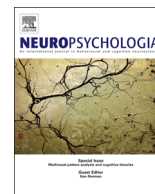




ELSEVIER

Contents lists available at ScienceDirect

## Neuropsychologia

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

## Spatiotemporal dynamics during processing of abstract and concrete verbs: An ERP study



Riccardo Dalla Volta<sup>a,b,\*</sup>, Maddalena Fabbri-Destro<sup>c,1</sup>, Maurizio Gentilucci<sup>b,c,d</sup>,  
Pietro Avanzini<sup>b</sup>

<sup>a</sup> Dipartimento di Scienze Mediche e Chirurgiche, Magna Graecia University, Viale Europa, Loc. Germaneto, 88100 Catanzaro, Italy

<sup>b</sup> Dipartimento di Neuroscienze, University of Parma, Parma, Italy

<sup>c</sup> Brain Center for Social and Motor Cognition, IIT (Italian Institute of Technology), Parma, Italy

<sup>d</sup> RTM (Rete Tecnologica Multidisciplinare), Italy

### ARTICLE INFO

#### Article history:

Received 8 June 2013

Received in revised form

13 June 2014

Accepted 13 June 2014

Available online 21 June 2014

#### Keywords:

Abstract verbs

Concrete verbs

High density EEG

ERPs

Embodied theory

### ABSTRACT

Different accounts have been proposed to explain the nature of concept representations. Embodied accounts claim a key involvement of sensory-motor systems during semantic processing while more traditional accounts posit that concepts are abstract mental entities independent of perceptual and motor brain systems. While the involvement of sensory-motor areas in concrete language processing is supported by a large number of studies, this involvement is far from being established when considering abstract language. The present study addressed abstract and concrete verb processing, by investigating the spatiotemporal dynamics of evoked responses by means of high density EEG while participants performed a semantic decision task. In addition, RTs to the same set of stimuli were collected. In both early and late time intervals, ERP scalp topography significantly differed according to word categories. Concrete verbs showed involvement of parieto-frontal networks for action, according to the implied body effector. In contrast, abstract verbs recruited mostly frontal regions outside the motor system, suggesting a non-motor semantic processing for this category. In addition, differently from what has been reported during action observation, the parietal recruitment related to concrete verbs presentation followed the frontal one. The present findings suggest that action word semantic is grounded in sensory-motor systems, provided a bodily effector is specified, while abstract concepts' representation cannot be easily explained by a motor embodiment.

© 2014 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/3.0/>).

### 1. Introduction

How does the brain represent the meaning of language? The precise nature of semantic knowledge is still controversial. According to a more traditional perspective, cognitive science defines semantic representations as mental entities that are abstract in nature, namely different from the brain perceptual and motor systems by which individuals interact with the world (Pylyshyn, 1984; Quillian, 1969; Tyler & Moss, 2001). *Amodal theories* claim that individuals initially represent the external and internal world in perceptual and motor systems by means of sensory and motor formats but when these representations are progressively integrated they lose their modality-specific attributes and become

coded by an amodal format. These amodal representations then are stored outside sensory and motor areas and are the substrate of semantic memories related to objects and events. Following this view, the attribution of meaning to language requires accessing information stored in heteromodal brain cortices, while the contribution of sensory and motor areas would be corollary (for review, see Mahon and Caramazza (2008)).

In contrast, *modality-specific* theories claim that the perceptual and motor systems are crucially involved in cognition and reject the notion that semantic processing primarily occurs in separate association cortices. This means that semantic knowledge is functionally and neuroanatomically grounded on these systems (*grounded cognition* or *embodiment theory*) (Barsalou, Kyle Simmons, Barbey, & Wilson, 2003; Gallese & Lakoff, 2005; Kiefer & Spitzer, 2001; Lakoff & Johnson, 1999; Pulvermüller, 2005; Warrington & Shallice, 1984; Zwaan & Taylor, 2006). Embodied cognition states that language understanding is grounded in the rehearsal of sensory and motor experiences related to the specific meaning that language carries on. For instance, comprehending

\* Corresponding author at: Dipartimento di Scienze Mediche e Chirurgiche, Magna Graecia University, Viale Europa, Loc. Germaneto, 88100 Catanzaro, Italy. Tel.: +39 961 3694138.

E-mail address: [riccardo.dallavolta@unicz.it](mailto:riccardo.dallavolta@unicz.it) (R. Dalla Volta).

<sup>1</sup> The authors contributed equally to the work.

the verb ‘to grasp’ involves the recruitment of sensory-motor experiences related to the action of grasping an object. Mechanistic models based on Hebbian principles of association learning (Hebb, Lambert, & Tucker, 1971; Braitenberg & Pulvermueller, 1992; Pulvermueller, 1999; Wennekers, Garagnani, & Pulvermueller, 2006) have been proposed to explain how sensory-motor areas of the brain become connected with core language areas. Pulvermueller (1999, 2001) noted that language acquisition tends to occur in the context of experiencing objects or acting in the real world. In general, during development, a meaningful relationship would be established by matching a word sound with simultaneously occurring sensory-motor experiences. Connecting perceptual and motor abilities with cognitive capacities contradicts with traditional views which assume a clear-cut separation between the former, low level and modality-specific processes and the latter, high level and amodal processes.

So far, a large amount of evidence has been accumulated showing sensory-motor involvement during processing of *concrete language* (for review, see Kiefer and Pulvermueller (2012)). A number of neuroimaging studies showed that specific motor circuits become active during action-related language comprehension (Hauk, Johnsrude, & Pulvermueller, 2004; Tettamanti et al., 2005; Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Kemmerer, Castillo, Talavage, Patterson, & Wiley, 2008; Boulenger, Hauk, & Pulvermueller, 2009; Willems, Toni, Hagoort, & Casasanto, 2010; Hauk & Pulvermueller, 2011). However, several studies suggest that the degree to which a modality-specific region contributes to a semantic representation may considerably vary (Raposo, Moss, Stamatakis, & Tyler, 2009; Rueschemeyer, Glenberg, Kaschak, Mueller, & Friederici, 2010; Van Dam, van Dijk, Bekkering, & Rueschemeyer, 2012). These findings have been interpreted by the authors as suggesting that the recruitment of sensory-motor system is not automatic but rather flexible and it may change as a function of the context in which action words are processed (e.g., focus on motor versus visual properties) and the type of strategy adopted to accomplish a task at hand. Finally, other investigations failed to find a clear link between motor areas and action or tool knowledge (Garcea, Dombovy, & Mahon, 2013; Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005; Negri et al. 2007).

Even if debated, a link between sensory-motor areas and concrete language is more plausible while instead the involvement of these same areas during *abstract language* processing does not appear so straightforward. By definition, abstract language does not refer to physical objects nor to actions performed with a body effector and, therefore, an embodied perspective does not seem to be well suited for representing abstract content in sensory and motor systems. Until recently, in fact, many influential accounts favored a non-embodied representation for this class of concepts. According to the dual coding theory (DCT) (Paivio, 1986), abstract concepts are exclusively represented in a verbal and symbolic system, while concrete terms rely also on a distinct non-verbal imagery system. This multiple coding for concrete words would explain the so-called *concreteness effect*, that is a processing advantage for concrete relative to abstract words (James, 1975). According to the context availability theory (CAT) (Schwanenflugel, 1991; Schwanenflugel & Shoben, 1983), abstract concepts are represented in a single symbolic system shared with concrete concepts. Processing differences between abstract and concrete words are attributable to the fact that concrete words have stronger semantic relations with the context represented by other words or supplied by comprehender’s own semantic memory.

While DCT and CAT are non-embodied perspectives as far as abstract language is concerned, also modality-specific approaches have been proposed. Lakoff and Johnson (1980), for instance, observed that abstract concepts are often defined *metaphorically*

by means of terms that are more concrete. Hence, abstract concepts may become closely linked to concrete concepts emerging directly from our experience. Basically, both concrete and abstract concepts are assumed to be similarly grounded in perception and action (Barsalou & Wiemer-Hastings, 2005; Kiefer & Barsalou, 2011; Pulvermueller, 2008). Glenberg, Sato, and Cattaneo (2008a) and Glenberg et al. (2008b) suggested a causal link between the motor system activation and the comprehension of both concrete and abstract language. In a behavioral study (Glenberg et al., 2008a), they showed that use-induced neural plasticity in the motor system affected processes involved in the comprehension of both concrete and abstract language. Moreover, abstract concepts are usually embedded in a concrete context that is experienced (and acted upon). Eventually, these contextual sensory-motor experiences come up to constitute the content of those concepts (Kiefer & Pulvermueller, 2012; Scorolli et al., 2011).

Differences between abstract and concrete language have been investigated by means of different techniques. Some functional Magnetic Resonance Imaging (fMRI) studies found more activation for abstract compared to concrete words in left inferior frontal cortex (Fiebach & Friederici, 2004; Noppeney & Price, 2004; Sabsevitz, Medler, Seidenberg, & Binder, 2005) while others investigated the embodiment of abstract sentences. Boulenger et al., 2009 reported somatotopic activation for idiomatic sentences (e.g., *he grasps the idea*) while two other studies failed to find such effects for abstract language (Aziz-Zadeh et al., 2006; Raposo et al., 2009).

While showing a high spatial resolution, metabolic neuroimaging data is affected by a low temporal resolution. Different techniques should then be employed when investigating the time course of language understanding. The time issue is crucial for determining whether a brain area is causally involved in word comprehension. In fact, it has been suggested that late post-comprehension processes occur following lexico-semantic information access (Glenberg & Kaschak, 2002). Electroencephalography (EEG) and magnetoencephalography (MEG) measure brain responses with millisecond temporal resolution. Using event-related responses, differences between concrete and abstract words have been found that are distributed in a wide temporal range. There is evidence suggesting that semantic information may be retrieved already within 250 ms after the stimulus presentation (Boulenger, Hoen, Jacquier, & Meunier, 2011; Hauk & Pulvermueller, 2004; Kellenbach, Wijers, Hovius, Mulder, & Mulder, 2002; Moscoso del Prado Martín, Hauk, & Pulvermueller, 2006; Pulvermueller, Haerle, & Hummel, 2001; Pulvermueller, Shtyrov, & Ilmoniemi, 2005; for review see Hauk, Shtyrov, and Pulvermueller (2008); Pulvermueller, Shtyrov, and Hauk (2009)). The same has been reported also in TMS studies (Buccino et al. 2005; Glenberg et al., 2008a; Innocenti, De Stefani, Sestito, & Gentilucci, 2014). Other studies found that the semantic content of a stimulus is capable of modulating the amplitude of a negative deflection of the EEG signal peaking at about 400 ms after stimulus onset, namely the well-known N400 effect (Kounios & Holcomb, 1994; Holcomb, Kounios, Anderson, & West, 1999; Nittono, Suehiro, & Hori, 2002; Swaab, Baynes, & Knight, 2002; Dhond, Witzel, Dale, & Halgren, 2007; Tsai et al., 2009; see review in Kutas and Federmeier (2011)). Summing up, the latency of neurophysiological responses may help in disambiguating between correlates of semantic information processing and secondary processes following early semantic information access.

