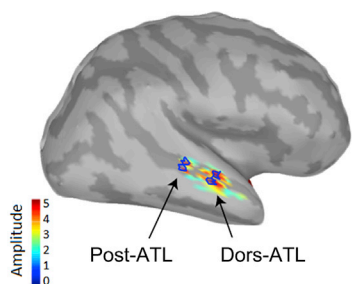


### 3. SVM classification

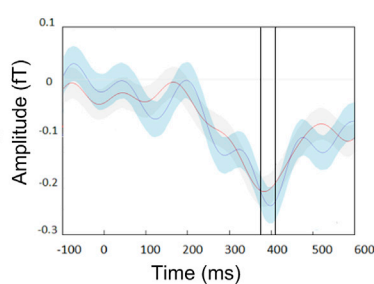


## B. Source-level ATL ROI

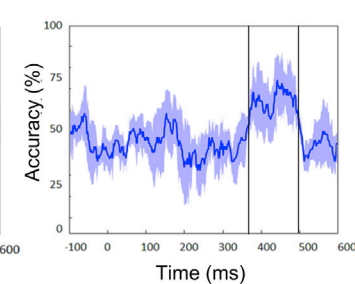
### 1. ROI location



### 2. Amplitude differences



### 3. SVM classification



**Fig. 3.** Source-level results. (A1) Results from the bilateral M1 ROI (signaled by two green dots). (A2) Amplitudes and for the AV and nAV trial averages for the bilateral M1 ROI (SEM in light blue for AVs and in light red for nAVs). (A3) Time-amplitude decoding via SVM. Classification accuracy in purple and SEM in light purple. The most significant classification cluster is marked within the time segment of 104–173 ms. (B1) Location of the right source-level ATL ROIs (signaled by blue dots). (B2) Amplitudes for the AV and nAV trial averages for the right source-level ATL ROIs (SEM in light blue for AVs and in light red for nAVs). (B3) Time-amplitude decoding via SVM. Classification accuracy in purple and SEM in light purple. The most significant classification cluster is signaled within the time segment of 373–499 ms. ROI: region of interest; M1: primary motor area; ATL: anterior temporal lobe; Dors-ATL: dorsal portion of the anterior temporal lobe; Post-ATL: posterior portion of the anterior temporal lobe. AVs: action verbs; nAVs: non-action verbs; SEM: standard error of the mean.

embodied effects in motor circuits.

The above conclusion is corroborated by SVM results. In M1, trial-by-trial classification of AVs and nAVs reached its peak in an early window (~100–175 ms). This result was consistent across sensor- and source-level data, the latter yielding maximal discrimination (71.15% accuracy) based on bilateral activity. Conversely, classification peaks for both data types (71.45% and 64.88%) emerged markedly later (~345–500 ms) in the ATL. These patterns mirror the time-course of our previous results and align with the windows evincing consistent semantic effects in embodied (Pulvermüller, 2018) and putative multimodal (Ralph et al., 2017) hubs. Even more crucially, they underscore the consistency of our findings across individual items. This is no trivial point, given that psycholinguistic variance in a stimulus set can bias average modulations in electrophysiological embodiment research (Shtyrov and Stroganova, 2015). Moreover, our SVM approach showed that discriminatory neural activity from a subset of subjects (training fold) affords high classification rates in another subsample (testing fold), attesting to the inter-individual robustness of the above results. In brief, our application of machine-learning analysis indicates that the presence of early M1 modulations for AV processing proves systematic across individual words and subjects.

Importantly, such AV-specific modulations were established relative to another verb category (nAVs). Thus, M1 effects cannot be attributed to the gross specialization of frontal circuits for verbs at large (Vigliocco et al., 2011). In fact, compared to nAVs (and other linguistic units), AVs can be distinctively impaired in patients with motor-network atrophy (García et al., 2016, 2018; Fernandino et al., 2013a, 2013b) and selectively boosted through whole-body motor training (Trevisan et al., 2017). Accordingly, we argue, the differential engagement of M1 during AV processing was specifically driven by these words' motoric associations rather than by unspecific properties of verbs in general. Importantly, note that all trials in our task were presented with an *identical* sentential structure –declarative, affirmative, active sentences, headed by a first-person singular pronoun (*I*) and followed by a present continuous structure for the verb phrase (*am verb + ing*). Therefore, the only difference between conditions was given by the semantic opposition between AVs and nAVs, which rules out potential morphosyntactic confounds.

