



## Special issue: Research report

# When syntax meets action: Brain potential evidence of overlapping between language and motor sequencing



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## ARTICLE INFO

## Article history:

Received 21 November 2016

Reviewed 09 March 2017

Revised 16 May 2017

Accepted 4 November 2017

Published online 15 November 2017

## Keywords:

Embodied cognition

Motor sequencing

Syntax

Relative clauses

ERPs

## ABSTRACT

This study aims to extend the embodied cognition approach to syntactic processing. The hypothesis is that the brain resources to plan and perform motor sequences are also involved in syntactic processing. To test this hypothesis, Event-Related brain Potentials (ERPs) were recorded while participants read sentences with embedded relative clauses, judging for their acceptability (half of the sentences contained a subject-verb morpho-syntactic disagreement). The sentences, previously divided into three segments, were self-administered segment-by-segment in two different sequential manners: linear or non-linear. Linear self-administration consisted of successively pressing three buttons with three consecutive fingers in the right hand, while non-linear self-administration implied the substitution of the finger in the middle position by the right foot. Our aim was to test whether syntactic processing could be affected by the manner the sentences were self-administered. Main results revealed that the ERPs LAN component vanished whereas the P600 component increased in response to incorrect verbs, for non-linear relative to linear self-administration. The LAN and P600 components reflect early and late syntactic processing, respectively. Our results convey evidence that language syntactic processing and performing non-linguistic motor sequences may share resources in the human brain.

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<sup>1</sup> <https://www.ucm.es/es-cech/cogneurosci>.

<https://doi.org/10.1016/j.cortex.2017.11.002>

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## 1. Introduction

There is a growing body of evidence in the literature emphasizing the relationship between language and sensorimotor processing in the so-called *embodied language* theoretical framework. This approach claims that sensorimotor simulation is at play during language processing and required for appropriate comprehension. From a neurobiological point of view, this notion implies that language comprehension relies at least partially on neural systems for perception and action (Barsalou, 2008; Fischer & Zwaan, 2008; Glenberg & Gallese, 2012; Pulvermüller, 2005; de Vega, Glenberg, & Graesser, 2008).

Evidence for this perspective has largely come from studies in which the motor activity associated with action language has been investigated with different methods, from behavioral measures to neuroimaging techniques. In a seminal paper, Glenberg and Kaschak (2002) reported that the processing time of action sentences was modulated by the preparation or internal simulation of an intended movement that either matched or mismatched the action described in the sentence. This experimental procedure is known as the *action-sentence compatibility effect* (ACE). In addition to these findings, a few electrophysiological studies have combined the ACE paradigm with the study of Event-Related brain Potentials (ERPs). For instance, Aravena et al. (2010) reported, on the one hand, that the incompatibility between a hand movement and the action depicted in a sentence significantly increases the N400 ERP component, a centro-parietal negativity reflecting semantic processing (Kutas & Federmeier, 2011). On the other hand, these authors showed a decrement in the ERP motor potential (MP) component associated with the hand movement, suggesting a bidirectional impact between language comprehension and motor processes. A similar pattern has also been found in studies of motor compatibility effects in language comprehension. Specifically, larger N400 amplitudes occur when participants read sentences referred to two simultaneous manual actions, which cannot be performed at once (Santana & de Vega, 2013). This type of data supports some common functional substrates for semantic processing of language and motor control.

Functional Magnetic Resonance Imaging (fMRI) studies, on the other hand, have reported activations of motor regions triggered by action language. For example, Pulvermüller and colleagues have described that understanding action verbs, in comparison with nouns referring to perceptual objects, elicited activations in fronto-central regions, including the pre-motor and motor cortex (Pulvermüller, 1996, 2005). Also, processing action verbs associated to different parts of the body elicited activations in somatotopic regions of the cortex that partially overlap with those specifically involved in the execution of those actions (Hauk & Pulvermüller, 2004; Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005). In addition, somatotopy in response to sentences describing actions has also been reported, yielding a strong activation of the fronto-parietal-motor network when compared with more abstract content sentences (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; de Vega et al., 2014; Tettamanti et al., 2005).

Embodied language theories, however, go beyond primary sensorimotor information and assume that embodiment could also entail abstraction. Comprehending words draws on reusing the whole sensorimotor representations that provided the basis for the acquisition of the corresponding concepts. Thus, the reactivation of multimodal states integrates conceptual information into a general and abstract representation, which is a function of cortical association areas as those described in classical neuroanatomical models of semantic memory (Barsalou, 2008, 2016a, 2016b). These areas of heteromodal cortex, which include the inferior parietal lobe and much of the temporal lobe –among others–, play an important role in the supramodal representations that allow the manipulation of abstract knowledge in semantic processing, having been cited as semantic “hubs” or high-level “convergence zones” (Binder & Desai, 2011; Damasio, 1989; Kiefer & Pulvermüller, 2012).

Importantly, the claim that embodied language also comprises abstract knowledge actually implies that syntax may as well be accounted for by this perspective. Several authors have indeed addressed this issue. In this regard, Kreiner and Eviatar (2014) propose that syntax is an emergent linguistic abstraction that can be embodied by different prosodic patterns in different languages. For example, hierarchic relationships between elements would be an abstraction that may be coded by intonation and/or by pauses in different languages. In turn, Glenberg and Gallese (2012), in their theory of *action-based language* (ABL), link language and action through the neural overlap between mirror neuron system for action and Broca's area for speech articulation. In this frame, these authors propose that syntax emerges from action control. Put simply, as the basic function of motor control is to combine movements in a way that produces goal-directed action and the main function of syntax is to combine linguistic components to produce a communicative goal, then syntax emerges from reusing control of action to produce control of speech (Glenberg & Gallese, 2012). Indeed, the well-known fact that Broca's area is functionally involved both in the syntax and in the sensorimotor systems supports this view (Clerget, Winderickx, Fadiga, & Olivier, 2009; Friederici, Bahlmann, Friedrich, & Makuuchi, 2011; Moro, 2014; Pulvermüller & Fadiga, 2010). In a similar vein, and from a mechanistic point of view, syntactic links (including agreement and other non-local syntactic relationships), have been proposed to be neurobiologically grounded in *discrete combinatorial neuronal assemblies*, or DCNAs, that bind together pairs of constituents (Pulvermüller, 2010). These combinatorial emerging aggregates of sequence detectors (similar to those found in a range of animals), do provide a candidate neuronal mechanism of syntactic binding circuits in establishing grammatical relationships in sentences (Pulvermüller & Knoblauch, 2009).

To date, however, empirical research on embodied language has mainly focused on the semantic domain, i.e., on how processing the *meaning* of action words (nouns and verbs), either presented in isolation or embedded into sentences, recruits our sensorimotor systems. By contrast, the relationship between syntax and embodiment has scarcely been addressed. Ensuing theoretical proposals that link

syntax and action systems of the brain (Glenberg & Gallese, 2012; Pulvermüller, 2010), this paper aims to contribute to this field by studying the impact of different concurring motor tasks on syntactic processing, by means of ERPs.