In conclusion, different theories have been put forward in order to account for the nature of semantic representations. According to embodied theories, a sensory-motor system involvement is expected during processing of concrete and possibly of abstract

language. On the contrary, according to a more traditional verbal-symbolic account, language should be primarily represented in a rather amodal fashion not directly linked to the perceptual and motor systems. Moreover, when considering the functional role of brain responses related to the processing of language it is mandatory to investigate their temporal relationships.

Starting from this premise, the general aim of the present work was to investigate the temporal and spatial dynamics of ERPs related to the presentation of abstract and concrete verbs by means of high density EEG and a behavioral study. The unique temporal resolution provided by ERP investigation will allow us to determine when the brain responses to abstract and concrete language diverge. The topographic analysis will not focus on the peaks of the ERP signal, as some previous reports did, but it will specifically consider the time intervals where the EEG scalp maps differ across conditions, in order to also capture more fine-grained dynamics of verb processing. Early differences (within the first 400 ms) during a semantic judgment would suggest that distinct types of lexico-semantic access characterize the two verbal categories, while later time intervals may reflect different post-understanding strategies. Concomitantly, by looking at the brain generators, we will be able to determine which areas are specifically involved in generating the observed differences among verb categories.

As far as concrete language is concerned, the embodied perspective postulates a sensory-motor involvement during comprehension. Consequently, an early recruitment of sensory and/or motor regions is expected to confirm embodiment assumptions. According to amodal perspectives, on the other hand, a recruitment of modality-specific brain regions is not expected at all or at least it may be observed in a late time interval, as part of post-understanding processes. As far as abstract language is concerned, finding a sensory-motor involvement would support a strong declination of embodiment, while according to amodal theories we should not obtain this type of findings. Finally, the observation that concrete and abstract verbs recruit different brain regions and different representational formats would be in line with proposals such as the DCT.

**2. Methods**

**2.1. Participants**

Twelve (4 males) native Italian speakers participated in the EEG study and 26 (12 males) native Italian speakers different from the previous ones participated in the behavioral study. They had normal or corrected-to-normal vision and no history of neurological or psychiatric disorder. The mean age of the volunteers was 27.5 ± 5.9 years. All were right-handed, as ascertained by the Edinburgh Handedness Inventory (Oldfield, 1971). The research was conducted according to the principles expressed in the Declaration of Helsinki. It has been approved by the Comitato Etico Unico per la Provincia di Parma, Italy. Before the experiment, participants gave written informed consent.

**2.2. Stimuli**

Stimuli were selected from a written Italian database (COLFIS; Laudanna, Thornton, Brown, Burani, & Marconi, 1995; 3.798.000 words) using psycholinguistic criteria. A preliminary list of 400 Italian verbs was evaluated in a validation study to assess the cognitive, emotional, and referential-semantic properties of the to-be-used words. This step was crucial to select verb categories homogeneous in terms of several variables known to elicit different neurophysiological responses (Kounios & Holcomb, 1992; Pulvermüller, 1999; Skrandies, 1998).

Native Italian speakers (N=80, different from those participating in the EEG and control studies) gave ratings on a 5-point Likert scale about the concreteness, arm-relatedness, Foot-relatedness, Mouth-relatedness, Imageability, Valence and Arousal of a subset of the preliminary list. Ratings were given on a continuum from 1 (i.e., very low) to 5 (i.e., very high). To index verb selectivity for a given body effector (e.g., hand) over the others, the ratio of the square of the effector-relatedness score (hand-relatedness<sup>2</sup>) to the quadratic sum of the other two

**Table 1** Mean values of psycholinguistic variables for each verb category. Lexical Frequency is number of occurrences per million according to the COLFIS database. Concreteness, Hand-, Foot-, Mouth-relatedness, visual Imageability, Valence and emotional Involvement scores are those of the validation questionnaire (N=80). Hand, foot and mouth Indexes indicate how much a verb category is related to one of the three body effectors compared to the other two (square of the specific effector score relative to the quadratic sum of the other two effector scores). Word Length is mean number of characters. p-Values of ANOVA's comparing the different verb categories for each psycholinguistic variable are shown below the corresponding variable. A=Abstract, F=Foot, H=Hand, M=Mouth.

	Lexical frequency	Concreteness	Hand-relatedness	Foot-relatedness	Mouth-relatedness	Visual imageability	Valence	Emotional involvement	Hand index	Foot index	Mouth index	Word length
Abstract	170.28 ± 221.74	1.03 ± 0.06	1.23 ± 0.24	1.06 ± 0.13	2.16 ± 0.51	2.18 ± 0.46	3.14 ± 0.47	3.09 ± 0.34	0.27	0.2	1.87	8.44 ± 1
Foot	95.2 ± 180.55	2.94 ± 0.11	1.42 ± 0.25	4.77 ± 0.31	1.32 ± 0.27	4.26 ± 0.4	3.14 ± 0.65	2.88 ± 0.55	0.08	6.53	0.07	8.88 ± 1.3
Hand	95.88 ± 312.47	2.91 ± 0.79	4.9 ± 1.44	1.1 ± 0.37	1.23 ± 0.5	4.37 ± 1.33	3.13 ± 1.37	2.77 ± 1.26	8.91	0.04	0.06	8.4 ± 1.1
Mouth	51.84 ± 92.08	2.81 ± 0.22	1.09 ± 0.17	1.01 ± 0.04	4.75 ± 0.2	4.25 ± 0.42	2.8 ± 0.75	3.01 ± 0.58	0.05	0.04	10.38	8.44 ± 1.5
p ANOVA	0.283	< .001				< .001	0.431	0.473				
(A - F - H - M)												
p ANOVA (F - H - M)	0.703	0.607				0.830	0.369	0.613				

effector-relatedness scores (Foot-relatedness<sup>2</sup>+Mouth-relatedness<sup>2</sup>) were computed. Subsequently, concrete items were selected so as to maximize the verb selectivity indices. To test if the verb groups were matched with respect to the main linguistic variables, a one-way ANOVA with Condition as factor (4 levels: Abstract, Foot-, Hand-, and Mouth-related) was conducted to check for Lexical Frequency (according to the COLFIS database), verb Length, Concreteness, visual Imageability, Valence and emotional Involvement. In addition, the same statistical analysis was conducted considering only the three concrete verb groups. On the basis of these evaluations, we selected 75 concrete content- (25 Foot-, 25 Hand- and 25 Mouth-related) and 25 abstract content-related verbs for subsequent experiments. Results of the validation procedure are shown in Table 1. The ANOVAs comparing the scores of the 4 different verb categories with respect to Lexical Frequency, verb Length, Valence and emotional Involvement are not significant, indicating that verb categories are balanced according to these linguistic variables. Moreover, a significant effect is present for Concreteness and Imageability, where abstract verbs scores are obviously smaller than those of concrete categories. In this case, however, ANOVAs computed only on the concrete verb categories did not show significant differences, indicating that they are homogenous.

### 2.3. Procedure

Participants were presented with the selected list of verbs (see Table 2), printed in white capital letters on a dark gray background at the center of a PC monitor. Each trial consisted of a fixation cross (700 ms), followed by the verb presentation (250 ms) and then a dark gray background used as inter-trial (random duration, range 2000–3000 ms). In the EEG study, a total of 3 blocks and 375 trials were administered, 75 for each verb category (Foot, Hand, Mouth and Abstract, 3 repetitions for each verb) and 75 catch trials (20% of the overall trials), which took up to a total of 40 min including breaks. In the behavioral study, a total of 2 blocks and 200 trials were administered (2 repetitions for each verb and no catch trials). Visual stimuli were presented using E-Prime software (<http://www.pstnet.com>). Participants were comfortably seated 90 cm away from a 19 in. monitor where verbs were centrally presented, subtending a horizontal visual angle smaller than 5°. They were instructed to perform a semantic decision task on the presented stimuli, namely to decide whether a concrete- or abstract-content verb appeared. In the EEG study an overt response from the participants (neither verbal nor manual) was not required, so as to avoid recording the activity related to the preparation and the execution of a motor response. However, catch trials were introduced to keep sustained and to monitor the attention of the participants. To this aim, when a question mark appeared on the screen 500 ms after verb offset participants were required to state aloud their semantic judgment about the last observed verb. The catch trials were balanced across the four conditions. A short training session was held to ensure the correct task understanding, administering 10 trials showing verbs other than those used in the experimental session. During EEG recordings, in order to avoid eye movements, participants were asked to fixate the central visual cross. All verb categories were equally well assigned to the correct label (abstract or

concrete) by the subjects during the experiment. The overall accuracy was more than 90%.

### 2.4. Behavioral experiment

Participants were instructed to press a button with either the index or the middle finger of the right hand according to the concreteness (abstract or concrete) of each presented verb. Half of the participants used the index finger to classify concrete verbs, while the remaining used the middle finger in order to counter-balance possible effects due to the fingers. They had to respond as soon and accurately as possible. Mean RTs and Accuracy (the percentage of correct responses) underwent a repeated measure ANOVA ( $\alpha \leq .05$ ) with verb-Category (Abstract, Foot-, Hand- and Mouth-related) as within-subjects factor and finger-Map as between-subjects factor. When a significant effect was found, post-hoc comparisons were evaluated with Bonferroni test.

### 2.5. EEG recording

Continuous EEG was acquired using the 128-channel Geodesic EEG System (Electrical Geodesics, Inc., Eugene, OR, USA) and the HydroCel Geodesic Sensor Net that arrays the sensors (AgCl coated electrodes) in a geodesic pattern over the surface of the head. It included 19 contacts at the equivalent 10–20 system locations. Consistent positioning was achieved by aligning the Sensor Net with skull landmarks (nasion, vertex, and pre-auricular points). With high input impedance amplifiers (Net Amps 300), low noise EEG was obtained with sensor-skin impedances maintained below 100 k $\Omega$ . The signal was digitized at 250 Hz sampling rate (0.01 Hz high-pass filter), recorded with a vertex reference.

### 2.6. EEG data preprocessing

EEG data were analyzed off-line by means of NetStation software (Electrical Geodesics, Inc., Eugene, OR, USA) and homemade MATLAB scripts (the Mathworks, Natick, MA, USA). Continuous recordings were segmented in epochs lasting 2700 ms, each including the fixation cross, the verb presentation and the first part of inter-trial (1750 ms). For artifact detection and removal, the epoch-file of each participant was high pass filtered (1 Hz), imported in EEGLAB tool and analyzed by means of Independent Component Analysis (ICA) (Delorme & Makeig, 2004), then back-transformed excluding components whose topography and time-course endowed eye (blink and saccades), cardiac, and muscular artifacts. A mean number of  $7.2 \pm 4.1$  components were removed. The resulting epoch-files were further visually inspected to exclude remaining bad trials (about 4% of trials removed) and re-referenced versus the average signal of all electrodes located above the axial plane passing through fronto-polar and occipital electrodes.