Of note, our findings were obtained through a shallow-processing paradigm. As corroborated here, these tasks typically fail to elicit behavioral differences between AVs and nAVs (Boulenger et al., 2006, 2008; Nazir et al., 2008; Sato et al., 2008; Pulvermüller et al., 2001), arguably because embodied manipulations typically require explicit conceptual access to modulate overt behavior (García and Ibáñez, 2016). Yet, neurally speaking, early sensorimotor reactivations may only be interpreted as primary embodied effects if obtained via *implicit* semantic tasks (Mollo et al., 2016; Kiefer et al., 2008; Hauk et al., 2008), as observed in other studies yielding null behavioral effects (Mollo et al., 2016; Klepp et al., 2014; Pulvermüller et al., 2001). Since explicit word-meaning judgments are not necessary to perform lexical decisions, our study fulfills this requirement and attests to the pervasiveness of embodied reactivations during language processing.

Given these considerations, the present results stand against the 'symbolic view' and its implication that sensorimotor circuits only play epiphenomenal, modulatory, or non-primary roles in semantic processing (Lotto et al., 2009; Hickok, 2015). Rather, insofar as semantic effects before the 200-ms mark are unlikely to reflect post-comprehension processes (Pulvermüller, 2005, 2018; Shtyrov et al., 2014; Mollo et al., 2016; Klepp et al., 2014; Boulenger et al., 2012; Pulvermüller and Fadiga, 2010), this study supports the 'grounded view', as defined at the outset. Furthermore, it challenges the notion that semantic processing "[does not present] a temporal sequence in which early sensory-motor activity is followed by later retrieval in ATL" (49: 1). Although this claim may be right for certain word categories, such as nouns, our findings suggest that, at least for the particular multimodal hubs tested herein, AV-related

meanings may indeed be construed with such functional coordination. Therefore, the time-course of embodied and multimodal systems seems sensitive to the specific semantic features evoked by the words at hand.

Beyond chronometric considerations, this research also offers insights for *neuroanatomical* models of language. First, the detection of primary embodied effects for AVs aligns with studies showing consistent modulations for this word class in motor networks, but not in the ATL and other multimodal regions (Raposo et al., 2009; Mollo et al., 2016; Bedny et al., 2012; Rodriguez-Ferreiro et al., 2011), even when compared to nAVs (van Dam et al., 2010, 2012). This further emphasizes the preeminence of sensorimotor reactivations for accessing AV-specific features.

Second, our results inform ongoing discussions on the topography of relevant embodied networks. In particular, it has been claimed that the semantic grounding of AVs is principally afforded by premotor, as opposed to primary motor, circuits, and that the latter become only artifactually engaged by post-conceptual imagery (Willems et al., 2010). However, current findings, in line with several other studies (Hauk et al., 2004; Tomasino et al., 2007, 2008; for reviews, see Pulvermüller, 2005, 2018), show that M1 activity is actually critical for accessing AV-evoked meanings –with equally primary contributions from other motor hubs being a certain possibility.

Third, note that both sensor- and source-level analyses of amplitude revealed AV-specific modulations over the left hemisphere, with the latter replicating it on the right hemisphere. Although the predominance of left-sided M1 activations for AVs in our right-handed sample mirrors previous results (e.g., Boulenger et al., 2012; Mollo et al., 2016; Shtyrov et al., 2014; Willems et al., 2010), the contributions of right-hemispheric motor systems have also been acknowledged in integrative theoretical accounts (Pulvermüller, 2013). More particularly, right M1 involvement in our study likely reflects the dominant presence of bimanual and bipedal AVs (e.g., *applauding*, *sprinting*), as these words are distinctively linked to bilateral motor-cortex activations (Klepp et al., 2014; Hauk and Pulvermüller, 2011). However, this conjecture should be tested directly in new MEG studies.

Finally, the evidence suggests that, in addition to somatotopic activations (e.g., Pulvermüller, 2005; Tomasino et al., 2007), AVs can also elicit widespread resonance patterns across the motor cortex (Trevisan et al., 2017). Indeed, although the M1 ROI was established via a hand-specific localizer task, AVs denoted actions involving diverse effectors (e.g., *typing*, *sneezing*, *jumping*), sometimes in combination (e.g., *dancing*). It follows that hand-specific circuits were likely activated, to some degree, by words denoting movements of varied body parts. While this cannot be directly ascertained given our design, effector-specific AVs are known to recruit extra-somatotopic motor sites (Ibanez et al., 2013; Arevalo et al., 2012; Melloni et al., 2015), with activation peaks that rarely match probabilistically defined maps of such regions (Kemmerer and Gonzalez-Castillo, 2010). Therefore, although somatotopic (Pulvermüller, 2018) and effector-specific (García and Ibáñez, 2016) effects are well-established in the literature, early embodied reactivations also seem characterized by coarse-grained modulations along modality-preferential circuits.