A customary procedure to study syntactic sentence processing with ERPs is the presentation of grammatical anomalies, such as morphosyntactic or word category violations (Carreiras & Clifton, 2004; Steinhauer & Connolly, 2008). Studies on sentence processing have usually granted different syntax-related ERP components to these types of anomalies, mainly consisting of anterior negativities and posterior positivities. Anterior negativities are typically labeled as LAN (left anterior negativity, after their leftmost usual distribution), peaking between roughly 250 and 550 msec, or ELAN (early LAN), appearing as early as 100–200 msec. Word category violations are the variations most frequently associated with ELAN (e.g., Friederici & Mecklinger, 1996), whereas other grammatical anomalies, including morphosyntactic violations (e.g., Coulson, King, & Kutas, 1998), usually elicit a LAN. Both anterior negativities may reflect highly automatic first-pass parsing processes, the detection of a morphosyntactic mismatch, and/or the inability to assign the incoming word to the current phrase structure (Friederici, 2002). In turn, a late positive-going component with a centro-parietal maximum, labeled P600, has typically been considered as a syntax-related ERP fluctuation since it is elicited by syntactic violations (e.g., Osterhout & Holcomb, 1992) and structurally ambiguous but correct sentences (Frisch, Schlesewsky, Saddy, & Alpermann, 2002). Accordingly, it has been suggested that the P600 indexes increased syntactic processing costs due to revisions and reanalyses of structural mismatches, possibly also reflecting subsequent repair processes (Müntz, Heinze, Matzke, Wieringa, & Johannes, 1998).

In the present study, we present to our participants center-embedded relative sentences that could contain a morphosyntactic error in the main verb, while recording ERPs. All our experimental sentences contained center-embedded relative clauses, because we wanted to use grammatical structures with certain degree of complexity; note therefore that sentence structure is not a manipulated but instead a controlled variable. On the other hand, the use of morphosyntactic violations is intended here as a means to elicit LAN and P600 ERP components and therefore to approach syntactic sentence processing, as customary in ERP research (see above). Accordingly, possible particularities on morphosyntactic processes relative to other types of grammatical features are not of interest here. Again, the type of grammatical process is not a manipulated but a controlled variable.

The sentences were divided into three consecutive segments, the segment in the middle consisting of the corresponding relative clause. Each segment was self-administered by the participants in one of either two manners. *Linear* self-administration consisted in successively pressing three buttons with three consecutive fingers of their right hand. *Non-linear* self-administration implied the substitution of the finger in the middle position—administering the relative clause—by pressing a button with their right foot.

These two types of sequences differ in the way their constituents are organized. Whereas in the linear mode of

administration the elements are concatenated sequentially, based on (body) local dependencies, the non-linear task implies a discontinuity between constituents characterized by long-distance dependencies (i.e., between two different body parts). The choice for these terms (linear and non-linear) is just intuitive as the linear sequence can be graphically represented as a straight line while the non-linear actually represents a V. Accordingly, it should not be seen as literally synonymous to syntactic linearity vs. non-linearity (or finite state vs. phrase structure grammar, as in, e.g., Friederici, Anwander, Heim, Schubotz, & Bahlmann, 2006). Even though, with the non-linear self-administration we aimed at paralleling to some extent the syntactic organization of relative sentences. In this regard, the non-linear self-administration implies a motor sequence structurally more complex than the linear one, in which the foot pressing depends on prior finger pressing and is followed back by another finger pressing. Therefore, this non-linear sequence constitutes a structure with non-adjacent or non-local dependencies—insofar as the hand and the foot represent different body loci. In this regard, sentences with center-embedded relative clauses are often considered as an exemplary case of structures with long distance and non-local combinations (Chomsky & Miller, 1958). In sum, the combinatorial configuration in our non-linear self-administration task can be assumed to partially equate the combinatorial operations involved in our non-linear, relative sentences. The similarities are nevertheless not straightforward, since we cannot assume specific properties of sentences, like a recursive or hierarchical organization (e.g., Hauser, Chomsky, & Fitch, 2002), in our non-linear motor sequences.

Our aim is to test whether the type of motor sequence (linear vs. non-linear) in which the sentences were self-administered affects syntactic processing as measured by the LAN and the P600 ERP components. To the extent that the neural processes recruited during the execution of structured motor tasks may be coextensive with neural processes implicated in syntactic structuring (as the embodied language approach suggests) some type of conflict or interplay should emerge when the motor sequence is more complex or non-linear, relative to linear sequences of self-administration.

## 2. Method and materials

### 2.1. Participants

Twenty-four healthy, native Spanish speakers (mean age 24 years, range 18–43, 10 males) participated in the study. All had normal or corrected-to-normal vision and were right-handed with average handedness scores of +82 (range 37–100), according to the Edinburgh Handedness Inventory (Oldfield, 1971). Prior to the experiment, the participants gave their informed consent and declared neither neurological nor psychiatric complaints. The volunteers were reimbursed for taking part in the experiment. The study was performed in accordance with the Declaration of Helsinki and approved by the ethics committee of the Center for Human Evolution and Behavior, UCM-ISCIII, Madrid, Spain.

## 2.2. Design and material

A  $2 \times 2$  repeated-measures experimental design was used in which Manner of sentence self-administration (linear/non-linear) and sentence Correctness (correct/incorrect, as a function of morphosyntactic violations) were manipulated independently.

The experimental language material consisted of a set of 210 Spanish relative sentences with a center-embedded subject-relative clause introduced by different subordinate conjunctions (i.e., “that”, “where”, “who”, “whose”, etc.), separated by commas from the main clause. Furthermore, next to the correct version of the relative sentences, an ungrammatical version was created containing a morpho-syntactic violation, that is, the verb of the main clause could present person, number, or both agreement violations.

From this initial pool of experimental sentences, a set of filler sentences was constructed by transforming each relative sentence into its copulative version, in which two transitive clauses were joined by the “and” conjunction. These fillers guaranteed different sentence structure while using the same linguistic material and sentence length as in the experimental sentences; they were never presented in both (relative and copulative) versions to the same subjects, and were always correct. Additionally, we also constructed 70 simple filler sentences of diverse syntactic structures, other than those in the experimental sentences. Half of these filler sentences were transitive, whereas the other half were intransitive. The entire set of simple fillers included a syntactic anomaly, at different points of the sentence, in order to overall equalize the number of correct and incorrect sentences within a session. The structure of all the sentences (experimental and fillers of either type) allows them to be divided into three segments to fit the self-administration motor task.

Length of target words (number of syllables) was matched across conditions (i.e., correct and incorrect sentences). Other linguistic variables, such as word frequency, familiarity, concreteness and imageability, were counterbalanced since all the verbs (correct and incorrect) were presented under both self-administration tasks.

Examples of the sentences, and their translations into English, are shown in Table 1.

With all this material, three experimental sets were constructed. Each set comprised 280 sentences: 70 correct relative sentences, 70 incorrect relative sentences, 70 copulative filler (correct) sentences, and the 70 other filler (incorrect) sentences. The sentences used in one set in their relative version, were in the copulative version in the other sets, and vice versa. Sentences used in one set in their correct version, were in the incorrect version in the other sets, and vice versa. Each sentence (whether copulative or relative, and correct or incorrect) was presented to a given participant only once. Every participant performed one of the three sets. The presentation of the sentences within a set was randomized.