**Table 2**

List of all verbs used as stimuli. Italian verbs with their English translation are listed according to the category (Hand, Foot, Mouth and Abstract).

Verb	Translation	Category	Verb	Translation	Category	Verb	Translation	Category	Verb	Translation	Category
Cucire	To knit	Hand	Zoppicare	To limp	Foot	Mordere	To bite	Mouth	Ritenerne	To believe	Abstract
Timbrare	To stamp	Hand	Scalciare	To kick	Foot	Leccare	To lick	Mouth	Prevedere	To foresee	Abstract
Cliccare	To click	Hand	Sgambettare	To patter	Foot	Grugnire	To grunt	Mouth	Desumere	To infer	Abstract
Modellare	To model	Hand	Pedalarare	To pedal	Foot	Soffiare	To blow	Mouth	Intendere	To mean	Abstract
Impastare	To knead	Hand	Calciare	To kick	Foot	Digrignare	To grind	Mouth	Ricordare	To remember	Abstract
Segare	To saw	Hand	Calpestare	To trample	Foot	Ululare	To yawl	Mouth	Influire	To affect	Abstract
Intagliare	To carve	Hand	Salire	To rise	Foot	Russare	To snore	Mouth	Stabilire	To establish	Abstract
Stappare	To uncork	Hand	Zampettare	To patter	Foot	Succhiare	To suck	Mouth	Presumere	To assume	Abstract
Digitare	To digit	Hand	Scendere	To go down	Foot	Blaterare	To blather	Mouth	Supporre	To suppose	Abstract
Bussare	To knock	Hand	Correre	To run	Foot	Gridare	To shout	Mouth	Reputare	To consider	Abstract
Applaudire	To clap	Hand	Camminare	To walk	Foot	Strillare	To scream	Mouth	Confutare	To refute	Abstract
Scrostare	To scrape	Hand	Marciare	To march	Foot	Sbuffare	To snort	Mouth	Preferire	To prefer	Abstract
Sbucciare	To peel	Hand	Maltellare	To skip	Foot	Masticare	To chew	Mouth	Dedurre	To deduce	Abstract
Impugnare	To grasp	Hand	Balzare	To leap	Foot	Borbottare	To mumble	Mouth	Arguire	To realize	Abstract
Spalmare	To smear	Hand	Passeggiare	To promenade	Foot	Alitare	To breathe	Mouth	Intuire	To guess	Abstract
Ricamare	To embroider	Hand	Pattinare	To skate	Foot	Sospirare	To sigh	Mouth	Riflettere	To reflect	Abstract
Scolpire	To sculpt	Hand	Pedinare	To shadow	Foot	Inghiottire	To swallow	Mouth	Dubitare	To doubt	Abstract
Maneggiare	To manipulate	Hand	Scivolare	To slide	Foot	Balbettare	To stutter	Mouth	Esigere	To require	Abstract
Tagliare	To cut	Hand	Inciampare	To stumble	Foot	Gemere	To groan	Mouth	Meditare	To meditate	Abstract
Palpare	To palpate	Hand	Discendere	To come down	Foot	Ridere	To laugh	Mouth	Appurare	To ascertain	Abstract
Spazzolare	To brush	Hand	Saltare	To jump	Foot	Bofonchiare	To grumble	Mouth	Influenzare	To influence	Abstract
Scrivere	To write	Hand	Rincorrere	To chase	Foot	Tossire	To cough	Mouth	Valutare	To evaluate	Abstract
Bastonare	To beat	Hand	Tallonare	To heel	Foot	Pronunciare	To pronounce	Mouth	Rinunciare	To give up	Abstract
Pugnalare	To stab	Hand	Balzellare	To jump	Foot	Deglutire	To swallow	Mouth	Ponderare	To ponder	Abstract
Dipingere	To paint	Hand	Dribblare	To dribble	Foot	Addentare	To bite	Mouth	Vagliare	To sift	Abstract



## 2.7. ERPs

Preprocessed data of each participant were imported and analyzed in Cartool software (version 3.52; <http://brainmapping.unige.ch/Cartool.htm>). Epoch-files were band-pass filtered (1–30 Hz). The outer most belt of electrodes of the sensor-net was discarded because they are more prone to show residual muscular artifacts. Eventually, only 110 electrodes entered subsequent analyses. The average for each subject and verb category was computed. The Foot-, Hand-, and Mouth-related verb categories were initially collapsed into a single Whole-Concrete-related verb category. In a second step analysis, we considered them as separated conditions so as to characterize brain activity specific for each concrete category.

In order to investigate topographic differences between electric field maps of different conditions, two topographic ANOVAs (TANOVA) (Murray, Brunet, & Michel, 2008) were conducted. The TANOVA compares the Global Map Dissimilarity (GMD), returning the time samples showing significant difference between electric field maps of two conditions, independently from the amplitude of the EEG signal. At a neurophysiologic level, because electric field changes are indicative of changes in the underlying generator configuration (Fender, 1987; Lehmann, 1987; Vaughan, 1982) this test provides a statistical means of determining whether and when the brain networks activated by two conditions differ. The first TANOVA compared the Whole-Concrete versus the Abstract, while the second compared each single concrete (Foot-, Hand- and Mouth-related) versus the Abstract verb category. Level of significance was set at  $p \leq .05$ . A temporal clustering was applied to each TANOVA so as to consider only significant periods lasting at least 5 consecutive time samples, i.e. 20 ms.

Once the periods of different scalp topographies were estimated, a spatial clustering algorithm was employed to determine if a stable topography was present within each significant interval returned by TANOVA. The first 600 ms of grand-averaged ERP data (i.e., the first 150 time points following the verb presentation) were processed using a space-oriented brain electric field analysis. This method is based on the notion of functional brain *microstates* introduced in 1980s by Lehmann (1987). It was observed that electric brain activity does not vary randomly over time. Rather, a discrete number of brain topographies remain stable over time from tens to hundred milliseconds (Michel, Seec, & Landis, 1999). Each stable brain topography (microstate) is sustained by a specific brain network and reflects a specific functional state of the brain (Lehmann, 1987; Michel et al., 1999). The analysis procedure implemented to identify the periods of topographic stability within and between experimental conditions is a modified agglomerative hierarchical clustering (Murray et al., 2008) termed 'AAHC' (Atomize and Agglomerate Hierarchical Clustering). Cluster analysis is reference-free, and insensitive to amplitude modulation of the same scalp potential field across conditions, since normalized maps are compared. The output is a set of template maps that describe the group-averaged ERPs over time. The optimal number of microstates explaining for the most of the considered data set variance was determined by a modified Krzanowski–Lai (K–L) criterion (Tibshirani, Walther, Botstein, & Brown, 2005). For each condition, the microstate segmentation allowed us to determine if the TANOVA significant intervals were characterized by a stable topographic scalp map.

To statistically assess the validity of the results emerging from the clustering algorithm, we applied a *fitting* procedure based on calculating the spatial correlation between single-subject ERPs and template maps previously identified on the group-averaged ERPs (Murray et al., 2008; Brandeis, Lehmann, Michel, & Mingrone, 1995). In each significant TANOVA interval, we computed the number of time samples spatially correlated with a given template map for each subject and condition. A repeated measurement ANOVA was conducted to evaluate if a significant MAP X Condition interaction was present and, if this was the case, post-hoc *t* test were conducted to evaluate significant ( $\alpha = .05$ ) differences within and between conditions.

Both TANOVA and AAHC can identify transitions in the scalp electric field that, in turn, indicate changes in the intracranial generator configuration (McCarthy & Wood, 1985; Vaughan, 1982). For this reason, they are useful in assisting subsequent computation of inverse solution. To investigate the neural sources responsible for the changes of scalp potential map, a distributed inverse solution was calculated with local autoregressive average (LAURA) model. This model is based on reconstruction of the brain electric activity in each point of a 3D grid of solution points. Each solution point is considered as a possible location of a current source, thus there is no a priori assumption on the number of dipoles in the brain. The computation provides a unique configuration of activity at each solution point that explains the surface measurements. Theoretically, since an infinite number of distributions of current sources within this 3D grid of solution points can lead to exactly the same scalp potential map, the inverse computation does not show a unique solution. LAURA incorporates biophysical laws as constraints driving the calculation of a unique solution. The solution space was computed on a locally spherical head model with anatomical constraints (LSMAC model; Brunet, Murray, & Michel, 2011) and comprised 3001 solution points equidistantly distributed within the brain structures of the Montreal Neurological Institute (MNI152) average brain.

The time intervals submitted to inverse solution computation were those in which the TANOVAs found significant topographic differences between conditions. The source localization comprised 2 steps: first, we computed the averaged intracranial source distribution for each condition and subject within the TANOVA significant time interval. Second, similar to the statistical parametric mapping used in fMRI analysis, a voxel-by-voxel paired *t*-test was applied (Esslen, Pascual-Marqui,

Hell, Kochi, & Lehmann, 2004; Murray, Imber, Javitt, & Foxe, 2006) to compare the sources between 2 conditions. Comparisons were conducted by performing paired *t*-tests at each solution point. This yielded the statistical parametric maps of the differential activation. First of all, we examined the differences between Abstract and Whole-Concrete, in order to get a general picture of the brain areas involved in processing abstract in contrast to concrete content of the stimuli. Then we moved on examining whether, within regions specific for Whole-Concrete stimuli, a further modulation according to different body effectors could be found.

## 3. Results

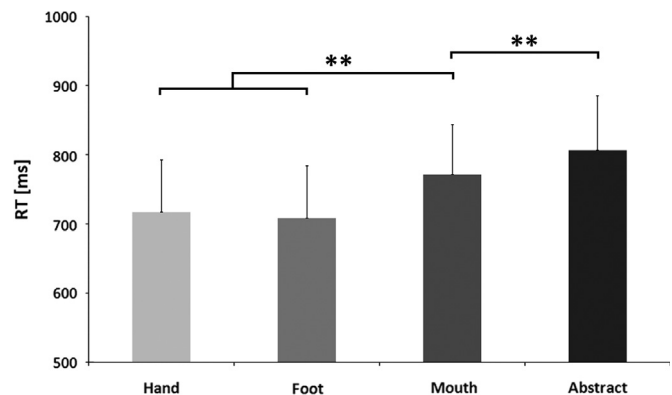
### 3.1. Behavioral experiment

In the behavioral study, mean RTs resulted to vary according to verb-Category (Fig. 1). Foot- and Hand-related verbs elicited the fastest RTs (Foot:  $709 \pm 75$  ms; Hand:  $718 \pm 87$  ms). Mouth-related and Abstract verbs showed instead longer RTs (Mouth:  $772 \pm 72$  ms; Abstract:  $807 \pm 79$  ms). Accuracy rates were as follows: Foot  $97 \pm 3\%$ , Hand  $97 \pm 4\%$ , Mouth  $89 \pm 7\%$ , and Abstract  $88 \pm 9\%$ . A repeated measurements ANOVA conducted on RTs showed a significant effect of verb-Category ( $F(3, 72) = 46.66, p < .0001$ ). Basically, post-hoc comparisons showed that RTs for Foot- and Hand-related verbs did not significantly differ each other, while they differed with respect to Mouth-related and Abstract verbs. In addition, Mouth-related and Abstract verbs significantly differed each other. The same statistical procedure applied to Accuracy, on the other hand, showed a significant effect of verb-Category ( $F(3, 72) = 17.44, p < .0001$ ), with Hand- and Foot-related verbs presenting higher Accuracy values. Finally, it must be noted that for both variables, neither finger-Map main effect nor verb-Category X finger-Map interaction was significant.