Succinctly, this work lends strong support to the 'grounded view', further indicating that embodied reactivations during AV processing are (i) driven by fast semantic effects (rather than by epiphenomenal modulations following multimodal operations), (ii) specifically guided by action-related meanings (as opposed to general features of verbs), (iii) primary even in the absence of explicit semantic access, (iv) consistent across sensor- and source-level dimensions, (v) potentially identifiable via trial-by-trial classification, (vi) observable in M1 (as a complement to premotor) regions, and (vii) characterized by bilateral and widespread (as opposed to exclusively left-sided and somatotopic) motor resonance. Insofar as they are precise, these conclusions afford non-trivial empirical constraints in the ongoing quest to understand how meaning is construed in the human brain.



## 5. Limitations and avenues for further research

Notwithstanding, our study presents some limitations. First, our sample size was modest. Although most previous MEG studies on AVs have employed similar or identical Ns (Mollo et al., 2016; Klepp et al., 2014; Pulvermuller et al., 2005; Boulenger et al., 2012), replications with larger groups would be desirable. Second, while our hypothesis was tested with a focus on objectively crucial ROIs, the neural circuits underpinning AVs are not restricted to them. Future MEG studies should thus aim to examine the role of other relevant embodied and multimodal regions, such as the premotor cortex (Hauk et al., 2004; Willems et al., 2010) and the angular gyrus (Seghier, 2013; Binder and Desai, 2011), respectively. Indeed, earlier non-embodied modulations could be revealed by considering other multimodal regions either individually or in combination; this is particularly true for the ATL, a very broad region which allows for numerous partitioning approaches. Note, however, that even if such results did emerge they would not challenge the key finding that embodied reactivations play primary (non-epiphenomenal) roles during semantic processing. Third, even though AVs and nAVs were carefully matched in our design, the former were not subdivided into comparable subsets capable of revealing intra-categorical distinctions. New implementations of our approach could address this issue by contrasting verbs that imply different effectors or denote bimanual/bipedal vs. unimanual/unipedal actions, among other oppositions. Finally, although the use of identical sentence structures for all stimuli allowed us to rule out potential morphosyntactic confounds, it would be informative for further studies to assess whether the spatiotemporal patterns observed for AVs are modulated by contrastive sentential patterns.

## 6. Conclusion

In sum, this study compared the time-course of embodied and multimodal systems during AV processing through a combination of inferential and machine-learning analyses on multidimensional MEG data obtained through an implicit and lexically unambiguous task. Crucially, we found that, whereas M1 dynamics discriminated and classified AVs from nAVs in an early window (~130–190 ms), the ATL networks targeted herein did so in a later time span (~250–410 ms). These results indicate that, at least for words denoting bodily movements, sensorimotor reactivations constitute primary semantic effects rather than epiphenomenal modulations subsequent to conceptual discriminations, which supports the ‘grounded view’ of meaning while challenging the ‘symbolic view’. More generally, our findings afford important constraints for spatiotemporal semantic models while paving the way for new cross-methodological research in the field.

## Data availability statement

All experimental data, as well as the scripts used for their collection and analysis, are fully available online (Moguilner et al., 2018).

## Author contributions

A.M.G. designed the research; E.M.C., T.K., and E.G.M. performed the research; S.M., K.T., L.S., A.M.G., E.H., and E.M. analyzed the data; A.M.G., S.M., K.T., and A.I. wrote the paper.

## Conflicts of interest

The authors declare no association that poses or could be perceived as a financial or intellectual conflict of interest in connection with the manuscript.

## Acknowledgments

This work was partially supported by grants from CONICET,

FONCYT-PICT (2017–1818, 2017–1820), CONICYT/FONDECYT Regular (1170010), FONDAF 15150012, Global Brain Health Institute (GBHI-UCSF); Programa Interdisciplinario de Investigación Experimental en Comunicación y Cognición (PIIECC), Facultad de Humanidades, USACH and the INECO Foundation.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuroimage.2019.05.002>.