## 2.3. Procedure

Participants were seated in a comfortable chair in an electrically shielded chamber. They were thoroughly informed about the experimental tasks and presented with a training set of

**Table 1 – Examples of experimental and filler sentences.**

Experimental sentences		Filler sentences	
Correct relative sentences	Incorrect relative sentences	Correct copulative sentences	Incorrect simple sentences
El agua [N, Sing.], que rebasó la presa, anegó [V, Sing, 3rd person] el poblado. The water [N, Sing.], that overflowed the dam, flooded [V, Sing., 3rd person] the village. El árbol [N, Sing.], donde anidaron los polluelos, floreció [V, Sing., 3rd person] en primavera. The tree [N, Sing.], where the chicks nested, blossomed [V, Sing, 3rd person] in spring. El pasajero [N, Sing.], cuya mochila descuidó, lamentó [V, Sing, 3rd person] el despiste. The passenger [N, Sing.], whose backpack neglected, regretted [V, Sing., 3rd person] the oversight.	El agua [N, Sing.], que rebasó la presa, anegaron [V, Pl., 3rd person] el poblado. The water [N, Sing.], that overflowed the dam, flooded [V, Pl., 3rd person] the village. El árbol [N, Sing.], donde anidaron los polluelos, florecí [V, Sing., 1st person] en primavera. The tree [N, Sing.], where the chicks nested, blossomed [V, Sing, 1st person] in spring. El pasajero [N, Sing.], cuya mochila descuidó, lamentaron [V, Pl., 3rd person] el despiste. The passenger [N, Sing.], whose backpack neglected, regretted [V, Pl., 3rd person] the oversight.	El agua [N, Sing.] rebasó la presa y anegó [V, Sing., 3rd person] el poblado. The water [N, Sing.] overflowed the dam and flooded [V, Sing, 3rd person] the village. En el árbol [N, Sing.] anidaron los polluelos y floreció [V, Sing., 3rd person] en primavera. In the tree [N, Sing.] the chicks nested and blossomed [V, Sing, 3rd person] in spring. El pasajero [N, Sing.] descuidó su mochila y lamentó [V, Pl., 3rd person] el despiste. The passenger [N, Sing.] neglected his backpack and regretted [V, Sing, 3rd person] the oversight.	El niño [N, Masc.,Sing.] consentida [Adj, Fem.,Sing.] aprende despacio sin las normas. The spoilt [Adj, Fem.,Sing.] boy [N, Masc.,Sing.] learns slowly without the rules. El gato bajo la mesa reposó en las [Det, Fem.,Pl.] manta [N, Fem.,Sing.]. The cat under the table rested in the [Det, Fem.,Pl.] blanket [N, Fem.,Sing.]. El coche [N, Masc., Sing.] con tres puertas chocamos [V, Pl., 2nd person] contra el muro. The three doors car [N, Masc.,Sing.] crashed [V, Pl., 2nd person] into the wall.



sentences, followed by one of the three sets of experimental sentences. Each sentence was partitioned into three consecutive segments, and participants were asked to self-administer these segments, avoiding body movements and blinks, in either two manners. In half of the sentences, a linear presentation manner was requested, in which participants pressed consecutively three buttons using the index, middle and ring fingers of their right hand, respectively. In the other half of the sentences, the non-linear presentation manner was used; the procedure was exactly the same as in the linear trials, except that the second segment of the sentence required pressing a pedal with the right foot rather than pressing a button with the middle finger (see Fig. 1). Participants were assigned randomly to one of the three sets of trials. Along the subjects, the presentation order of the sets was counterbalanced, as well as the order of the two manners of self-administering the sentence within a set. As the self-administering manner changed at the middle of the experimental session, a training set was repeated at this stage, practicing the new manner of self-administration.

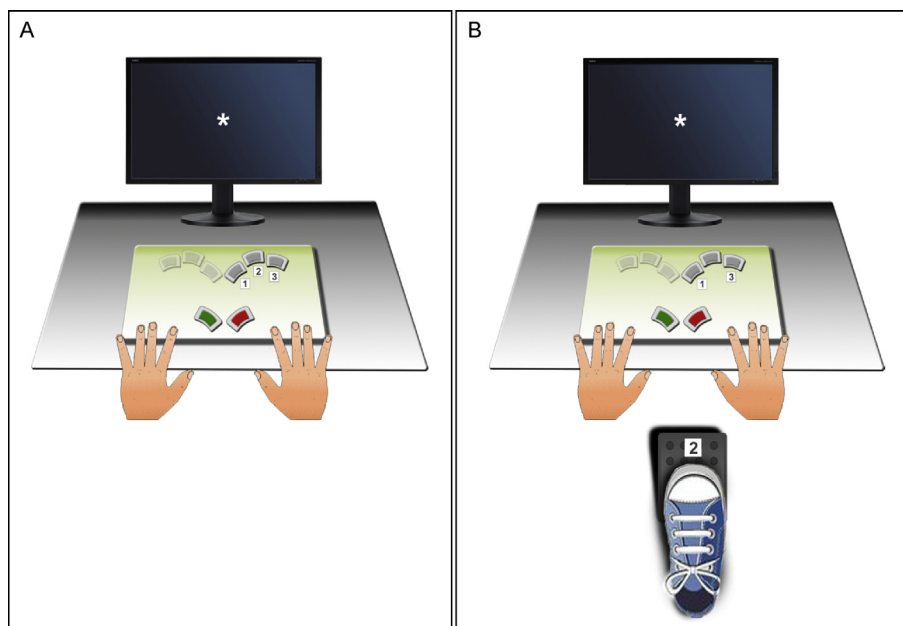
Stimuli were presented white-on-black on an LCD screen, controlled by Presentation<sup>®</sup> Software. Participants' eyes were located 65 cm from the screen yielding viewing angles of the stimuli around 0.8° in height and 0.8° to 4° in width. Each trial started with a fixation cross presented on the center of the screen for 500 msec and followed by 200 msec blank. Subsequently, an asterisk appeared indicating the participants to press the first button to get the first segment displayed. As soon as the participants pressed the button, a 300-ms blank appeared followed by the first segment which was presented word-by-word, for 300 msec each, with a stimulus onset asynchrony (SOA) of 600 msec. The schema of events was the same for the next two segments of every sentence,

both in the linear and in the non-linear presentation manners. The first word of the first segment always began with a capital letter and the last word of the third segment was presented together with a period at the end. One second after the offset of the last word, a question mark appeared for 1, 5 sec as a prompt to judge whether the sentence was correct or not. The judgment was performed by pressing one of two keys with the thumb either of the right or the left hand. Hand assignment to decision alternative (correct/incorrect) was counterbalanced. The outline of a trial is illustrated in Fig. 2. The experimental session lasted about 50 min, plus electrode preparation.

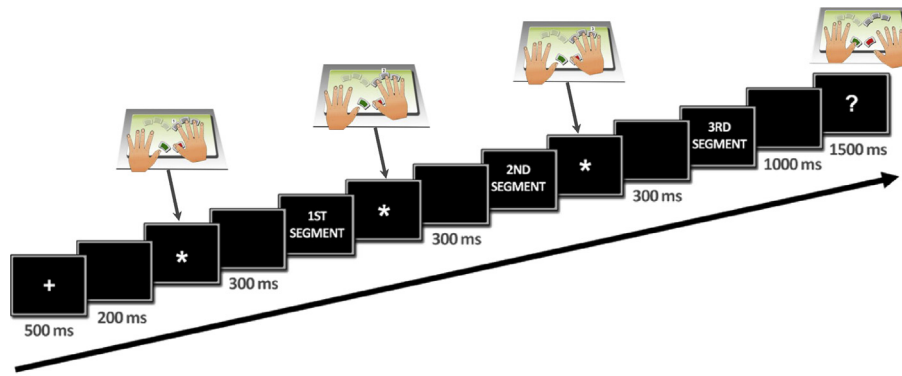
#### 2.4. Electrophysiological recording and analysis

EEG was recorded from 59 scalp channels; electrodes were mounted in an electrode cap (EasyCap), following the 10/20 International System. The impedance of all electrodes was kept below 5 K $\Omega$ . Raw data were sampled at 250 Hz and recorded with a band-pass from .01 to 40 Hz. Bipolar vertical and horizontal EOGs were recorded to monitor eye movements and blinks. During recording all scalp electrodes as well as one electrode at the left mastoid, were originally referenced to one electrode at the right mastoid; offline they were re-referenced to the average of the right and left mastoids.