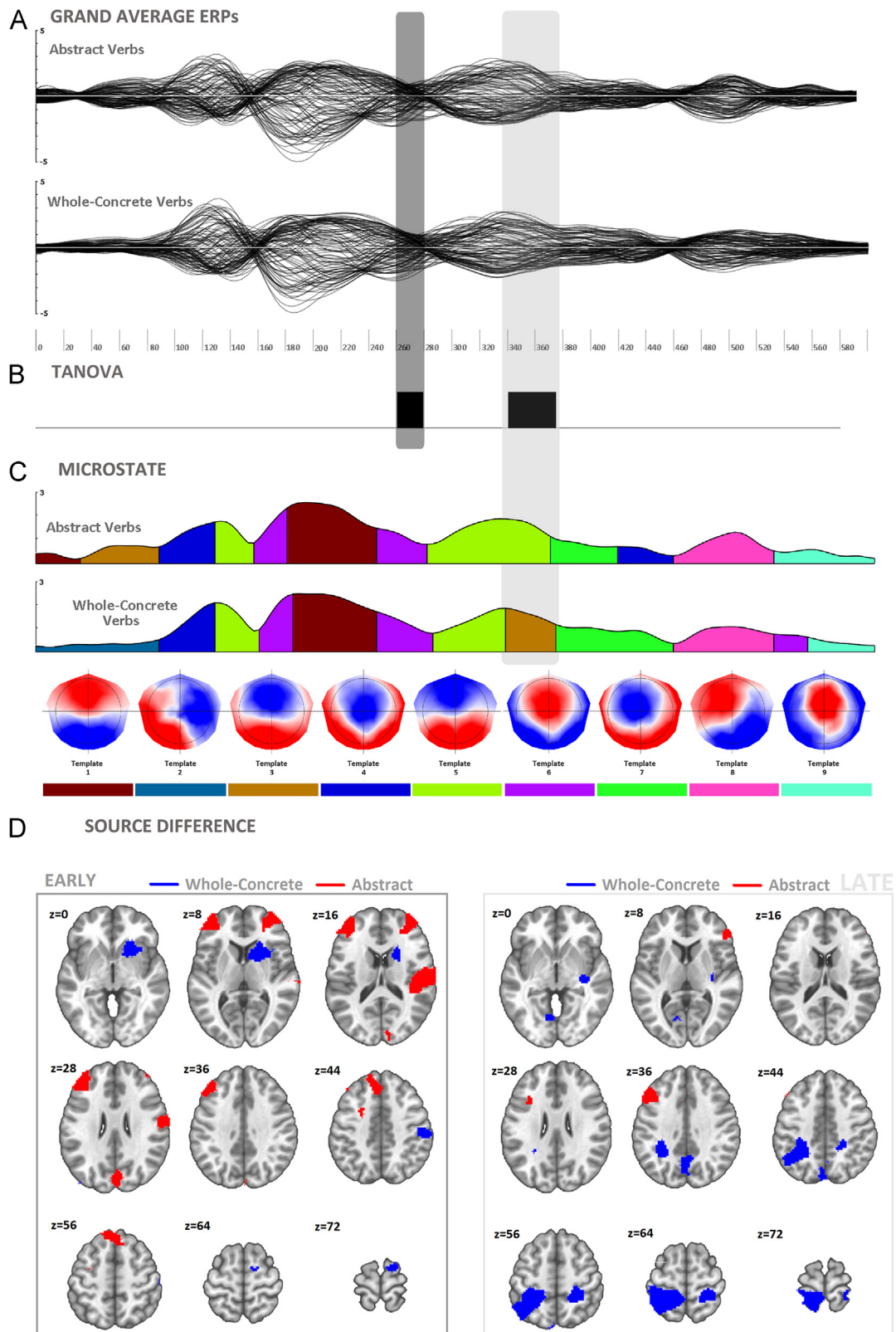
### 3.2. ERPs

Results are displayed in Figs. 2 and 3. Since we were interested in core semantic processing of the presented stimuli, early visual processing indexed in the first 100 ms after stimulus onset will not be considered. Significant differences among comparisons were identified in 2 main time intervals: either an *early* one occurring between 200 and 300 ms either a *later* one between 300 and 400 ms after verb presentation.

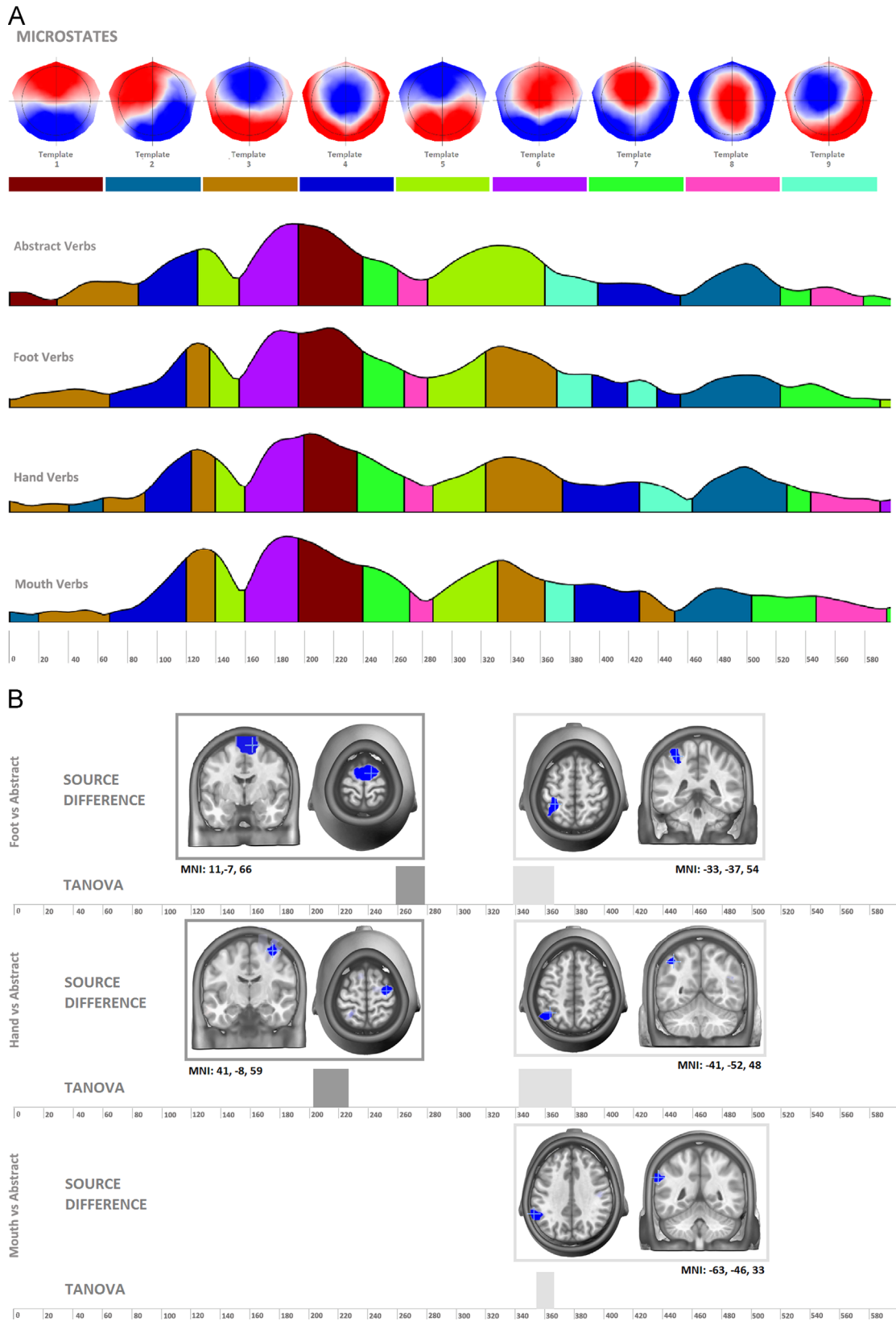
In the early interval, TANOVA analysis showed a significant difference in the time window 260–280 ms for Abstract versus Whole-Concrete (Fig. 2), in 260–280 ms for Abstract versus Foot and in 204–228 ms for Abstract versus Hand comparisons (Fig. 3),



**Fig. 1.** Behavioral experiment's results. The graph shows mean RTs in a categorization task of different verb categories. The repeated measurements ANOVA showed a significant effect of verb-Category ( $p < .0001$ ). Post-hoc analysis indicates that Abstract verbs significantly differ from Hand, Foot and Mouth verb categories and, in addition, Mouth verbs are significantly different from Hand and Foot ones. Bars are SD.



**Fig. 2.** Abstract versus Whole-Concrete verbs comparison. Panel A: Grand-averaged ERPs for Abstract and Whole-Concrete verbs. The x-axis reports the time relative to the verb onset. The y-axis indicates the ERP amplitude, ranging from  $-5 \mu\text{V}$  to  $+5 \mu\text{V}$ . Panel B: Time samples showing a significant ( $p < .05$ ) topographic difference at the TANOVA between the 2 verb categories are reported. Two intervals were identified: early (260–280 ms) and late (340–376 ms). Two shaded rectangles (dark gray for the early interval, light gray for the late one) align the significant TANOVA intervals to the grand-averaged ERPs. Panel C: microstate segmentation of Abstract and Whole-Concrete verbs. Different colors and numbers indicate different periods of stable scalp topography. The microstate profile indicates the GFP, computed for each condition as the variance of the channels over the whole scalp at a given time point. It is always positive and it ranges from 0 up to  $3 \mu\text{V}^2$ . The template maps relative to each microstate are reported below highlighted with the color corresponding to the microstates sequence. In the late TANOVA interval, as different microstates occur, the shaded rectangle is extended over the microstate segmentation. Panel D: the statistical comparisons between Abstract and Whole-Concrete verbs' current source densities are plotted on brain (MNI152) axial slices for both early and late TANOVA significant time intervals. All significant voxels ( $p < .05$ ) are colored: red indicates a higher density for Abstract verbs, blue for Whole-Concrete ones. The z-coordinate relative to each slice is reported.