## References

- Abel, T.J., et al., 2015. Direct physiologic evidence of a heteromodal convergence region for proper naming in human left anterior temporal lobe. *J. Neurosci.* 35 (4), 1513–1520.
- Ahlfors, S.P., Han, J., Belliveau, J.W., Hamalainen, M.S., 2010. Sensitivity of MEG and EEG to source orientation. *Brain Topogr.* 23 (3), 227–232.
- Arevalo, A.L., Baldo, J.V., Dronkers, N.F., 2012. What do brain lesions tell us about theories of embodied semantics and the human mirror neuron system? *Cortex* 48 (2), 242–254.
- Aziz-Zadeh, L., Wilson, S.M., Rizzolatti, G., Iacoboni, M., 2006. Congruent embodied representations for visually presented actions and linguistic phrases describing actions. *Curr. Biol.* 16 (18), 1818–1823.
- Bedny, M., Caramazza, A., 2011. Perception, action, and word meanings in the human brain: the case from action verbs. *Ann. N. Y. Acad. Sci.* 1224, 81–95.
- Bedny, M., Caramazza, A., Pascual-Leone, A., Saxe, R., 2012. Typical neural representations of action verbs develop without vision. *Cerebr. Cortex* 22 (2), 286–293.
- Beltran, D., Muneton-Ayala, M., de Vega, M., 2018. Sentential negation modulates inhibition in a stop-signal task. Evidence from behavioral and ERP data. *Neuropsychologia* 112, 10–18.
- Binder, J.R., Desai, R.H., 2011. The neurobiology of semantic memory. *Trends Cognit. Sci.* 15 (11), 527–536.
- Binder, J.R., Desai, R.H., Graves, W.W., Conant, L.L., 2009. Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebr. Cortex* 19 (12), 2767–2796.
- Binney, R.J., Embleton, K.V., Jefferies, E., Parker, G.J., Ralph, M.A., 2010. The ventral and inferolateral aspects of the anterior temporal lobe are crucial in semantic memory: evidence from a novel direct comparison of distortion-corrected fMRI, rTMS, and semantic dementia. *Cerebr. Cortex* 20 (11), 2728–2738.
- Birba, A., et al., 2017. Losing ground: frontostriatal atrophy disrupts language embodiment in Parkinson's and Huntington's disease. *Neurosci. Biobehav. Rev.* 80, 673–687.
- Boulenger, V., et al., 2006. Cross-talk between language processes and overt motor behavior in the first 200 msec of processing. *J. Cogn. Neurosci.* 18 (10), 1607–1615.
- Boulenger, V., et al., 2008. Subliminal display of action words interferes with motor planning: a combined EEG and kinematic study. *J. Physiol. Paris* 102 (1–3), 130–136.
- Boulenger, V., Shtyrov, Y., Pulvermuller, F., 2012. When do you grasp the idea? MEG evidence for instantaneous idiom understanding. *Neuroimage* 59 (4), 3502–3513.
- Capitani, E., Laiacona, M., Mahon, B., Caramazza, A., 2003. What are the facts of semantic category-specific deficits? A critical review of the clinical evidence. *Cogn. Neuropsychol.* 20 (3), 213–261.
- Carota, F., Moseley, R., Pulvermüller, F., 2012. Body-part-specific representations of semantic noun categories. *J. Cogn. Neurosci.* 24 (6), 1492–1509.
- Chen, Y., et al., 2016. The 'when' and 'where' of semantic coding in the anterior temporal lobe: temporal representational similarity analysis of electrocorticogram data. *Cortex* 79, 1–13.
- Cheyne, D., Weinberg, H., 1989. Neuromagnetic fields accompanying unilateral finger movements: pre-movement and movement-evoked fields. *Exp. Brain Res.* 78 (3), 604–612.
- Clarke, A., Taylor, K.I., Tyler, L.K., 2011. The evolution of meaning: spatio-temporal dynamics of visual object recognition. *J. Cogn. Neurosci.* 23 (8), 1887–1899.
- Clarke, A., Taylor, K.I., Devereux, B., Randall, B., Tyler, L.K., 2013. From perception to conception: how meaningful objects are processed over time. *Cerebr. Cortex* 23 (1), 187–197.
- Cruz-Garza, J.G., Hernandez, Z.R., Nepal, S., Bradley, K.K., Contreras-Vidal, J.L., 2014. Neural decoding of expressive human movement from scalp electroencephalography (EEG). *Front. Hum. Neurosci.* 8, 188.
- van Dam, W.O., Rueschemeyer, S.A., Bekkering, H., 2010. How specifically are action verbs represented in the neural motor system: an fMRI study. *Neuroimage* 53 (4), 1318–1325.
- van Dam, W.O., van Dijk, M., Bekkering, H., Rueschemeyer, S.A., 2012. Flexibility in embodied lexical-semantic representations. *Hum. Brain Mapp.* 33 (10), 2322–2333.
- Davis, C.J., 2005. N-watch: a program for deriving neighborhood size and other psycholinguistic statistics. *Behav. Res. Methods* 37 (1), 65–70.
- Dreyer, F.R., Pulvermuller, F., 2018. Abstract semantics in the motor system? - an event-related fMRI study on passive reading of semantic word categories carrying abstract emotional and mental meaning. *Cortex* 100, 52–70.
- Esteppe, J.R., Christensen, J.C., 2015. Electrode replacement does not affect classification accuracy in dual-session use of a passive brain-computer interface for assessing cognitive workload. *Front. Neurosci.* 9, 54.