The EEG data was analyzed with Brain Vision Analyzer<sup>®</sup> software. Raw data were filtered off-line with a band-pass from .05 to 20 Hz. The continuous EEG was segmented into 1200 msec epochs, starting 200 msec before the onset of the main verb in the relative sentences. Ocular correction was applied following the algorithm of Gratton, Coles, and Donchin (1983), and a semi-automatic mode for artifact rejection was implemented to eliminate remaining epochs



**Fig. 1 – Buttons for self-administration. A) Linearly sequenced manner of self-administration. The participants were told to press three buttons (signaled with numbers 1, 2 and 3) only with three consecutive fingers in their right hand. B) Non-linearly sequenced manner of self-administration. The participants were told to replace the finger pressing the button in the middle position by the right foot pressing a pedal (number 2).**



**Fig. 2 – Schematic representation of the stimulation procedures. Participants were presented the three segments word by word. Participants' task consisted of pressing a button to get the segments displayed every time they saw an asterisk in the center of the monitor in order to continue the task. At the end of each sentence, a judgment of grammaticality was requested. Examples of the buttons to press are included.**

with artifacts from the data. Additionally, incorrectly classified stimuli (correct sentences judged as incorrect and vice versa) were also excluded from the ERP averages. The final mean rejection rate was 35.5% of epochs, and at least 20 trials could be analyzed for every condition. There were no significant differences between conditions nor interactions in this regard (repeated-measures analyses of variance (ANOVA) with the factors sentence Correctness and Manner of sentence self-administration: all  $F_s(1,23) < 2.56$ ; all  $p_s > .1$ ).

Separate average ERPs were calculated for 1200 msec-epochs containing verbs in the experimental sentences as a function of whether they were self-administered in a linear or a non-linear manner, correct or incorrect.

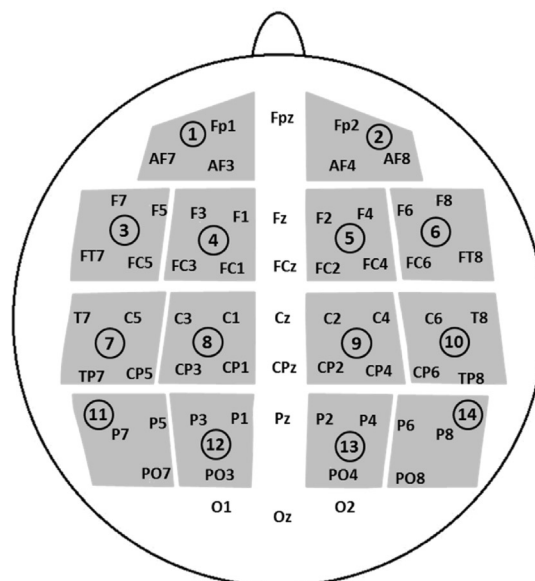
Overall repeated-measures ANOVA were first performed for amplitude comparisons. Amplitude was measured as the mean amplitude within a particular time interval. To avoid a loss of statistical power when repeated-measures ANOVAs are used to quantify a large number of electrodes, fourteen

regions of interest (ROIs) were computed out of 59 cephalic electrodes, each containing the mean of three or four electrodes (see Fig. 3). ANOVAs included four factors: sentence Correctness (correct vs. incorrect), Manner of sentence self-administration (linear vs. non-linear), Region (7 levels), and Hemisphere (2 levels). The Greenhouse-Geisser correction (Greenhouse & Geisser, 1959) was always applied when appropriate. Effect sizes were calculated by computing partial eta-square ( $\eta_p^2$ ).

### 3. Results

#### 3.1. Performance

Regarding sentences correctness judgment, the results were as follows: correct sentences were judged as correct in 96.6% and 96.8% of cases, for sentences self-administered in linear



- Region 1: left antero-lateral
- Region 2: right antero-lateral
- Region 3: left fronto-lateral
- Region 4: left fronto-medial
- Region 5: right fronto-medial
- Region 6: right fronto-lateral
- Region 7: left centro-lateral
- Region 8: left centro-medial
- Region 9: right centro-medial
- Region 10: right centro-lateral
- Region 11: left parieto-lateral
- Region 12: left parieto-medial
- Region 13: right parieto-medial
- Region 14: right parieto-lateral

**Fig. 3 – Layout of the 14 regions of interest in relation to the measured electrodes.**

**Table 2 – Performance on correctness judgment task. Percentage of errors and mean reaction times (RTs) in milliseconds as a function of manner of self-administration and sentence correctness. SDs are shown in parentheses.**

		Manner of self-administration	
		Linear	Non-linear
Correct sentences	Errors	3.4 (3.9)	3.2 (2.6)
	RTs	727.1 (271.7)	715.9 (272.9)
Incorrect sentences	Errors	1.6 (1.9)	1.9 (2.6)
	RTs	629.9 (223.9)	567.2 (247.3)

and non-linear manner, respectively. Incorrect sentences in turn were classified as incorrect in 98.4%, and 98.1% of cases, respectively. The difference between appropriate classifications of correct and incorrect sentences ( $M = 96.70\%$  vs.  $98.21\%$ ) was significant [ $F(1,23) = 4.781$ ,  $p = .05$ ,  $\eta_p^2 = .15$ ]. No significant main effects of Manner of self-administration, or interaction with Correctness were obtained. Overall, the Manner of self-administering the sentences did not impact final correctness judgments of the participants. This is probably the consequence of correctness judgments being requested 1 sec after the offset of the last word (i.e., 2,800 msec after the onset of the verb), and therefore this information will not be considered of interest for the main purposes of the present study and will not be discussed.