**Fig. 3.** Comparison between Abstract versus each concrete verb category. Panel A: microstate segmentation of Abstract, Foot, Hand and Mouth verbs. The top line shows the template maps relative to the 9 computed microstates. The sequences of microstates are then reported for the four investigated conditions. Each microstate is color-coded according to the relative template map. The microstate profile indicates the GFP, ranging from 0 up to  $3 \mu V^2$ . The timeline (ms) is aligned to the verb onset. Panel B: the TANOVA and the corresponding difference of brain generators (significant  $p$ -Value) between Abstract and each single concrete verb category are reported. The early and late time intervals are depicted in dark and light gray, respectively. Voxels reaching a statistical significance ( $p < .05$ ) for each concrete category relative to the Abstract one are colored in blue and plotted onto brain axial and coronal slices (MNI152). The white cross indicates the voxel exhibiting the lowest  $p$ -Value over the whole brain, and its MNI coordinates are reported.



indicating the presence of different electric field distributions between compared verb categories. No significant time window emerged in the Abstract versus Mouth comparison. In the late interval, significant differences appeared in the time window 340–376 ms for Abstract versus Whole-Concrete comparison (Fig. 2) and in a similar time window for Abstract versus each separate concrete category (Abstract versus Foot: 340–368 ms; Abstract versus Hand: 344–380 ms; Abstract versus Mouth: 356–368 ms, Fig. 3).

Results of spatiotemporal segmentation of the Abstract and Whole-Concrete categories are shown in Fig. 2. Nine was the optimal number (according to K–L criterion) of template potential maps, explaining 89.9% of the variance of the dataset. In the late time window indicated by the TANOVA (340–376 ms), the segmentation procedure showed the presence of different microstates according to different categories. Template map 5 was assigned to the Abstract, while map 3 to the Whole-Concrete category. A fitting procedure was applied in the same interval to determine for each subject how many time samples were better explained by map 3 rather than map 5. The ANOVA returned a significant Map (2 levels) X Condition (2 levels) interaction ( $F(1, 11) = 6.38, p < .05$ ). Post-hoc comparisons showed that occurrence of map 3 was significantly higher in the Whole-Concrete (mean: 77% of the late TANOVA interval) with respect to Abstract condition (51%) across participants, further confirming that this map is more characterizing the concrete rather than the abstract verbs processing in the late TANOVA interval.

Spatiotemporal segmentation of the Abstract, Foot-, Hand- and Mouth-related verb categories is shown in Fig. 3. K–L criterion indicated 9 as the optimal number of microstates, explaining 89.1% of the variance. In the same time window indicated by the TANOVA (340–380 ms), the segmentation procedure showed the presence of different microstates according to different conditions. Template map 5 was assigned to the Abstract, while map 3 was specific for Foot-, Hand- and Mouth-related conditions. The fitting procedure showed a significant Map (2 levels) X Condition (4 levels) interaction ( $F(3, 33) = 4.23, p < .05$ ). Post-hoc comparisons showed that occurrence of map 3 was significantly higher than that of map 5 in Foot-, Hand- and Mouth-related conditions across participants. Vice versa, map 5 was more represented in Abstract than concrete conditions.

### 3.3. Source estimation

The results of *t*-tests between averaged current density maps computed in the time periods of significant differences in scalp topography are displayed in Figs. 2 and 3, where significant solution points are rendered on corresponding slices of a MNI152 brain.

In the early time window, 5 cortical clusters (3 in frontal and 2 in more posterior regions) of significant differences emerged where Abstract verbs elicited a stronger activation than Whole-Concrete ones. More in detail, 2 frontal clusters occupy roughly symmetrical regions of the Middle Frontal gyri (MFG) in the prefrontal cortex (right side: Brodmann area (BA) 10 and BA 46; left side: BA 10) while a more dorsal frontal cluster occupies the Superior Frontal gyrus (SFG), especially on the right side (BA 8). One of the posterior clusters is located in a perisylvian region of the right hemisphere at the conjunction of Temporal, Parietal and Frontal cortices while the other one is located in the right Cuneus (BA 19). In addition, Whole-Concrete verbs elicited a stronger response than Abstract ones in a cortical cluster located in a sensory-motor region of the right hemisphere around the rolandic fissure and characterized by two spots, one more dorsal and one more ventral (Fig. 2).

In the late time interval, 2 frontal clusters showed stronger current density for Abstract verbs while 3 posterior clusters were

stronger for the Whole-Concrete ones. More in detail, the frontal clusters occupy right sectors of the Inferior Frontal gyrus (IFG, BA 46) and left sectors of MFG (BA 8, 9). Two of the posterior clusters are located in the parietal convexity. The left one occupies sectors of Inferior Parietal Lobule (IPL, BA 40), Superior Parietal Lobule (SPL, BA 5, 7) and extends toward the Post-Central gyrus (postC), while the right one is restricted to postC and SPL (BA 5). The last posterior cluster lies in mesial SPL (BA 7), bilaterally (Fig. 2).

When considering specific body effectors, in the early time interval a functional organization was found within the premotor region, which is compatible with the classical somatotopic motor representation of different body parts. In fact, when compared to Abstract, Foot-related verbs activation prevails in a bilateral posterior sector of SFG and Medial frontal gyrus (BA 6), while Hand-related verbs prevail in a more ventral sector comprising the Pre-Central gyrus (BA 6) in the right hemisphere (Fig. 3).

Similarly, a somatotopic-like organization was found in the late interval within the left parietal region. Foot-related verbs prevail in a more anteriorly and dorsally located sector of IPL (BA 40) while Mouth-related ones prevail in more posterior and ventral sectors of IPL extending to Supramarginal gyrus (BA 39, 40). Finally, the Hand-related ones lie in between (IPL, BA 40) (Fig. 3).

## 4. Discussion

The present study investigated the dynamics of semantic processing of healthy individuals when presented with abstract and concrete verbs, both at behavioral and electrophysiological levels. Clear differences in the processing of these two categories are highlighted. First, the behavioral data confirmed a processing advantage for concrete items (*concreteness effect*). This effect has been long known (James, 1975; Rubin, 1980; Whaley, 1978) and it is generally assumed that it reflects a higher imageability of concrete items. Our set of concrete verbs is, indeed, characterized by higher scores regarding imageability and thus our behavioral data are compatible with this assumption.

According to different categories, ERPs showed different scalp topographies and, consequently, different brain generators in two separate time intervals, one early and one late. In particular, in the early interval (at around 270 ms) Whole-Concrete verbs showed stronger activation in a sensory-motor region of the right hemisphere. This finding is in line with EEG studies by Hauk & Pulvermueller (2004); Pulvermueller (1999); Pulvermueller (2001) that found a motor cortex involvement for action words approximately 200–250 ms after word onset. In addition, concrete verbs showed specific activations in the motor strip, according to the body effector. The observation of Foot verbs elicited activation of a dorso-mesial sector of premotor areas bilaterally, while the observation of Hand verbs a more ventro-lateral part of the right premotor area. The representation of these effectors in the premotor cortex is congruent with the classical organization of this region as described by Penfield and Rasmussen (1952) and with functional imaging studies showing that action observation activates premotor areas in a somatotopic manner (Buccino et al., 2001; Wheaton, Thompson, Syngeniotis, Abbott, & Puce, 2004). The location of Hand verbs representation in the right motor strip should not sound unexpected. Hauk and Pulvermueller (2004) found a comparable result in a similar EEG experiment. This finding is consistent with the interpretation that in the healthy human brain, right hemispheric motor areas play a role in processing certain subtypes of action words, as it has been reported that focal lesions in the right frontal cortex can lead to specific deficits in processing action-related words (Neininger & Pulvermueller, 2001, 2003).

Here we should note that, on one hand, our data did not highlight a motor activation for Mouth verbs and, on the other hand, their categorization appears more difficult compared to that of the other



concrete categories, as demonstrated by longer RTs and lower accuracies. In our opinion these two points are not directly linked. It is well-known that during language comprehension individuals activate the motor program related to the pronunciation of the listened or read words (Watkins, Strafella, & Paus, 2003; for a review see Pickering and Garrod (2007)). In our study, this kind of covert speech is common to all verb categories and recruits the same motor areas expected to be elicited by Mouth verbs according to the embodied theory. Thus, it is reasonable to assume that in a direct comparison aimed at detecting scalp differences, the early mouth motor activation representing the meaning of Mouth-related verbs may be masked by a concomitant mouth motor activation related to the covert pronunciation of the Abstract verbs.

The behavioral data, on the other hand, shows slower response times for Mouth-related verbs. Here it must be considered that the differences in RT data among verb categories arise from the sum of both bottom-up (e.g., verb understanding) and top-down (e.g., task-related verb categorization and motor response) operations. Instead, ERP data essentially reflects bottom up (i.e., automatic) operations such as those related to understanding the meaning of the presented verb, since ERPs are time-locked with the verb presentation and not, for instance, with the hand response. Starting from this premise, we suggest that the behavioral results relative to Mouth verbs are likely due to a task-related, top down process of categorization that was more difficult than that of Foot and Hand verbs. All verb categories were matched in terms of many psycholinguistic variables (including Concreteness and Imageability) according to the scores returned by 80 volunteers during the preliminary stimuli validation. However, this validation procedure took into account only the returned scores and not the time needed to achieve them. It is therefore possible that labeling as concrete a Mouth-related verb was an equally efficient, but more time-consuming process with respect to the other two concrete categories. In the behavioral study, where participants were required to respond as fast as possible and where response latencies were collected, longer RTs and lower accuracies were observed.

In the late interval, Whole-Concrete verbs elicited stronger activation of the parietal lobe, mainly involving the left hemisphere. Moreover, the contrasts between Abstract and single concrete categories returned distinct although partially overlapping activations in the same area for verbs describing Mouth, Hand, and Foot actions. The motor organization of the parietal lobe is clearly established in non-human primates, where mouth movements are represented in the rostral part of PF area (Leinonen & Nyman, 1979; Fogassi, Gallese, Fadiga, & Rizzolatti, 1998), distal hand movements in the anterior intraparietal area (Sakata, Taira, Murata, & Mine, 1995) and arm reaching movements posteriorly in the medial bank of the intraparietal sulcus (Colby & Duhamel, 1991; Snyder, Batista, & Andersen, 1997). Furthermore, clinical and brain imaging studies strongly suggest that body effectors are represented in a segregated fashion in the parietal lobe also in humans (Buccino et al., 2001; De Renzi, 1982; Jeannerod, 1986; Pause, Kunesch, Binkofski, & Freund, 1989; Seitz, Roland, Bohm, Greitz, & Stone-Elander, 1991).