- Farahibozorg, S.R., Henson, R.N., Hauk, O., 2017. Adaptive cortical parcellations for source reconstructed EEG/MEG connectomes. *Neuroimage* 169, 23–45.
- Fernandino, L., et al., 2013. Parkinson's disease disrupts both automatic and controlled processing of action verbs. *Brain Lang.* 127 (1), 65–74.
- Fernandino, L., et al., 2013. Where is the action? Action sentence processing in Parkinson's disease. *Neuropsychologia* 51 (8), 1510–1517.
- Gaonkar, B., Davatzikos, C., 2013. Analytic estimation of statistical significance maps for support vector machine based multi-variate image analysis and classification. *Neuroimage* 78, 270–283.
- García, A.M., Ibáñez, A., 2016. A touch with words: dynamic synergies between manual actions and language. *Neurosci. Biobehav. Rev.* 68, 59–95.
- García, A.M., et al., 2016. The cerebellum and embodied semantics: evidence from a case of genetic ataxia due to STUB1 mutations. *J. Med. Genet.* 54, 114–124.
- García, A.M., et al., 2018. Parkinson's disease compromises the appraisal of action meanings evoked by naturalistic texts. *Cortex* 100, 111–126.
- Gerfo, E.L., et al., 2008. The influence of rTMS over prefrontal and motor areas in a morphological task: grammatical vs. semantic effects. *Neuropsychologia* 46 (2), 764–770.
- Gramfort, A., et al., 2014. MNE software for processing MEG and EEG data. *Neuroimage* 86, 446–460.
- Gross, J., et al., 2013. Good practice for conducting and reporting MEG research. *Neuroimage* 65, 349–363.
- Hamalainen, M., Ilmoniemi, R., 1984. Interpreting Measured Magnetic Fields of the Brain: Estimates of Current Distributions. Technical Report, Helsinki.
- Hauk, O., Pulvermüller, F., 2004. Neurophysiological distinction of action words in the fronto-central cortex. *Hum. Brain Mapp.* 21 (3), 191–201.
- Hauk, O., Pulvermüller, F., 2011. The lateralization of motor cortex activation to action-words. *Front. Hum. Neurosci.* 5 (149).
- Hauk, O., Johnsrude, I., Pulvermüller, F., 2004. Somatotopic representation of action words in human motor and premotor cortex. *Neuron* 41 (2), 301–307.
- Hauk, O., Shtyrov, Y., Pulvermüller, F., 2008. The time course of action and action-word comprehension in the human brain as revealed by neurophysiology. *J. Physiol. Paris* 102 (1), 50–58.
- Hickok, G., 2015. The motor system's contribution to perception and understanding actions: clarifying mirror neuron myths and misunderstandings. *Lang. Cognit.* 7 (3), 476–484.
- Hirshorn, E.A., Li, Y., Ward, M.J., Richardson, R.M., Fiez, J.A., Ghuman, A.S., 2016. Decoding and disrupting left midfusiform gyrus activity during word reading. *Proc. Natl. Acad. Sci. U.S.A.* 113 (29), 8162–8167.
- Humphreys, G.F., Hoffman, P., Visser, M., Binney, R.J., Lambon Ralph, M.A., 2015. Establishing task- and modality-dependent dissociations between the semantic and default mode networks. *Proc. Natl. Acad. Sci. Unit. States Am.* 112 (25), 7857–7862.
- Ibáñez, A., et al., 2013. Motor-language coupling: direct evidence from early Parkinson's disease and intracranial cortical recordings. *Cortex* 49 (4), 968–984.
- Jackson, R.L., Lambon Ralph, M.A., Pobric, G., 2015. The timing of anterior temporal lobe involvement in semantic processing. *J. Cogn. Neurosci.* 27 (7), 1388–1396.
- Jefferies, E., Patterson, K., Jones, R.W., Lambon Ralph, M.A., 2009. Comprehension of concrete and abstract words in semantic dementia. *Neuropsychology* 23 (4), 492–499.
- Kemmerer, D., Gonzalez-Castillo, J., 2010. The two-level theory of verb meaning: an approach to integrating the semantics of action with the mirror neuron system. *Brain Lang.* 112 (1), 54–76.
- Kiefer, M., Sim, E.-J., Herrnberger, B., Grothe, J., Hoenig, K., 2008. The sound of concepts: four markers for a link between auditory and conceptual brain systems. *J. Neurosci.* 28 (47), 12224–12230.
- Klepp, A., et al., 2014. Neuromagnetic hand and foot motor sources recruited during action verb processing. *Brain Lang.* 128 (1), 41–52.