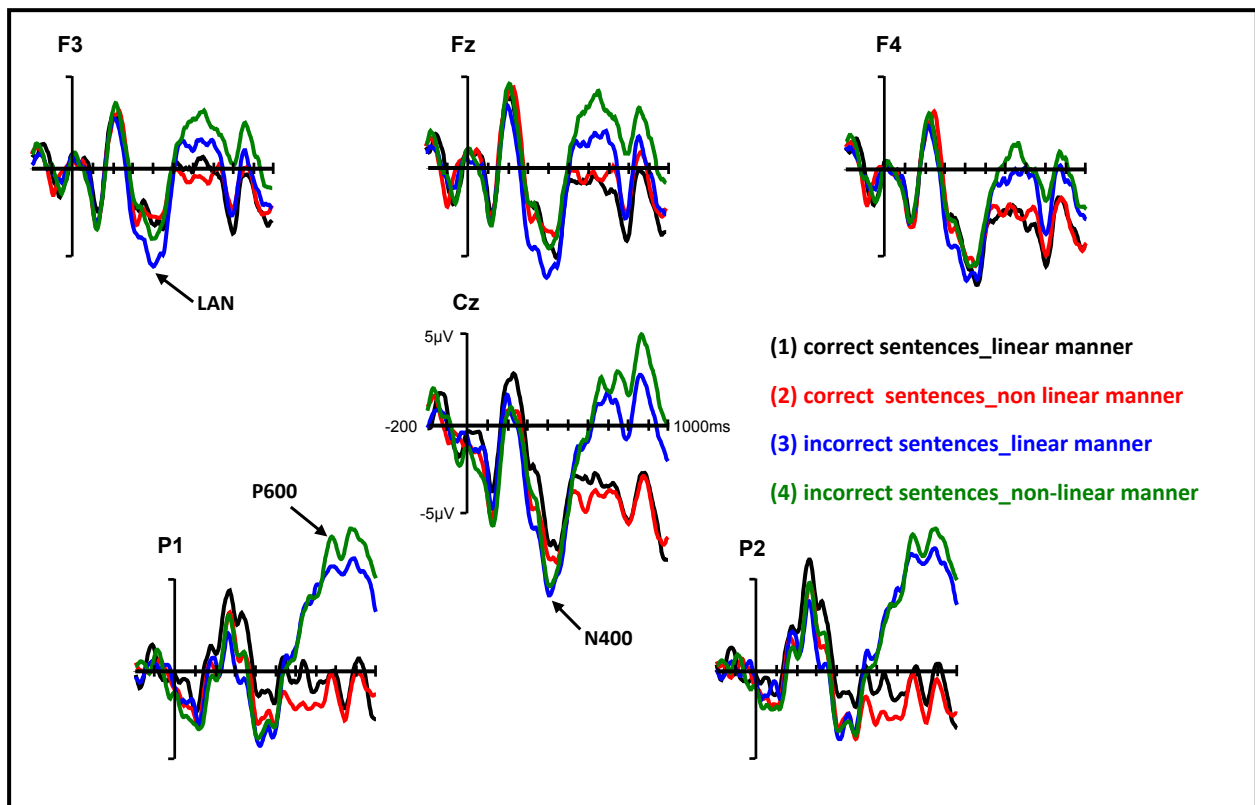
The mean reaction times (RTs) were 727.1 msec for correct sentences delivered in linear manner, 629.9 msec for incorrect

sentences delivered in linear manner, 715.9 msec for correct sentences delivered in non-linear manner and 567.2 msec for incorrect sentences delivered in non-linear manner. An ANOVA indicated a significant effect of Correctness,  $F(1,23) = 25.622$ ,  $p = .001$ ,  $\eta_p^2 = .53$ . Again, no significant main effects of Manner of self-administration, or in interaction with Correctness were obtained. Yet again, the long interval between the presentation of the critical word (the verb) and the response request render these results not relevant for discussion. Table 2 shows performance on sentence correctness judgment.

### 3.2. Event-related potentials

Visual inspection of the ERPs (Fig. 4) revealed two main effects of sentence Correctness, associated with linear self-administration; namely, incorrect sentences elicited a negativity maximal at left frontal electrodes and peaking around 400 msec (a LAN effect), and a long-lasting posterior positivity (P600) around 600 to 1000 msec. Strikingly, however, for the non-linear self-administration, the LAN does not appear, while the P600 component increases in amplitude.

Repeated-measures ANOVA for mean ERP amplitudes in the time window from 350 to 450 msec substantiated this description for the LAN, revealing a significant interaction of Hemisphere by Region by Correctness by Manner of self-administration. Based upon these results as well as on visual inspection, a post-hoc ANOVA was performed in the left fronto-medial region (ROI number 4 in Fig. 3), yielding a main



**Fig. 4 – ERP waveforms at selected electrodes to syntactically correct and incorrect verbs in the two manners of self-administering. For display purposes only, the ERP waves were high-pass filtered at 15 Hz.**

effect of Correctness [ $F(1,23) = 8.302, p = .008, \eta_p^2 = .27$ ], as well as a significant Correctness by Manner of self-administration interaction [ $F(1,23) = 6.385, p = .019, \eta_p^2 = .22$ ].

The depiction of the P600 effects, in turn, was supported by main effects of Correctness, which was qualified by interactions with Hemisphere, with Region, and with both, Hemisphere and Region in the windows 600–700, 700–800, 800–900, and 900–1000 msec. Further, differences in amplitude between linear and non-linear manners of self-administration in the P600 were also statistically supported by significant results in the Correctness by Hemisphere by Region by Manner of self-administration interaction in the 600–700 and 700–800 msec time window. ANOVA results are reported in Table 3.

Interestingly, Fig. 4 also reveals an apparent difference in posterior electrodes between the correct trials in the linear manner of administration and the rest of conditions. This consisted in a more positive-going fluctuation starting about 250–300 msec and resolving by 700 msec. After 500 msec, however, this difference remains only for the comparison between both correct stimuli, since in the incorrect ones the P600 effects arise. To substantiate this observation, post-hoc ANOVAs were performed only for correct sentences as a function of the manner of self-administration, in the windows 300–400, 400–500, 500–600, and 600–700 msec in the 4 ROIs around centro-parietal areas (ROIs numbers 8, 9, 12, and 13 in Fig. 3).

Results showed significant effects of Manner of self-administration in the four regions for 300–400 msec and for

500–600 msec windows. For 600–700 msec window, we found significant effects for the left centro-medial, left parieto-medial and right parieto-medial regions (Table 4). Given its distribution and time-course, we interpreted this modulation as a possible reduction of the N400 effects in the condition that happened to be the easiest in the experimental setup (i.e., correct sentences in linear self-administration).

Fig. 5 summarizes our main results through their topographic representations. Given the posterior positivity (or reduced negativity) in the correct sentences linearly delivered, the LAN effects in the corresponding incorrect sentences are better viewed by comparison with the incorrect sentences delivered non-linearly, where no LAN emerged (Fig. 5B) while devoid of the posterior positivity.

#### 4. Discussion

Our study frames into embodied language approaches, according to which brain resources to plan and perform motor sequences are also used in generating and comprehending some linguistic structures. In the present study, we have explored the brain reactions (ERPs) to morphosyntactic violations in relative sentences, as a function of the type of concurrent motor task used by the participants to self-administer the fragments of the sentence. While linear self-administrations yielded the typical pattern of LAN and P600 components to grammatical anomalies, non-linear self-administrations resulted in LAN vanishment and P600