More generally, a large number of studies has shown a parietal involvement in planning of complex visually-guided actions, in tool use knowledge and in processing spatial interaction between manipulated tool and body's effectors (Peeters et al., 2009; for reviews see Glover (2004); Goldenberg (2009)). In addition, it has been suggested a role of the parietal lobe in describing objects for the purpose of acting upon them (Jeannerod, 1994; Milner & Goodale, 1995) and also during the observation of object-related actions (Buccino et al., 2001). In contrast, far less evidence is available about how parietal regions contribute to the comprehension of linguistically encoded actions. An fMRI study by Tettamanti

et al. (2005) showed parietal activation during listening to sentences describing actions upon objects. Of note, this study showed activation of different sectors of parietal lobe according to the specific body effector involved in the interaction with the object. More recently, (Kemmerer, Rudrauf, Manzel, & Tranel 2012) in a clinical study where 226 brain damaged patients were evaluated, demonstrated that impaired lexical and conceptual knowledge of actions is often associated with a damage to the left parietal cortex, in particular the Supramarginal gyrus. Considering the mentioned evidence, we propose that our late parietal activations reflect a multimodal representation of actions and objects implied by the concrete verbs. In fact, the majority of concrete items of our study were transitive verbs implying actions upon an object while, instead, abstract items did not imply physical objects. This multimodal representation may cover aspects related to action planning such as a parietal pragmatic description of objects potentially implied in the interaction with the effector, the spatial relations among the components of the action (body effectors, objects, tools, etc.) and possible sensory feedback related to action execution.

An original finding of the present study is represented by the delay between frontal and parietal activations during concrete verbs processing. Both premotor and parietal areas are known to be part of a network subserving visuo-motor transformations for action (Rizzolatti, Luppino, & Matelli, 1998) and anatomic connections between these regions are direct and bidirectional (Cavada & Goldman-Rakic, 1989; Matelli, Camarda, Glickstein, & Rizzolatti, 1986). To our knowledge, no temporal relation between the recruitment of different frontal and parietal areas has been previously described during action-related word processing, at least in metabolic imaging studies. Nevertheless, these studies are affected by low temporal resolution, making it difficult to establish the precise temporal dynamics of brain activations. On the contrary, our EEG study allowed us to track the time line of different activations during semantic processing, showing that the frontal ones occurred about 100 ms before the parietal ones. However, previous studies reported that during action observation parietal activity precedes the premotor one by 20–100 ms (Nishitani & Hari, 2002; Ortigue, Sinigaglia, Rizzolatti, & Grafton, 2010). In a speculative view, we suggest that the inverted recruitment observed here depends on the different nature of the stimuli. Generally, while observing an action its details (e.g. the objects, the effectors, the space, etc.) are immediately made available to the observer. At brain level, this information is represented in the parietal lobe (Kemmerer et al., 2012) that is strongly connected with premotor areas where also the goal of the action is coded (Rizzolatti & Sinigaglia, 2010). Conversely, when reading a concrete verb, the same type of information is not immediately available, while the action goal, i.e. the verb meaning, is initially accessed and coded in premotor areas. Afterwards, parietal regions could be automatically recruited to instantiate a 'full' representation of the action. In line with this speculation, previous studies highlighted that the visual word form area (VWFA) (for review see McCandliss, Cohen, and Dehaene (2003)), an area playing a key role in the rapid and effortless transformation of a group of letters into integrated visual percepts is functionally connected with remote brain areas of the core language network (Matsumoto et al., 2004; Van der Mark et al., 2011). Given its proximity with premotor regions, Broca's area could be a plausible candidate for mediating the recruitment of premotor neurons related to the meaning of the verb. However, the technique employed in our study (scalp EEG and ERP) does not constitute an efficient tool to precisely identify the anatomical connections that mediate between the activation of occipito-temporal areas recruited in a reading task and parieto-premotor networks.

In summary, the present findings are compatible with an embodied account of concrete verb processing, according to which the

same sensory and motor areas involved in processing actions are recruited when accessing the correspondent concept (Barsalou et al., 2003; Gallese & Lakoff, 2005; Pulvermueller, 2005). Parieto-frontal areas activated by action execution and observation (Binkofski et al., 1999; Buccino et al., 2001; Buccino et al., 2004) are indeed activated also by concrete verbs.

One may argue that in order to accomplish the categorization task, participants were induced to use a motor imagery strategy, potentially responsible for the observed sensory-motor activations. Recently, the role of the motor system in language understanding has been reviewed in light of a number of studies showing that motor representations can or cannot be activated on the basis of the type of strategy that participants adopt to perform tasks involving motor phrases (Tomasino & Rumiati, 2013). The authors argue that implicit motor imagery is neither automatic nor necessary to language understanding. In our study, the short latency of the observed effects, starting from 200 ms after verb presentation and compatible with the emergence of lexical and semantic effects (Boulenger et al., 2006; Pulvermueller et al., 2001; Pulvermueller, Hauk, Nikulin, & Ilmoniemi, 2005; Pulvermueller et al., 2005), strongly speaks against the possibility that this motor activation during action words processing reflects secondary imaginary processes. Before performing any mental imagery, we believe that one has to preliminary access the semantic level of a presented action word by means of an early and automatic recruitment of the motor system in order to understand its meaning. This activation is different from a top-down motor recruitment such as a strategy-dependent motor imagery of the action implied by a given presented word. Willems, Toni, Hagoort, and Casasanto (2010) showed that understanding action words and performing a motor imagery on the same action words may involve different types of motor representations. In conclusion, even though, we cannot rule out that a motor imagery strategy has been adopted in our study to accomplish the task at hand, we believe that the early involvement of the motor system reflects action word understanding rather than top-down motor imagery. While RT values show a difference of 50–100 ms according to the presented verb category, ERPs do not present any comparable shift in terms of latency among the categories, making it difficult to explain the concreteness effect of behavioral data with a different timing at level of bottom up processing locked to stimulus onset. The differences in RTs may instead be due to a top down type of processing related to the categorization of the verb.

While the processing of concrete items showed a temporally different recruitment of the sensory-motor areas, Abstract verbs showed a similar pattern of generators in both early and late time intervals. Abstract verbs predominate in clusters located outside sensory-motor regions, mainly in dorsal and ventral sectors of the prefrontal cortex. A dorso-lateral sector of prefrontal cortex has been linked with verbal short-term memory and lexical retrieval (Fiez, 1997; Paulesu et al., 1993). On the basis of lesion studies (Alexander & Benson, 1993; Freedman, Alexander, & Naeser, 1984; Luria & Tsvetkova, 1967) it has been suggested that this area is engaged in self-guided, goal-directed retrieval of semantic information. Inferior frontal gyrus is implicated in semantic, syntactic and phonological processing (for a review see Binder, Desai, Graves, and Conant (2009); Bookheimer (2002); Fiez (1997)). More specifically, it is engaged when tasks require effortful selection of semantic information, when many alternative responses are possible or when ambiguity elicits competing semantic representations (Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005; Martin & Chao, 2001; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). The greater activation of IFG for abstract verbs suggests that it may subserve the integration of abstract concepts into an appropriate context by selecting one of the competing instantiations and complementing missing information in order to reach an unequivocal interpretation. According to CAT, different

representations need to be integrated/compared to get a coherent picture of abstract language meanings (Schwanenflugel & Akin, 1994). Summing up, in the present study, the predominance of Abstract verbs activation in clusters located outside sensory-motor regions is not in line with an embodiment account. This discrepancy between our findings and those of other authors who did find a motor system involvement even for abstract language (Glenberg et al., 2008a, 2008b) may depend on the type of stimuli adopted. Here, abstract verbs are presented in isolation while in others studies an abstract transfer is indicated by abstract verbs embedded in an appropriate context (e.g., *Jim delegated the power to you*). We suggest that just reading the verb *to delegate* would not activate the motor system while the abstract transfer indicated by the entire sentence is likely mapped onto the motor system.

In conclusion, Abstract versus Concrete verbs comparison suggests a different processing between the two categories. As far as Abstract verbs are concerned, first the behavioral study confirms that these verbs pose a greater demand in a categorization task and consequently they take more time compared to Concrete verbs. Second, the EEG source analysis shows that they activate areas outside sensory-motor areas such as prefrontal regions. In contrast, as far as concrete language is concerned, we reported a clear recruitment of sensory-motor areas somatotopically organized according to the effector implied by the verb. Thus, a link between the sensory-motor system and the comprehension of abstract verbs is not supported by our data. On the contrary, this link appears to be crucial for concrete verbs, in line with embodied theories claiming that language understanding relies on rehearsal of sensory and motor experiences related to the specific meaning of language. Taken together the present findings are not compatible with theories such as CAT that state the existence of one single verbal and symbolic code for both abstract and concrete concepts. In contrast, they appear to well fit with theories proposing a multiple coding of language, such as DCT, where coding concrete concepts would rely on sensory-motor system activation while a more symbolic code would subserve abstract concepts processing.

## Acknowledgments

We thank Gaetano Cantalupo and Annalisa Pascarella for their contribution to this work and Luca Bonini and Stefano Rozzi for their fruitful comments to our findings. Supported by Grant MIUR (Ministero dell'Istruzione, Università e Ricerca) to MG.

## References

- Alexander, M. P., & Benson, D. F. (1993). The aphasia and related disturbances. In: R. J. Joynt (Ed.), *Clinical neurology* (pp. 1–58). Philadelphia: Lipincott JB.
- Aziz-Zadeh, L., Wilson, S. M., Rizzolatti, G., & Iacoboni, M. (2006). Congruent embodied representations for visually presented actions and linguistic phrases describing actions. *Current Biology: CB*, 16(18), 1818–1823.
- Badre, D., Poldrack, R. A., Paré-Blagoev, E. J., Insler, R. Z., & Wagner, A. D. (2005). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. *Neuron*, 47(6), 907–918.
- Barsalou, L. W., Kyle Simmons, W., Barbey, A. K., & Wilson, C. D. (2003). Grounding conceptual knowledge in modality-specific systems. *Trends in Cognitive Sciences*, 7(2), 84–91.
- Barsalou, L. W., & Wiemer-Hastings, K. (2005). Situating abstract concepts. In: D. Pecher, & R. Zwaan (Eds.), *Grounding cognition: the role of perception and action in memory, language, and thought* (pp. 129–163). New York: Cambridge University Press.
- 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. *Cerebral Cortex*, 19(12), 2767–2796.
- Binkofski, F., Buccino, G., Stephan, K. M., Rizzolatti, G., Seitz, R. J., & Freund, H. J. (1999). A parieto-premotor network for object manipulation: evidence from neuroimaging. *Experimental Brain Research*, 128(1–2), 210–213.