- Klepp, A., Nicolai, V., Buccino, G., Schnitzler, A., Biermann-Ruben, K., 2015. Language-motor interference reflected in MEG beta oscillations. *Neuroimage* 109, 438–448.
- Kristeva-Feige, R., et al., 1994. A neuromagnetic study of the functional organization of the sensorimotor cortex. *Eur. J. Neurosci.* 6 (4), 632–639.
- Kuperman, V.H., Stadthagen-Gonzalez, 2012. Age-of-acquisition ratings for 30,000 English words. *Behav. Res. Methods* 44 (4), 978–990.
- Lambon Ralph, M.A., Lowe, C., Rogers, T.T., 2007. Neural basis of category-specific semantic deficits for living things: evidence from semantic dementia, HSVE and a neural network model. *Brain* 130 (Pt 4), 1127–1137.
- Lambon Ralph, M.A., Ehsan, S., Baker, G.A., Rogers, T.T., 2012. Semantic memory is impaired in patients with unilateral anterior temporal lobe resection for temporal lobe epilepsy. *Brain* 135 (Pt 1), 242–258.
- Lambon Ralph, M.A., Jefferies, E., Patterson, K., Rogers, T.T., 2017. The neural and computational bases of semantic cognition. *Nat. Rev. Neurosci.* 18 (1), 42–55.
- Lau, E.F., Gramfort, A., Hämäläinen, M.S., Kuperberg, G.R., 2013. Automatic semantic facilitation in anterior temporal cortex revealed through multimodal neuroimaging. *J. Neurosci.* 33 (43), 17174–17181.
- Liljestrom, M., et al., 2008. Perceiving and naming actions and objects. *Neuroimage* 41 (3), 1132–1141.
- Lin, F.H., et al., 2006. Assessing and improving the spatial accuracy in MEG source localization by depth-weighted minimum-norm estimates. *Neuroimage* 31 (1), 160–171.
- Liuzzi, G., et al., 2010. The involvement of the left motor cortex in learning of a novel action word lexicon. *Curr. Biol.* 20 (19), 1745–1751.
- Lotto, A.J., Hickok, G.S., Holt, L.L., 2009. Reflections on mirror neurons and speech perception. *Trends Cognit. Sci.* 13 (3), 110–114.
- Melloni, M., et al., 2015. Cortical dynamics and subcortical signatures of motor-language coupling in Parkinson's disease. *Sci. Rep.* 5, 11899.
- Moguliner, S., García, A.M., Castillo, E.M., 2018. Data from “How meaning unfolds in neural time.” GIN G-Node. [https://web.gin.g-node.org/Sebastian\\_Moguliner/How\\_meaning\\_unfolds\\_in\\_neural\\_time](https://web.gin.g-node.org/Sebastian_Moguliner/How_meaning_unfolds_in_neural_time).
- Mollo, G., Pulvermüller, F., Hauk, O., 2016. Movement priming of EEG/MEG brain responses for action-words characterizes the link between language and action. *Cortex* 74, 262–276.
- Mollo, G., Cornelissen, P.L., Millman, R.E., Ellis, A.W., Jefferies, E., 2017. Oscillatory dynamics supporting semantic cognition: MEG evidence for the contribution of the anterior temporal lobe hub and modality-specific spokes. *PLoS One* 12 (1), e0169269.
- Moreno, I., de Vega, M., Leon, I., 2013. Understanding action language modulates oscillatory mu and beta rhythms in the same way as observing actions. *Brain Cogn.* 82 (3), 236–242.
- Moreno, I., de Vega, M., León, I., 2013. Understanding action language modulates oscillatory mu and beta rhythms in the same way as observing actions. *Brain Cogn.* 82 (3), 236–242.
- Moreno, I., et al., 2015. Brain dynamics in the comprehension of action-related language. A time-frequency analysis of mu rhythms. *Neuroimage* 109, 50–62.
- Nazir, T.A., et al., 2008. Language-induced motor perturbations during the execution of a reaching movement. *Q. J. Exp. Psychol. (Hove)* 61 (6), 933–943.
- Papeo, L., Caramazza, A., 2014. When “ultrapid” word-related motor activity is not faster than “early”. *Front. Hum. Neurosci.* 8, 842.
- Papeo, L., Vallesi, A., Isaia, A., Rumiati, R.I., 2009. Effects of TMS on different stages of motor and non-motor verb processing in the primary motor cortex. *PLoS One* 4 (2), e4508.
- Patterson, K., Nestor, P.J., Rogers, T.T., 2007. Where do you know what you know? The representation of semantic knowledge in the human brain. *Nat. Rev. Neurosci.* 8 (12), 976–987.
- Pobric, G., Jefferies, E., Lambon Ralph, M.A., 2010. Category-specific versus category-general semantic impairment induced by transcranial magnetic stimulation. *Curr. Biol.* 20 (10), 964–968.