**Table 3 – Main ANOVA of ERP results.**

	d.f.	Window (ms)				
		350–450	600–700	700–800	800–900	900–1000
Hemisphere	1,23		20.8*** $\eta_p^2 = .48$	12.8*** $\eta_p^2 = .36$	4.7* $\eta_p^2 = .17$	5.5* $\eta_p^2 = .20$
Region	6,138	14.2*** $\eta_p^2 = .38$	2.7* $\eta_p^2 = .11$	7.9*** $\eta_p^2 = .26$	4.7** $\eta_p^2 = .17$	13.8*** $\eta_p^2 = .38$
Correctness	1,23	5.4* $\eta_p^2 = .20$	15.8*** $\eta_p^2 = .41$	24.7*** $\eta_p^2 = .52$	35.7*** $\eta_p^2 = .61$	50.9*** $\eta_p^2 = .70$
Manner of self-administration	1,23					
Hemisphere $\times$ Region	6,138	12.8*** $\eta_p^2 = .36$	6.0** $\eta_p^2 = .21$	9.8*** $\eta_p^2 = .30$	10.5*** $\eta_p^2 = .31$	4.8** $\eta_p^2 = .17$
Hemisphere $\times$ Correctness	1,23		22.1*** $\eta_p^2 = .50$	38.8*** $\eta_p^2 = .63$	26.6*** $\eta_p^2 = .54$	50.7*** $\eta_p^2 = .70$
Region $\times$ Correctness	6,138		4.5* $\eta_p^2 = .16$	14.2*** $\eta_p^2 = .38$	23.0*** $\eta_p^2 = .50$	15.7*** $\eta_p^2 = .41$
Hemisphere $\times$ Region $\times$ Correctness	6,138		13.0*** $\eta_p^2 = .36$	15.3*** $\eta_p^2 = .40$	22.3*** $\eta_p^2 = .50$	14.3*** $\eta_p^2 = .38$
Hemisphere $\times$ Manner of self-administration	1,23		4.2* $\eta_p^2 = .15$	12.5*** $\eta_p^2 = .35$	25.8*** $\eta_p^2 = .53$	17.6*** $\eta_p^2 = .43$
Region $\times$ Manner of self-administration	6,138	6.04** $\eta_p^2 = .21$	5.2** $\eta_p^2 = .19$	5.9** $\eta_p^2 = .21$	6.3** $\eta_p^2 = .22$	4.5*** $\eta_p^2 = .17$
Hemisphere $\times$ Region $\times$ Manner of self-administration	6,138		14.7*** $\eta_p^2 = .40$	16.0*** $\eta_p^2 = .41$	24.8*** $\eta_p^2 = .52$	21.7*** $\eta_p^2 = .50$
Correctness $\times$ Manner of self-administration	1,23					
Hemisphere $\times$ Correctness $\times$ Manner of self-administration	1,23					
Region $\times$ Correctness $\times$ Manner of self-administration	6,138					
Hemisphere $\times$ Region $\times$ Correctness $\times$ Manner of self-administration	6,138	3.8* $\eta_p^2 = .14$	5.0** $\eta_p^2 = .18$	4.3** $\eta_p^2 = .16$		

F-values with  $p$  (\* $<.05$ , \*\* $<.01$ , \*\*\* $<.001$ ) and partial eta-square ( $\eta_p^2$ ). Only significant results are reported.



**Table 4 – Post-hoc ANOVAs for correct stimuli in four centro-parietal regions showing effects of Manner of self-administration.**

	Window (ms)		
	300–400	500–600	600–700
Left Centro Medial Region	8.0*** $\eta_p^2 = .26$	6.8** $\eta_p^2 = .23$	4.5* $\eta_p^2 = .16$
Right Centro Medial Region	4.8* $\eta_p^2 = .17$	4.2* $\eta_p^2 = .15$	
Left Parieto Medial Region	5.9* $\eta_p^2 = .21$	4.5* $\eta_p^2 = .16$	5.3* $\eta_p^2 = .19$
Right Parieto Medial Region	7.1** $\eta_p^2 = .24$	5.2* $\eta_p^2 = .19$	5.3* $\eta_p^2 = .19$

F-values (d.f. = 1.23) with  $p$  (\* < .05, \*\* < .01, \*\*\* < .001) and partial eta-square ( $\eta_p^2$ ). Only significant results are reported.

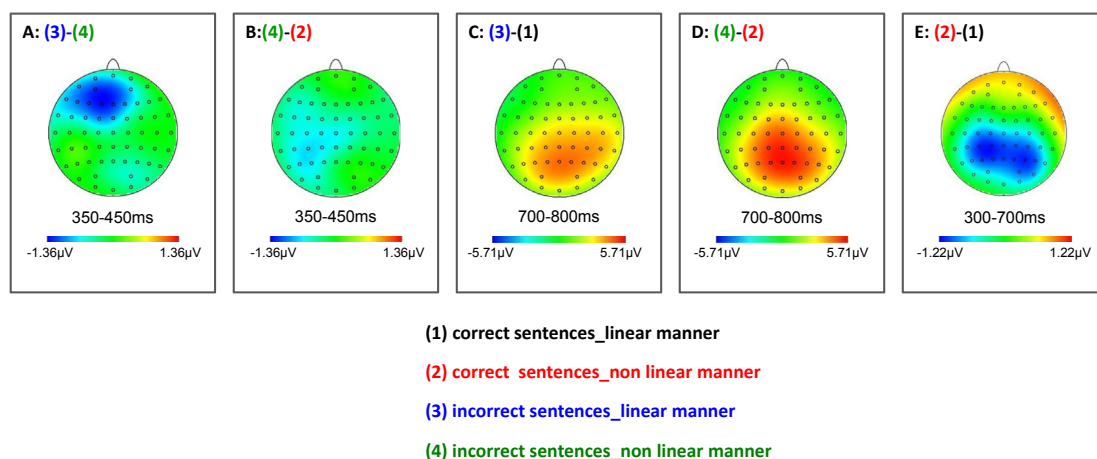
enhancement. As we will argue, this seems to support an embodied language approach.

To our knowledge, this is the first time that a motor task is conflated with a concurring sentence processing to explore a possible mutual interplay at the syntactic domain. Our experimental paradigm was initially inspired in previous literature on the ACE paradigm, reviewed in the introduction. The ACE studies have shown that understanding the *meaning* of action sentences and performing simultaneously matching or mismatching motor actions significantly modulates behavior and brain responses. In this article, we use an ACE-like procedure, but going one step further, by focusing on syntactic processing rather than lexically driven meaning. The rationale is that processing the structural (syntactic) features of the sentence, regardless of its specific meaning, is affected by the processing of the structural features of the concurring motor task. However, whereas many ACE studies have found a facilitation of language processing in trials with matching movements (e.g., Aravena et al., 2010; Glenberg &

Kaschak, 2002), our results are rather indexing interference between matching non-linear motor sequences and non-linear syntactic processing. The interplay between motor actions and syntactic processing would have yielded a depletion of the available resources, which in our case was detrimental for syntactic processing.

A similar resources depletion explanation for compatible conditions was proposed in some ACE studies, in which the motor response was requested immediately after the action verb onset. In such case, the reaction times were slower for matching than mismatching conditions (Buccino et al., 2005; de Vega, Moreno, & Castillo, 2013). These apparent discrepancies between facilitatory and interfering ACE results could be explained by a recent model accounting for motor-language coupling. The Hand-Action-Network Dynamic Language Embodiment (HANDLE) model (García & Ibáñez, 2016) proposes that relevant networks related to the coupling of motor action and embodied semantics could be activated in different thresholds and predicts that if the action is prepared before sentence onset or during sentence unfolding, facilitation or interference would occur, respectively. In the same line, previous studies have described significant amplitude modulations of the biphasic LAN-P600 pattern when processing conflicts tap on shared resources (King & Kutas, 1995; Tanner & van Hell, 2014; Vos, Gunter, Kolk, & Mulder, 2001). This would be suggestive of our results reflecting that syntax and motor task computations draw upon interdependent resources, this leading to syntactic processing impairment when sentences are non-linearly self-administered.

Some authors have proposed the existence of a domain-general hierarchical sequential processor in the inferior frontal lobe (Fadiga, Craighero, & D'Ausilio, 2009; Fiebach & Schubotz, 2006; Tettamanti & Weniger, 2006), which is in line with the sensorimotor theory of syntax, i.e., the involvement of action and perception circuits to mediate syntactic processing in language (Pulvermüller & Fadiga, 2010; van Schie, Toni, & Bekkering, 2006). Our results reinforce this



**Fig. 5 – Summary of main results. Difference maps of the LAN, P600 and N400 effects. A:** LAN effect in incorrect sentences, when they were linearly self-administered. **B:** Absence of LAN effect in incorrect sentences when they were non-linearly administered. **C and D:** The P600 component to morphosyntactic violations, which seems to increase in amplitude with non-linear administrations (in D). **E:** The posterior positivity in correct sentences delivered linearly is here represented with inverted polarity, in line with its interpretation as a reduction of the N400 component in this condition.

idea, supporting that the production of a non-linear motor task apparently recruits neural resources of this supramodal processor, turning it unavailable for the syntactic processing of the morphosyntactic violations. Reports that the LAN component of the ERPs, which was strongly affected in our study, appears to be generated in left inferior frontal regions (e.g., Molinaro, Barber, & Carreiras, 2011) would harmonize well with this assumption.