- Bookheimer, S. (2002). Functional MRI of language: new approaches to understanding the cortical organization of semantic processing. *Annual Review of Neuroscience*, 25, 151–188.
- Boulenger, V., Hauk, O., & Pulvermueller, F. (2009). Grasping ideas with the motor system: semantic somatotopy in idiom comprehension. *Cerebral Cortex*, 19(8), 1905–1914.
- Boulenger, V., Hoen, M., Jacquier, C., & Meunier, F. (2011). Interplay between acoustic/phonetic and semantic processes during spoken sentence comprehension: an ERP study. *Brain and Language*, 116(2), 51–63.
- Boulenger, V., Roy, A. C., Paulignan, Y., Deprez, V., Jeannerod, M., & Nazir, T. A. (2006). Cross-talk between language processes and overt motor behavior in the first 200 msec of processing. *Journal of Cognitive Neuroscience*, 18(10), 1607–1615.
- Braitenberg, V., & Pulvermueller, F. (1992). [Model of a neurological theory of speech]. *Die Naturwissenschaften*, 79(3), 103–117.
- Brandeis, D., Lehmann, D., Michel, C. M., & Mingrone, W. (1995). Mapping event-related brain potential microstates to sentence endings. *Brain Topography*, 8(2), 145–159.
- Brunet, D., Murray, M. M., & Michel, C. M. (2011). Spatiotemporal analysis of multichannel EEG: CARTOOL. *Computational Intelligence and Neuroscience*, 2011, 813870.
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *The European Journal of Neuroscience*, 13(2), 400–404.
- Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., et al. (2004). Neural circuits involved in the recognition of actions performed by noncon-specific: an fMRI study. *Journal of Cognitive Neuroscience*, 16(1), 114–126.
- Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., & Rizzolatti, G. (2005). Listening to action-related sentences modulates the activity of the motor system: a combined TMS and behavioral study. *Brain Research Cognitive Brain Research*, 24(3), 355–363.
- Cavada, C., & Goldman-Rakic, P. S. (1989). Posterior parietal cortex in rhesus monkey: II. Evidence for segregated corticocortical networks linking sensory and limbic areas with the frontal lobe. *The Journal of Comparative Neurology*, 287(4), 422–445.
- Colby, C. L., & Duhamel, J. R. (1991). Heterogeneity of extrastriate visual areas and multiple parietal areas in the macaque monkey. *Neuropsychologia*, 29(6), 517–537.
- De Renzi, E. (1982). *Disorders of space exploration and cognition*. New York: Wiley.
- Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134(1), 9–21.
- Dhond, R. P., Witzel, T., Dale, A. M., & Halgren, E. (2007). Spatiotemporal cortical dynamics underlying abstract and concrete word reading. *Human Brain Mapping*, 28(4), 355–362.
- Esslen, M., Pascual-Marqui, R. D., Hell, D., Kochi, K., & Lehmann, D. (2004). Brain areas and time course of emotional processing. *NeuroImage*, 21(4), 1189–1203.
- Fender, D. H. (1987). Source localization of brain electrical activity. In: A. S. Gevins, & A. Remond (Eds.), *Handbook of electroencephalography and clinical neurophysiology*, vol. 1 (pp. 355–399). Amsterdam: Elsevier.
- Fiebach, C. J., & Friederici, A. D. (2004). Processing concrete words: fMRI evidence against a specific right-hemisphere involvement. *Neuropsychologia*, 42(1), 62–70.
- Fiez, J. A. (1997). Phonology, semantics, and the role of the left inferior prefrontal cortex. *Human Brain Mapping*, 5(2), 79–83.
- Fogassi, L., Gallese, V., Fadiga, L., & Rizzolatti, G. (1998). Neurons responding to the sight of goal-directed hand/arm actions in the parietal area PF (7b) of the macaque monkey. *Society for Neuroscience Abstract*, 24, 154.
- Freedman, M., Alexander, M. P., & Naeser, M. A. (1984). Anatomic basis of transcortical motor aphasia. *Neurology*, 34(4), 409–417.
- Gallese, V., & Lakoff, G. (2005). The Brain's concepts: the role of the sensory-motor system in conceptual knowledge. *Cognitive Neuropsychology*, 22(3), 455–479.
- Garcea, F. E., Dombovy, M., & Mahon, B. Z. (2013). Preserved tool knowledge in the context of impaired action knowledge: implications for models of semantic memory. *Frontiers in Human Neuroscience*, 7, 120.
- Glenberg, A. M., & Kaschak, M. P. (2002). Grounding language in action. *Psychonomic Bulletin & Review*, 9(3), 558–565.
- Glenberg, A. M., Sato, M., & Cattaneo, L. (2008a). Use-induced motor plasticity affects the processing of abstract and concrete language. *Current Biology: CB*, 18(7), R290–R291.
- Glenberg, A. M., Sato, M., Cattaneo, L., Riggio, L., Palumbo, D., & Buccino, G. (2008b). Processing abstract language modulates motor system activity. *Quarterly Journal of Experimental Psychology*, 61(6), 905–919.
- Glover, S. (2004). Separate visual representations in the planning and control of action. *The Behavioral and Brain Sciences*, 27(1), 3–24 (discussion 24–78).
- Goldenberg, G. (2009). Apraxia and the parietal lobes. *Neuropsychologia*, 47(6), 1449–1459.
- Hauk, O., Johnsrude, I., & Pulvermueller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, 41(2), 301–307.
- Hauk, O., & Pulvermueller, F. (2004). Neurophysiological distinction of action words in the fronto-central cortex. *Human Brain Mapping*, 21(3), 191–201.
- Hauk, O., & Pulvermueller, F. (2011). The lateralization of motor cortex activation to action-words. *Frontiers in Human Neuroscience*, 5, 149.
- Hauk, O., Shtyrov, Y., & Pulvermueller, F. (2008). The time course of action and action-word comprehension in the human brain as revealed by neurophysiology. *Journal of Physiology*, 102(1–3), 50–58.
- Hebb, D. O., Lambert, W. E., & Tucker, G. R. (1971). Language, thought and experience\*. *The Modern Language Journal*, 55(4), 212–222.
- Holcomb, P. J., Kounios, J., Anderson, J. E., & West, W. C. (1999). Dual-coding, context-availability, and concreteness effects in sentence comprehension: an electrophysiological investigation. *Journal of Experimental Psychology Learning, Memory, and Cognition*, 25(3), 721–742.
- Innocenti, A., De Stefani, E., Sestito, M., & Gentilucci, M. (2014). Understanding of action-related and abstract verbs in comparison: a behavioral and TMS study. *Cognitive Processing*, 15, 85–92.
- James, C. T. (1975). The role of semantic information in lexical decisions. *Journal of Experimental Psychology: Human Perception and Performance*, 104, 130–136.
- Jeannerod, M. (1986). The formation of finger grip during prehension. A cortically mediated visuomotor pattern. *Behavioural Brain Research*, 19(2), 99–116.
- Jeannerod, M. (1994). The representing brain: neural correlates of motor intention and imagery. *Behavioral and Brain Sciences*, 17, 187–245.
- Kable, J. W., Kan, I. P., Wilson, A., Thompson-Schill, S. L., & Chatterjee, A. (2005). Conceptual representations of action in the lateral temporal cortex. *Journal of Cognitive Neuroscience*, 17(12), 1855–1870.
- Kellenbach, M. L., Wijers, A. A., Hovius, M., Mulder, J., & Mulder, G. (2002). Neural differentiation of lexico-syntactic categories or semantic features? event-related potential evidence for both. *Journal of Cognitive Neuroscience*, 14(4), 561–577.
- Kemmerer, D., Castillo, J. G., Talavage, T., Patterson, S., & Wiley, C. (2008). Neuroanatomical distribution of five semantic components of verbs: evidence from fMRI. *Brain and Language*, 107(1), 16–43.
- Kemmerer, D., Rudrauf, D., Manzel, K., & Tranel, D. (2012). Behavioral patterns and lesion sites associated with impaired processing of lexical and conceptual knowledge of actions. *Cortex*, 48(7), 826–848.
- Kiefer, M., & Barsalou, L. W. (2011). Grounding the human conceptual system in perception, action, and introspection. In: W. Prinz, M. Beisert, & A. Herwig (Eds.), *Tutorials in action science*. Cambridge: MIT Press.
- Kiefer, M., & Pulvermueller, F. (2012). Conceptual representations in mind and brain: theoretical developments, current evidence and future directions. *Cortex*, 48(7), 805–825.
- Kiefer, M., & Spitzer, M. (2001). The limits of a distributed account of conceptual knowledge. *Trends in Cognitive Sciences*, 5(11), 469–471.
- Kounios, J., & Holcomb, P. J. (1992). Structure and process in semantic memory: evidence from event-related brain potentials and reaction times. *Journal of Experimental Psychology General*, 121(4), 459–479.
- Kounios, J., & Holcomb, P. J. (1994). Concreteness effects in semantic processing: ERP evidence supporting dual-coding theory. *Journal of Experimental Psychology Learning, Memory, and Cognition*, 20(4), 804–823.
- Kutas, M., & Federmeier, K. D. (2011). Thirty years and counting: finding meaning in the N400 component of the event-related brain potential (ERP). *Annual Review of Psychology*, 62, 621–647.
- Lakoff, G., & Johnson, M. (1980). *Metaphors we live by*. Chicago and London: University of Chicago Press.
- Lakoff, G., & Johnson, M. (1999). *Philosophy in the flesh: the embodied mind and its challenge to western thought*. New York: Basic Books.
- Laudanna, A., Thornton, A. M., Brown, G., Burani, C., & Marconi, L. (1995). Un corpus dell'italiano scritto contemporaneo dalla parte del ricevente. In: S. Bolasco, L. Lebart, & A. Salem (Eds.), *III Giornate internazionali di Analisi Statistica dei Dati Testuali*, 1 (pp. 103–109). Roma: Cisu.
- Lehmann, D. (1987). Principles of spatial analysis. In: A. S. Gevins, & A. Remond (Eds.), *Handbook of electroencephalography and clinical neurophysiology*, 1 (pp. 309–354). Amsterdam: Elsevier.
- Leinonen, L., & Nyman, G. (1979). II. Functional properties of cells in anterolateral part of area 7 associative face area of awake monkeys. *Experimental Brain Research. Experimentelle Hirnforschung. Expérimentation Cérébrale*, 34(2), 321–333.
- Luria, A. R., & Tsvetkova, L. S. (1967). Towards the mechanisms of "dynamic aphasia". *Acta Neurologica et Psychiatrica Belgica*, 67, 1045–1057.
- Mahon, B. Z., & Caramazza, A. (2008). A critical look at the embodied cognition hypothesis and a new proposal for grounding conceptual content. *Journal of Physiology*, 102(1–3), 59–70.
- Martin, A., & Chao, L. L. (2001). Semantic memory and the brain: structure and processes. *Current Opinion in Neurobiology*, 11(2), 194–201.
- Matelli, M., Camarda, R., Glickstein, M., & Rizzolatti, G. (1986). Afferent and efferent projections of the inferior area 6 in the macaque monkey. *The Journal of Comparative Neurology*, 251(3), 281–298.
- Matsumoto, R., Nair, D. R., LaPresto, E., Najm, I., Bingaman, W., Shibusaki, H., et al. (2004). Functional connectivity in the human language system: a cortico-cortical evoked potential study. *Brain: A Journal of Neurology*, 127(Pt. 10), 2316–2330.
- McCandliss, B. D., Cohen, L., & Dehaene, S. (2003). The visual word form area: expertise for reading in the fusiform gyrus. *Trends in Cognitive Sciences*, 7(7), 293–299.
- McCarthy, G., & Wood, C. C. (1985). Scalp distributions of event-related potentials: an ambiguity associated with analysis of variance models. *Electroencephalography and Clinical Neurophysiology*, 62(3), 203–208.
- Michel, C. M., Seeck, M., & Landis, T. (1999). Spatiotemporal dynamics of human cognition. *News in Physiological Sciences*, 14, 206–214.
- Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. Oxford: Oxford University Press.
- Moscoso del Prado Martín, F., Hauk, O., & Pulvermueller, F. (2006). Category specificity in the processing of color-related and form-related words: an ERP study. *NeuroImage*, 29(1), 29–37.



