



Where is the action? Action sentence processing in Parkinson's disease



Leonardo Fernandino*, Lisa L. Conant, Jeffrey R. Binder, Karen Blindauer, Bradley Hiner, Katie Spangler, Rutvik H. Desai

Department of Neurology, Medical College of Wisconsin, USA

ARTICLE INFO

Article history:

Received 31 January 2013

Received in revised form

1 April 2013

Accepted 18 April 2013

Available online 25 April 2013

Keywords:

Conceptual processing

Embodiment

Figurative language

Language comprehension

Metaphor

Idiom

Sentence processing

Parkinson's disease

ABSTRACT

According to an influential view of conceptual representation, action concepts are understood through motoric simulations, involving motor networks of the brain. A stronger version of this embodied account suggests that even figurative uses of action words (e.g., *grasping the concept*) are understood through motoric simulations. We investigated these claims by assessing whether Parkinson's disease (PD), a disorder affecting the motor system, is associated with selective deficits in comprehending action-related sentences. Twenty PD patients and 21 age-matched controls performed a sentence comprehension task, where sentences belonged to one of four conditions: literal action, non-idiomatic metaphoric action, idiomatic action, and abstract. The same verbs (referring to hand/arm actions) were used in the three action-related conditions. Patients, but not controls, were slower to respond to literal and idiomatic action than to abstract sentences. These results indicate that sensory-motor systems play a functional role in semantic processing, including processing of figurative action language.

© 2013 Elsevier Ltd. All rights reserved.

1. Introduction

Embodied theories of semantics maintain that language comprehension depends, at least to some extent, on the reactivation of the sensory-motor representations that shaped the meanings of the words in question as they were incorporated into one's lexical repertoire. According to this view, accessing the meaning of a word such as *apple*, for instance, consists in reactivating the neural traces of one's prior experiences with apples, including visual, gustatory, olfactory, auditory, and somatosensory representations¹, presumably stored in modality-specific cortical regions of the brain. Likewise, words whose meanings have a strong motor component, such as action verbs (e.g., *grasp*, *bite*, *run*, etc.), are thought to rely to a significant degree on the reactivation of specific motor programs, stored in motor cortical areas (Barsalou, 1999; Binder & Desai, 2011; Damasio, 1989; Gallese & Lakoff, 2005; Glenberg & Robertson, 2000; Kemmerer & Gonzalez-Castillo, 2010; Pulvermüller, 2005).

Converging lines of evidence attest to the selective involvement of the motor system in the semantic processing of action-related

words and sentences (Meteyard, Cuadrado, Bahrami, & Vigliocco, 2012). Most of these studies rely on demonstrations that semantic processing of action-related language is accompanied by (1) increased neural activity in motor cortical areas, as shown by functional MRI (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Desai, Binder, Conant, & Seidenberg, 2010; Hauk, Johnsrude, & Pulvermüller, 2004; Raposo, Moss, Stamatakis, & Tyler, 2009), magnetoencephalography (Boulenger, Shtyrov, & Pulvermüller, 2012; Pulvermüller, Shtyrov, & Ilmoniemi, 2005b), electroencephalography (Hauk & Pulvermüller, 2004; van Elk, van Schie, Zwaan, & Bekkering, 2010), and motor evoked potentials induced by transcranial magnetic stimulation (TMS) (Buccino et al., 2005; Glenberg et al., 2008b; Oliveri et al., 2004), or by (2) activation of specific motor action programs, observed in the form of behavioral interactions between action language processing and compatible or incompatible motor responses (Glenberg & Kaschak, 2002; Scorilli & Borghi, 2007; Zwaan & Taylor, 2006). The correlational nature of this evidence has led some authors to suggest that motor activations may not play any functional role in semantic processing, arising instead as epiphenomenal byproducts of comprehension (Chatterjee, 2010; Mahon & Caramazza, 2008). Other studies, however, indicate that the motor system does play a functional role in the process, either by showing that experimental modulation of motor cortical activity can selectively influence recognition of action words (Papeo, Vallesi, Isaja, & Rumiati, 2009; Pulvermüller et al., 2005b; Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005a; Willems, Labruna, D'Esposito, Ivry, & Casasanto, 2011) or that pathologies affecting primarily the motor

* Correspondence to: Department of Neurology, Medical College of Wisconsin, Center for Imaging Research, MEB 4671, 8701 Watertown Plank Road, Milwaukee, WI 53226, USA. Tel.: +1414 955 7388.