Syntactic processing has been traditionally considered as an encapsulated process, that is, impervious to other non-syntactic or extralinguistic processes (Friederici & Weissenborn, 2007; Hauser et al., 2002; Ullman, 2001). Nevertheless, there is evidence that other types of information, such as semantics or emotional context, can significantly affect syntactic processing (e.g., Jiménez-Ortega et al., 2012; Martín-Loeches, Nigbur, Casado, Hohnfeld & Sommer, 2006). In line with this, our experimental results demonstrate that syntactic processing can be affected by a concurrent motor task, adding new evidence to the proposal that syntax processing might interact with other domains, and might therefore be less independent and encapsulated than traditionally postulated.

In this respect, it could be the case that our observed effects are not straightforwardly the consequence of our motor task, but instead depend on more general resources. That is, effects may not be necessarily specific of motor actions, but tapped by the cognitive shift involved by our non-linearly sequenced motor task, i.e., the required alternation between hand and foot in participants' self-administration. In this line, other possibilities may also be admissible, such as shared resources related to attentional control, prediction and expectation, or other top-down processes (e.g., Simanova, Francken, de Lange, & Bekkering, 2015). Our experimental design does not permit to fully clarify these points. However, no modulation typically related to attention, executive control or other cognitive processes could be observed. Besides, the fact that our non-linear self-administration task modulated ERP components typically related to syntax, i.e., LAN and P600 (as well as the semantic N400 –see below), would support that processes extraneous to the manipulated factors were not involved. In any event, our main conclusion could hold: performing a non-linear motor task appears detrimental – compared to a linear motor task – for morphosyntactic processing in center-embedded relative sentences, this being the case regardless of the specific internal neurocognitive operations involved. It is also the case – and this is another limitation of the present study – that our experimental design does not allow testing the interplay between motor tasks and other syntactic structures than the one used here. This is also the situation for the type of grammatical anomaly (morphosyntactic violations) used to explore syntactic processing. Future studies including sentences differing in the dependencies established between their constituents, as well as other types of grammatical violations or manipulations are needed. Finally, the field is open for the use in future research of other types of motor sequences than the one used here, and that might differentially tap on resources involved in specific grammatical constructions.

One more feature that deserves some comment is the fact that we found a centro-parietal positivity to syntactically (and semantically) correct sentences when they were delivered in a

linear manner, as compared with the rest of conditions. As outlined in the results section, it is our opinion that this positivity can be explained as an overall reduction of the N400 in the easiest condition. On the one hand, it has been established that the N400 component is evoked by every content word, regardless of its correctness value (Kutas & Federmeier, 2011). On the other hand, previous studies have reported an N400 reduction for words with facilitated semantic processing (e.g., Herbert, Junghofer, & Kissler, 2008; Martín-Loeches et al., 2012). Since this modulation was not found in the correct sentences delivered non-linearly, it can be assumed that the type of motor task has been also able to affect somehow the processes reflected by the N400 component. This component has been shown to be sensitive not only to the semantic content of linguistic expressions but it also can be elicited by action-related material. Recently, a study reviews data from experiments that explored the N400 related to the action events processing (Amoruso et al., 2013) and proposed that the processes indexed by the N400 component are clearly modulated by motor information. In this regard, the N400 for correct and incorrect verbs administered in a non-linear manner and incorrect verbs in the linear condition could be explained as a boosting of the semantic processing biased by the motor task.

In sum, we have designed a paradigm that has demonstrated to be successful in the study of the relationships between action performance and sentence syntactic processing. Our findings support the idea that motor and linguistic structural processing seem to share common neurocognitive mechanisms, providing additional support for the embodied view of language syntactic processing and theoretical accounts of embodied cognition.

## Acknowledgements

This research was supported by Spanish Ministry of Science and Innovation and by the European Regional Development Funds, grants PSI2013-43107-P to PC, MML, DHD, JE, FM, LJO and SF, and PSI2015-66277-R to MdV and IL.

## REFERENCES

- Amoruso, L., Gelormini, C., Aboitiz, F., Alvarez González, M., Manes, F., Cardona, J. F., et al. (2013). N400 ERPs for actions: Building meaning in context. *Frontiers in Human Neuroscience*, 7, 57.
- Aravena, P., Hurtado, E., Riveros, R., Cardona, J. F., Manes, F., & Ibáñez, A. (2010). Applauding with Closed Hands: Neural signature of action-sentence compatibility effects. *PLoS One*, 5(7), e11751. <https://doi.org/10.1371/journal.pone.0011751>.
- 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*, 16(18), 1818–1823.
- Barsalou, L. W. (2008). Grounded cognition. *Annual Review of Psychology*, 59, 617–645.
- Barsalou, L. W. (2016a). On staying grounded and avoiding Quixotic dead ends. *Psychonomic Bulletin & Review*, 23, 1122–1142.