- Pobric, G., Jefferies, E., Ralph, M.A., 2010. Amodal semantic representations depend on both anterior temporal lobes: evidence from repetitive transcranial magnetic stimulation. *Neuropsychologia* 48 (5), 1336–1342.
- Del Prato, P., Pykkänen, L., 2014. MEG evidence for conceptual combination but not numeral quantification in the left anterior temporal lobe during language production. *Front. Psychol.* 5 (524).
- Pulvermüller, F., 2005. Brain mechanisms linking language and action. *Nat. Rev. Neurosci.* 6 (7), 576–582.
- Pulvermüller, F., 2013. How neurons make meaning: brain mechanisms for embodied and abstract-symbolic semantics. *Trends Cognit. Sci.* 17 (9), 458–470.
- Pulvermüller, F., 2018. Neural reuse of action perception circuits for language, concepts and communication. *Prog. Neurobiol.* 160, 1–44.
- Pulvermüller, F., Fadiga, L., 2010. Active perception: sensorimotor circuits as a cortical basis for language. *Nat. Rev. Neurosci.* 11 (5), 351–360.
- Pulvermüller, F., Harle, M., Hummel, F., 2001. Walking or talking? Behavioral and neurophysiological correlates of action verb processing. *Brain Lang.* 78 (2), 143–168.
- Pulvermüller, F., Hauk, O., Nikulin, V.V., Ilmoniemi, R., 2005. Functional links between motor and language systems. *Eur. J. Neurosci.* 21, 793–797.
- Pulvermüller, F., Shtyrov, Y., Ilmoniemi, R., 2005. Brain signatures of meaning access in action word recognition. *J. Cogn. Neurosci.* 17 (6), 884–892.
- Pulvermüller, F., Kherif, F., Hauk, O., Mohr, B., Nimmo-Smith, I., 2009. Distributed cell assemblies for general lexical and category-specific semantic processing as revealed by fMRI cluster analysis. *Hum. Brain Mapp.* 30 (12), 3837–3850.
- Ralph, M.A., Jefferies, E., Patterson, K., Rogers, T.T., 2017. The neural and computational bases of semantic cognition. *Nat. Rev. Neurosci.* 18 (1), 42–55.
- Raposo, A., Moss, H.E., Stamatakis, E.A., Tyler, L.K., 2009. Modulation of motor and premotor cortices by actions, action words and action sentences. *Neuropsychologia* 47 (2), 388–396.
- Repetto, C., Colombo, B., Cipresso, P., Riva, G., 2013. The effects of rTMS over the primary motor cortex: the link between action and language. *Neuropsychologia* 51 (1), 8–13.
- Rodriguez-Ferreiro, J., Gennari, S.P., Davies, R., Cueto, F., 2011. Neural correlates of abstract verb processing. *J. Cogn. Neurosci.* 23 (1), 106–118.
- Ruschmeyer, S.A., Brass, M., Friederici, A.D., 2007. Comprehending prehearing: neural correlates of processing verbs with motor stems. *J. Cogn. Neurosci.* 19 (5), 855–865.
- Santana, E.J., de Vega, M., 2013. An ERP study of motor compatibility effects in action language. *Brain Res.* 1526, 71–83.
- Sato, M., Mengarelli, M., Riggio, L., Gallese, V., Buccino, G., 2008. Task related modulation of the motor system during language processing. *Brain Lang.* 105 (2), 83–90.
- Schneider, W., Eschman, A., Zuccolotto, A., 2002. E-prime Reference Guide. Psychology Software Tools, Pittsburgh, PA).
- Seghier, M.L., 2013. The angular gyrus: multiple functions and multiple subdivisions. *Neuroscientist: Rev. J. Bringing Neurobiol. Neurol. Psychiatr.* 19 (1), 43–61.
- Shimotake, A., et al., 2015. Direct exploration of the role of the ventral anterior temporal lobe in semantic memory: cortical stimulation and local field potential evidence from subdural grid electrodes. *Cerebr. Cortex* 25 (10), 3802–3817.
- Shtyrov, Y.Y., Stroganova, T.A., 2015. When ultrarapid is ultrarapid: on importance of temporal precision in neuroscience of language. *Front. Hum. Neurosci.* 9, 576.
- Shtyrov, Y., Hauk, O., Pulvermüller, F., 2004. Distributed neuronal networks for encoding category-specific semantic information: the mismatch negativity to action words. *Eur. J. Neurosci.* 19 (4), 1083–1092.
- Shtyrov, Y., Butorina, A., Nikolaeva, A., Stroganova, T., 2014. Automatic ultrarapid activation and inhibition of cortical motor systems in spoken word comprehension. *Proc. Natl. Acad. Sci. U. S. A.* 111 (18), E1918–E1923.