E-mail address: lfernandino@mcw.edu (L. Fernandino).

¹ As well as more abstract representations associated to that word through symbolic communication, such as the fact that apples play a role in the reproduction of the apple tree, for instance.

system can lead to selective deficits in the semantic processing of pictures and individual words related to actions (Bak, O'Donovan, Xuereb, Boniface, & Hodges, 2001; Bak et al., 2006; Boulenger et al., 2008; Buxbaum & Saffran, 2002; Fernandino et al., 2012; Grossman et al., 2008; Neining & Pulvermüller, 2003).

To our knowledge, only two studies have directly tested the claim that the motor system plays a causal role in the comprehension of sentences related to bodily actions. Glenberg, Sato, and Cattaneo (2008a) showed that, after participants execute a manual transfer action between two locations (e.g., away from the body) a large number of times, they are slower to process sentences describing transfer of objects in the same direction as the previously executed action (e.g., *You are dealing Mark the cards*). The authors interpret this result in terms of “use-induced motor plasticity”, in which a motor program becomes temporarily inhibited after repeated execution, making it less available for semantic simulation. Interestingly, the same effect was found for sentences describing transfer of abstract information (e.g., *You are delegating the responsibilities to Anna*). The other study, by Ibáñez et al. (2012), used the action-sentence compatibility paradigm of Glenberg and Kaschak (2002) to show that action execution affects the amplitude of the N400 brain potential as measured by electrocorticography over language and motor areas, and that the action-sentence compatibility effect (ACE) is reduced in patients with a motor disorder (Parkinson's disease; PD) relative to healthy participants.

Some authors have proposed that metaphoric language is also grounded in sensory-motor simulations, such that comprehension is achieved by means of an analogy with the embodied literal sense. In this view, reactivation of sensory-motor representations is required even when processing abstract and figurative language (Gallese & Lakoff, 2005; Gibbs, 2006; Lakoff, 1999; Lakoff & Johnson, 2003). This claim is only partially supported by the existing literature: Three studies have found activation in or near the visual motion processing area MT+ for both literal and figurative motion-related sentences (e.g., *The man fell under her spell; The bridge jumped over the brook*) compared with sentences unrelated to motion (Chen, Widick, & Chatterjee, 2008; Saygin, McCullough, Alac, & Emmorey, 2010; Wallentin, Lund, Ostergaard, Ostergaard, & Roepstorff, 2005). A study by Cacciari et al. (2011) used single-pulse TMS to assess cortical activity in the motor leg area of the left hemisphere as subjects read different kinds of sentences. Sentences employing motion verbs (e.g., *walk, run, jump*) in literal, metaphoric, or fictive senses elicited higher motor cortical activity than sentences employing those same verbs in idiomatic senses, or sentences involving mental verbs (e.g., *deceive, notice, hope*). Using fMRI, Boulenger, Hauk, & Pulvermüller (2009) found somatotopic activation in the premotor cortex for both figurative and literal action sentences involving leg and arm verbs, although Aziz-Zadeh et al. (2006) found somatotopic premotor activation only for literal action sentences, not for idiomatic phrases (e.g., *biting off more than you can chew*). Likewise, a study by Raposo et al. (2009) found activation in motor and premotor regions for isolated action verbs and for literal action sentences, but not for figurative sentences using action verbs. Finally, Desai, Binder, Conant, Mano, & Seidenberg (2011) found activation in the anterior supramarginal gyrus—a region involved in motor planning—for both literal and metaphoric sentences using action verbs, as well as a negative correlation between metaphor familiarity and activity in the primary motor cortex.

The finding by Desai et al. (2011) of a negative correlation between metaphor familiarity and motor cortex activation suggests that the process by which the brain accesses the meaning of a given metaphor may depend on how familiar one is with that particular construction. While a novel metaphor can only be understood by analogy with its literal sense, a well-known,

conventionalized metaphoric construction can, in principle, be processed as an abstract concept, independently of the literal meaning (Bowdle & Gentner, 2005). According to this view, the comprehension of common idioms (which are highly conventionalized phrases that are often metaphoric) should not require reactivation of the sensory-motor representations associated with the words' literal meanings.