- Murray, M. M., Brunet, D., & Michel, C. M. (2008). Topographic ERP analyses: a step-by-step tutorial review. *Brain Topography*, 20(4), 249–264.
- Murray, M. M., Imber, M. L., Javitt, D. C., & Foxe, J. J. (2006). Boundary completion is automatic and dissociable from shape discrimination. *The Journal of Neuroscience*, 26(46), 12043–12054.
- Negri, G. A. L., Rumiati, R. I., Zadini, A., Ukmar, M., Mahon, B. Z., & Caramazza, A. (2007). What is the role of motor simulation in action and object recognition? Evidence from apraxia. *Cognitive Neuropsychology*, 24(8), 795–816.
- Neininger, B., & Pulvermueller, F. (2001). The right hemisphere's role in action word processing: a double case study. *Neurocase*, 7(4), 303–317.
- Neininger, B., & Pulvermueller, F. (2003). Word-category specific deficits after lesions in the right hemisphere. *Neuropsychologia*, 41(1), 53–70.
- Nishitani, N., & Hari, R. (2002). Viewing lip forms: cortical dynamics. *Neuron*, 36(6), 1211–1220.
- Nitto, H., Suehiro, M., & Hori, T. (2002). Word imageability and N400 in an incidental memory paradigm. *International Journal of Psychophysiology*, 44(3), 209–229.
- Noppeney, U., & Price, C. J. (2004). Retrieval of abstract semantics. *NeuroImage*, 22(1), 164–170.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113.
- Ortigue, S., Sinigaglia, C., Rizzolatti, G., & Grafton, S. T. (2010). Understanding actions of others: the electrodynamics of the left and right hemispheres. A high-density EEG neuroimaging study. *PLoS One*, 5(8), e12160.
- Paivio, A. (1986). *Mental representations: a dual coding approach*. New York: Oxford University Press.
- Paulesu, P., Frith, C. D., Bench, C. J., Bottini, G., Grasby, G., & Frackowiak, S. J. (1993). Functional anatomy of working memory: the articulatory loop. *Journal of Cerebral Blood Flow & Metabolism*, 13, 551.
- Pause, M., Kunesch, E., Binkofski, F., & Freund, H. J. (1989). Sensorimotor disturbances in patients with lesions of the parietal cortex. *Brain*, 112(Pt. 6), 1599–1625.
- Peeters, R., Simone, L., Nelissen, K., Fabbri-Destro, M., Vanduffel, W., Rizzolatti, G., et al. (2009). The representation of tool use in humans and monkeys: common and uniquely human features. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 29(37), 11523–11539.
- Penfield, W., & Rasmussen, T. (1952). *The cerebral cortex of man*. New York: Macmillan.
- Pickering, M. J., & Garrod, S. (2007). Do people use language production to make predictions during comprehension? *Trends in Cognitive Sciences*, 11(3), 105–110.
- Pulvermueller, F. (1999). Words in the brain's language. *The Behavioral and Brain Sciences*, 22(2), 253–279 (discussion 280–336).
- Pulvermueller, F. (2001). Brain reflections of words and their meaning. *Trends in Cognitive Sciences*, 5(12), 517–524.
- Pulvermueller, F. (2005). Brain mechanisms linking language and action. *Nature Reviews Neuroscience*, 6(7), 576–582.
- Pulvermueller, F. (2008). Grounding language in the brain. In de. In: M. Vega, A. Graesser, & A. M. Glenberg (Eds.), *Symbols, embodiment, and meaning* (pp. 85–116). Oxford: Oxford University Press.
- Pulvermueller, F., Haerle, M., & Hummel, F. (2001). Walking or talking? Behavioral and neurophysiological correlates of action verb processing. *Brain and Language*, 78(2), 143–168.
- Pulvermueller, F., Hauk, O., Nikulin, V. V., & Ilmoniemi, R. J. (2005). Functional links between motor and language systems. *The European Journal of Neuroscience*, 21(3), 793–797.
- Pulvermueller, F., Shtyrov, Y., & Hauk, O. (2009). Understanding in an instant: neurophysiological evidence for mechanistic language circuits in the brain. *Brain and Language*, 110(2), 81–94.
- Pulvermueller, F., Shtyrov, Y., & Ilmoniemi, R. (2005). Brain signatures of meaning access in action word recognition. *Journal of Cognitive Neuroscience*, 17(6), 884–892.
- Pylshyn, Z. W. (1984). *Computation and cognition: towards a foundation for cognitive science*. Cambridge: MIT Press.
- Quillian, M. R. (1969). The teachable language comprehender. *Communications of the ACM*, 12(8), 459–476.
- 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.
- Rizzolatti, G., Luppino, G., & Matelli, M. (1998). The organization of the cortical motor system: new concepts. *Electroencephalography and Clinical Neurophysiology*, 106(4), 283–296.
- Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nature Reviews Neuroscience*, 11(4), 264–274.
- Rubin, D. C. (1980). 51 properties of 125 words: a unit analysis of verbal behaviour. *Journal of Verbal Learning and Verbal Behavior*, 19, 736–755.
- Rueschemeyer, S. A., Glenberg, A. M., Kaschak, M. P., Mueller, K., & Friederici, A. D. (2010). Top-down and bottom-up contributions to understanding sentences describing objects in motion. *Front Psychology*, Nov 5;1:183.
- Sabsevitz, D. S., Medler, D. A., Seidenberg, M., & Binder, J. R. (2005). Modulation of the semantic system by word imageability. *NeuroImage*, 27(1), 188–200.
- Sakata, H., Taira, M., Murata, A., & Mine, S. (1995). Neural mechanisms of visual guidance of hand action in the parietal cortex of the monkey. *Cerebral Cortex*, 5(5), 429–438.
- Schwaneflugel, P. (1991). Why are abstract concepts hard to understand?. In: P. Schwaneflugel (Ed.), *The psychology of word meanings* (pp. 223–250). Hillsdale, NJ: Erlbaum.
- Schwaneflugel, P. J., & Akin, C. E. (1994). Developmental trends in lexical decisions for abstract and concrete words. *Reading Research Quarterly*, 29, 251–264.
- Schwaneflugel, P. J., & Shoben, E. J. (1983). Differential context effects in the comprehension of abstract and concrete verbal materials. *Journal of Experimental Psychology Learning Memory and Cognition*, 9, 82–102.
- Scorolli, C., Binkofski, F., Buccino, G., Nicoletti, R., Riggio, L., & Borghi, A. M. (2011). Abstract and concrete sentences, embodiment, and languages. *Frontiers in Psychology*, 2, 227.
- Seitz, R. J., Roland, P. E., Bohm, C., Greitz, T., & Stone-Elander, S. (1991). Somatosensory discrimination of shape: tactile exploration and cerebral activation. *The European Journal of Neuroscience*, 3(6), 481–492.
- Skrandies, W. (1998). Evoked potential correlates of semantic meaning – A brain mapping study. *Brain Research. Cognitive Brain Research*, 6(3), 173–183.
- Snyder, L. H., Batista, A. P., & Andersen, R. A. (1997). Coding of intention in the posterior parietal cortex. *Nature*, 386(6621), 167–170.
- Swaab, T. Y., Baynes, K., & Knight, R. T. (2002). Separable effects of priming and imageability on word processing: an ERP study. *Brain Research. Cognitive Brain Research*, 15(1), 99–103.
- Tettamanti, M., Buccino, G., Saccuman, M. C., Gallese, V., Danna, M., Scifo, P., et al. (2005). Listening to action-related sentences activates fronto-parietal motor circuits. *Journal of Cognitive Neuroscience*, 17(2), 273–281.
- Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proceedings of the National Academy of Sciences of the United States of America*, 94(26), 14792–14797.
- Tibshirani, R., Walther, G., Botstein, D., & Brown, P. (2005). Cluster validation by prediction strength. *Journal of Computational and Graphical Statistics*, 14, 511–528.
- Tomasino, B., & Rumiati, R. I. (2013). At the mercy of strategies: the role of motor representations in language understanding. *Frontiers in Psychology*, 4, 4–27.
- Tsai, P.-S., Yu, B. H.-Y., Lee, C.-Y., Tzeng, O. J.-L., Hung, D. L., & Wu, D. H. (2009). An event-related potential study of the concreteness effect between Chinese nouns and verbs. *Brain Research*, 1253, 149–160.
- Tyler, L. K., & Moss, H. E. (2001). Towards a distributed account of conceptual knowledge. *Trends in Cognitive Sciences*, 5(6), 244–252.
- Van Dam, W. O., van Dijk, M., Bekkering, H., & Rueschemeyer, S. A. (2012). Flexibility in embodied lexical-semantic representations. *Human Brain Mapping*, 33(10), 2322–2333.
- Van der Mark, S., Klaver, P., Bucher, K., Maurer, U., Schulz, E., Brem, S., et al. (2011). The left occipitotemporal system in reading: disruption of focal fMRI connectivity to left inferior frontal and inferior parietal language areas in children with dyslexia. *NeuroImage*, 54(3), 2426–2436.
- Vaughan, H. G., Jr. (1982). The neural origins of human event-related potentials. *Annals of the New York Academy of Sciences*, 388, 125–138.
- Warrington, E. K., & Shallice, T. (1984). Category specific semantic impairments. *Brain*, 107, 829–854.
- Watkins, K. E., Strafella, A. P., & Paus, T. (2003). Seeing and hearing speech excites the motor system involved in speech production. *Neuropsychologia*, 41(8), 989–994.
- Wennekers, T., Garagnani, M., & Pulvermueller, F. (2006). Language models based on Hebbian cell assemblies. *Journal of Physiology*, 100(1–3), 16–30.
- Whaley, C. P. (1978). Word-nonword classification times. *Journal of Verbal Learning and Verbal Behavior*, 17, 143–154.
- Wheaton, K. J., Thompson, J. C., Syngieniotis, A., Abbott, D. F., & Puce, A. (2004). Viewing the motion of human body parts activates different regions of premotor, temporal, and parietal cortex. *NeuroImage*, 22(1), 277–288.
- Willems, R. M., Toni, I., Hagoort, P., & Casasanto, D. (2010). Neural dissociations between action verb understanding and motor imagery. *Journal of Cognitive Neuroscience*, 22(10), 2387–2400.
- Zwaan, R. A., & Taylor, L. J. (2006). Seeing, acting, understanding: motor resonance in language comprehension. *Journal of Experimental Psychology General*, 135(1), 1–11.