- Tadel, F., Baillet, S., Mosher, J.C., Pantazis, D., Leahy, R.M., 2011. Brainstorm: a user-friendly application for MEG/EEG analysis. *Comput. Intell. Neurosci.* 2011, 879716.
- Tan, H.M., Gross, J., Uhlhaas, P.J., 2016. MEG sensor and source measures of visually induced gamma-band oscillations are highly reliable. *Neuroimage* 137, 34–44.
- Taulu, S., Simola, J., 2006. Spatiotemporal signal space separation method for rejecting nearby interference in MEG measurements. *Phys. Med. Biol.* 51 (7), 1759–1768.
- Tettamanti, M., et al., 2005. Listening to action-related sentences activates fronto-parietal motor circuits. *J. Cogn. Neurosci.* 17 (2), 273–281.
- Tomasino, B., Werner, C.J., Weiss, P.H., Fink, G.R., 2007. Stimulus properties matter more than perspective: an fMRI study of mental imagery and silent reading of action phrases. *Neuroimage* 36, T128–T141.
- Tomasino, B., Fink, G.R., Sparing, R., Dafotakis, M., Weiss, P.H., 2008. Action verbs and the primary motor cortex: a comparative TMS study of silent reading, frequency judgments, and motor imagery. *Neuropsychologia* 46 (7), 1915–1926.
- Trevisan, P., Sedeño, L., Birba, A., Ibáñez, A., García, A.M., 2017. A moving story: whole-body motor training selectively improves the appraisal of action meanings in naturalistic narratives. *Sci. Rep.* 7 (1), 12538.
- Urrutia, M., de Vega, M., Bastiaansen, M., 2012. Understanding counterfactuals in discourse modulates ERP and oscillatory gamma rhythms in the EEG. *Brain Res.* 1455, 40–55.
- Vigliocco, G., Vinson, D.P., Druks, J., Barber, H., Cappa, S.F., 2011. Nouns and verbs in the brain: a review of behavioural, electrophysiological, neuropsychological and imaging studies. *Neurosci. Biobehav. Rev.* 35 (3), 407–426.
- Visser, M., Jefferies, E., Embleton, K.V., Lambon Ralph, M.A., 2012. Both the middle temporal gyrus and the ventral anterior temporal area are crucial for multimodal semantic processing: distortion-corrected fMRI evidence for a double gradient of information convergence in the temporal lobes. *J. Cogn. Neurosci.* 24 (8), 1766–1778.
- Dalla Volta, R., Fabbri-Destro, M., Gentilucci, M., Avanzini, P., 2014. Spatiotemporal dynamics during processing of abstract and concrete verbs: an ERP study. *Neuropsychologia* 61, 163–174.
- Dalla Volta, R., Avanzini, P., De Marco, D., Gentilucci, M., Fabbri-Destro, M., 2018. From meaning to categorization: the hierarchical recruitment of brain circuits selective for action verbs. *Cortex* 100, 95–110.
- White, L.E., et al., 1997. Structure of the human sensorimotor system. *Cerebr. Cortex* 7 (1), 18–30.
- Willems, R.M., Hagoort, P., Casasanto, D., 2010. Body-specific representations of action verbs: neural evidence from right- and left-handers. *Psychol. Sci.* 21 (1), 67–74.
- Willems, R.M., Labruna, L., D'Esposito, M., Ivry, R., Casasanto, D., 2011. A functional role for the motor system in language understanding: evidence from theta-burst transcranial magnetic stimulation. *Psychol. Sci.* 22 (7), 849–854.
- Zwaan, R.A., 2014. Embodiment and language comprehension: reframing the discussion. *Trends Cognit. Sci.* 18 (5), 229–234.