- Barsalou, L. W. (2016b). Situated conceptualization: Theory and applications. In Y. Coello, & M. H. Fischer (Eds.), *Foundations of embodied cognition, Volume 1: Perceptual and emotional embodiment* (pp. 11–37). East Sussex, UK: Psychology Press.
- Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences*, 15(11), 527–536.
- Buccino, G., Riggio, L., Melli, G., Binkofski, F., Gallese, V., & Rizzolatti, G. (2005). Listening to action-related sentences modulates the activity of the motor system: A combined TMS and behavioral study. *Cognitive Brain Research*, 24(3), 355–363. <https://doi.org/10.1016/j.cogbrainres.2005.02.020>.
- Carreiras, M., & Clifton, C. (2004). *The on-line study of sentence Comprehension: Eyetracking, ERPs and beyond*. New York: Psychology Press.
- Chomsky, N., & Miller, G. A. (1958). Finite state languages. *Information & Control*, 1, 91–112.
- Clerget, E., Winderickx, A., Fadiga, L., & Olivier, E. (2009). Role of Broca's area in encoding sequential human actions: A virtual lesion study. *NeuroReport*, 20, 1496–1499.
- Coulson, S., King, J., & Kutas, M. (1998). Expect the unexpected: Event-related brain responses to morphosyntactic violations. *Language and Cognitive Processes*, 13, 21–58.
- Damasio, A. R. (1989). The brain binds entities and events by multiregional activation from convergence zones. *Neural Computation*, 1(1), 123–132.
- de Vega, M., Glenberg, A., & Graesser, A. (2008). *Symbols and Embodiment: Debates on meaning and cognition*. New York: Oxford University Press.
- de Vega, M., León, I., Hernández, J. A., Valdés, M., Padrón, I., & Ferstl, E. C. (2014). Action sentences activate sensory motor regions in the brain independently of their status of reality. *Journal of Cognitive Neuroscience*, 26(7), 1363–1376. [https://doi.org/10.1162/jocn\\_a\\_00559](https://doi.org/10.1162/jocn_a_00559).
- de Vega, M., Moreno, V., & Castillo, D. (2013). The comprehension of action-related sentences may cause interference rather than facilitation on matching actions. *Psychological Research*, 77(1), 20–30. <https://doi.org/10.1007/s00426-011-0356-1>.
- Fadiga, L., Craighero, L., & D'Ausilio, A. (2009). Broca's area in language, action, and music. *Annals of the New York Academy of Sciences*, 1169, 448–458.
- Fiebach, C. J., & Schubotz, R. I. (2006). Dynamic anticipatory processing of hierarchical sequential events: A common role for Broca's area and ventral premotor cortex across -domains? *Cortex*, 42(4), 499–502.
- Fischer, M. H., & Zwaan, R. A. (2008). Embodied language: A review of the role of the motor system in language comprehension. *The Quarterly Journal of Experimental Psychology*, 61(6), 825–850.
- Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Science*, 6, 78–84.
- Friederici, A., Anwander, A., Heim, S., Schubotz, R. I., & Bahlmann, J. (2006). The brain differentiates human and non-human grammars: Functional localization and structural connectivity. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 2458–2463.
- Friederici, A. D., Bahlmann, J., Friedrich, R., & Makuuchi, M. (2011). The neural basis of recursion of complex syntactic hierarchy. *Biolinguistics*, 5(1–2), 87–104.
- Friederici, A. D., & Mecklinger, A. (1996). Syntactic parsing as revealed by brain responses: First-pass and second-pass parsing processes. *Journal of Psycholinguistic Research*, 25, 157–176.
- Friederici, A. D., & Weissenborn, J. (2007). Mapping sentence form onto meaning: The syntax-semantic interface. *Brain Research*, 1146, 50–58.
- Frisch, S., Schlesewsky, M., Saddy, D., & Alpermann, A. (2002). The P600 as an indicator of syntactic ambiguity. *Cognition*, 85, B83–B92.
- García, A., & Ibáñez, A. (2016). A touch with words: Dynamic synergies between manual actions and language. *Neuroscience and Biobehavioral Reviews*, 68, 59–95.
- Glenberg, A. M., & Gallese, V. (2012). Action-based language: A theory of language acquisition, comprehension, and production. *Cortex*, 48, 905–922.
- Glenberg, A. M., & Kaschak, M. P. (2002). Grounding language in action. *Psychonomic Bulletin & Review*, 9, 558–565.
- Gratton, G., Coles, M. G. H., & Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, 55, 468–484.
- Greenhouse, W. S., & Geisser, S. (1959). On methods in the analysis of profile data. *Psychometrika*, 24(2), 95–112.
- Hauk, O., & Pulvermüller, F. (2004). Neurophysiological distinction of action words in the fronto-central cortex. *Human Brain Mapping*, 21, 191–201.
- Hauser, M., Chomsky, N., & Fitch, T. (2002). The faculty of language: What is it, who has it, and how did it evolve. *Science*, 198, 1569–1579.
- Herbert, C., Junghofer, M., & Kissler, J. (2008). Event related potentials to emotional adjectives during reading. *Psychophysiology*, 45, 487–498.
- Jiménez-Ortega, L., Martín-Loeches, M., Casado, P., Sel, S., Fondevila, S., Herreros de Tejada, P., et al. (2012). How the emotional content of discourse affects language comprehension. *PLoS One*, 7(3), e33718. <https://doi.org/10.1371/journal.pone.0033718>.
- Kiefer, M., & Pulvermüller, F. (2012). Conceptual representations in mind and brain: Theoretical developments, current evidence and future directions. *Cortex*, 48(7), 805–825.
- King, J. W., & Kutas, M. (1995). Who did what and When? Using word- and clause-level ERPs to monitor working memory usage in reading. *Journal of Cognitive Neuroscience*, 7, 376–395.
- Kreiner, H., & Eviatar, Z. (2014). Prosody: The missing link in the embodiment of syntax. *Brain and Language*, 137(2014), 91–102.
- 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.
- Martín-Loeches, M., Fernández, A., Schacht, A., Sommer, W., Casado, P., Jiménez-Ortega, L., et al. (2012). The influence of emotional words on sentence processing: Electrophysiological and behavioral evidence. *Neuropsychologia*, 50, 3262–3272.
- Martín-Loeches, M., Nigbur, R., Casado, P., Hohlfeld, A., & Sommer, W. (2006). Semantics prevalence over syntax during sentence processing: A brain potential study of noun-adjective agreement in Spanish. *Brain Research*, 1093, 178–189.
- Molinero, N., Barber, H., & Carreiras, M. (2011). Grammatical agreement processing in reading: ERP findings and future directions. *Cortex*, 47, 908–930.
- Moro, A. (2014). On the similarity between syntax and actions. *Trends in Cognitive Sciences*, 18(3), 109–110.
- Münte, T. F., Heinze, H. J., Matzke, M., Wieringa, B. M., & Johannes, S. (1998). Brain potentials and syntactic violations revisited: No evidence for specificity of the syntactic positive shift. *Neuropsychologia*, 36, 217–226.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9, 97–113.
- Osterhout, L., & Holcomb, P. J. (1992). Event-related brain potentials elicited by syntactic anomaly. *Journal of Memory and Language*, 31, 785–806.
- Pulvermüller, F. (1996). Hebb's concept of cell assemblies and the psychophysiology of word processing. *Psychophysiology*, 33, 317–333.
- Pulvermüller, F. (2005). Brain mechanisms linking language and action. *Nature Reviews Neuroscience*, 6, 576–582.

- Pulvermüller, F. (2010). Brain embodiment of syntax and grammar: Discrete combinatorial mechanisms spelt out in neuronal circuits. *Brain and Language*, 112(3), 167–179.
- Pulvermüller, F., & Fadiga, L. (2010). Active perception: Sensorimotor circuits as a cortical basis for language. *Nature Reviews Neuroscience*, 11(5), 351–360.
- Pulvermüller, F., Hauk, O., Nikulin, V., & Ilmoniemi, R. J. (2005). Functional interaction of language and action: A TMS study. *European Journal of Neuroscience*, 21(3), 793–797.
- Pulvermüller, F., & Knoblauch, A. (2009). Discrete combinatorial circuits emerging in neural networks: A mechanism for rules of grammar in the human brain? *Neural Networks*, 22(1), 161–172.
- Santana, E., & de Vega, M. (2013). An ERP study of motor compatibility effects in action language. *Brain Research*, 1526, 71–83.
- van Schie, H. T., Toni, I., & Bekkering, H. (2006). Comparable mechanisms for action and language: Neural systems behind intentions, goals, and means. *Cortex*, 42(4), 495–498.
- Simanova, I., Francken, J. C., de Lange, F. P., & Bekkering, H. (2015). Linguistic priors shape categorical perception. *Language, Cognition and Neuroscience, Special Issue: Prediction in language comprehension and production*, 31(1), 159–165.
- Steinhauer, K., & Connolly, J. F. (2008). Event-related potentials in the study of language. In B. Stemmer, & H. A. Whitaker (Eds.), *Handbook of the neuroscience of language* (pp. 91–104). San Diego: Academic Press.
- Tanner, D., & van Hell, J. G. (2014). ERPs reveal individual differences in morphosyntactic processing. *Neuropsychologia*, 56, 289–301.
- Tettamanti, M., & Weniger, D. (2006). Broca's area: A supramodal hierarchical processor? *Cortex*, 42(4), 491–494.
- 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.
- Ullman, M. T. (2001). A neurocognitive perspective on language: The declarative/procedural model. *Nature Reviews Neuroscience*, 2, 717–726.
- Vos, S. H., Gunter, T. C., Kolk, H. H. J., & Mulder, G. (2001). Working memory constraints on syntactic processing: An electrophysiological investigation. *Psychophysiology*, 38, 41–63.