The aim of the present study is to investigate the functional contributions of the motor system to the comprehension of literal, non-idiomatic metaphoric, and idiomatic action sentences, using a paradigm in which the action required for response is unrelated to the semantic content of the stimuli (i.e., neutral relative to the action implied by the sentence). We compared the performance of patients in the early stages of PD with that of healthy controls on a task that required semantic processing of action and non-action sentences. PD is a neurodegenerative disorder characterized by motor deficits such as rigidity, bradykinesia (slowness of movement), postural instability, and tremor during rest (Dauer & Przedborski, 2003). These motor symptoms result from abnormal activity in the primary motor cortex (M1) and supplementary motor area (SMA) caused, in turn, by dopamine deficiency in the basal ganglia (Jahanshahi et al., 1995; Jenkins et al., 1992; Pasquereau & Turner, 2011; Rascol et al., 1992; Suppa et al., 2010; Wu et al., 2011). We hypothesized that PD patients' ability to perform semantic judgments on action-related sentences would be reduced relative to healthy controls. Performance was assessed in terms of response time (RT) and accuracy (Acc). To account for any group differences in overall processing speed and/or latency of motor responses, we included a control condition consisting of sentences involving abstract (non-action-related) verbs (e.g., *The war caused food shortages in some places*).

In order to separately investigate the role of the motor system in the processing of literal and figurative action sentences, we included three action-related conditions: In the literal action condition, sentences described physical actions performed with the body (e.g., *The craftsman lifted the pebble from the ground*). In the metaphoric action condition, action verbs were used in a metaphoric sense that was not completely conventionalized (e.g., *The discovery lifted the nation out of poverty*), while in the idiomatic action condition, sentences included common idioms involving action verbs (e.g., *The country lifted the veil on its nuclear program*). The same set of action verbs was used in the literal, metaphoric, and idiomatic sentences. Based on the previous literature, we predicted an interaction between sentence type and participant group such that performance on the literal action sentences would be worse, relative to the abstract sentences, for PD patients than for healthy controls. This interaction could be found in RT, Acc, or both. A similar result for the metaphoric sentences would indicate that motor simulations are also required for comprehension of action-related metaphoric language. Finally, if motor representations also play a role in the processing of highly conventionalized metaphoric constructions, a similar pattern of results should also be observed in the idiomatic sentences.

2. Methods

2.1. Participants

Twenty PD patients (mean age=64.5, 9 females) and 21 healthy older adults (mean age=65.6, 11 females) participated in the study. PD patients had been previously diagnosed with idiopathic PD by a movement disorders specialist. Seventeen patients were taking dopaminergic medication and were in the ON state during testing. Two patients were in the OFF state (off medication for at least 12 h) at the time of testing because they were being evaluated for deep brain stimulation surgery. One patient had not yet started taking anti-parkinsonian medication (Table 1). All participants were screened for dementia (MMSE2>25) and other neurological conditions. Handedness was assessed with the Edinburgh

Table 1
Individual patient information and group means (standard deviations) for age (years), education (years), WTAR standard score (max=34), MMSE2 (max=30), UPDRS (max=108), time since diagnosis (years), Hoehn–Yahr stage (max=4), medication status at time of testing, and daily medication DOPA-equivalent dose (mg).

Patients	Gender	Age	Education	WTAR-Std	MMSE2	UPDRS	Years since diagnosis	Hoehn–Yahr	Status at testing	DOPA equivalence
P1	M	75	21	107	27	17	3.5	2	ON	750
P2	F	77	12	108	30	24	4.5	3	ON	350
P3	M	60	15	123	30	12	2	1	OFF	0
P4	F	59	16	110	26	21	4	2	ON	up to 600
P5	F	52	16	104	30	25	9	2	ON	700–1000
P6	F	63	13	102	29	21	2	2	ON	800
P7	M	65	19	104	26	47	14	4	ON	750
P8	F	72	14	104	27	22	10	2	ON	600
P9	F	68	16	113	30	29	10	2	ON	800
P10	M	60	14	107	27	57	2.5	3	OFF	600
P11	M	64	12	96	27	45	6	3	ON	150
P12	M	67	19	93	28	68	5	4	OFF	1550
P13	M	74	14	99	28	43	6	2	ON	200
P14	F	60	18	102	28	24	7	2	ON	variable
P15	M	37	17	113	30	10	5	2	ON	750
P16	M	65	18	123	30	26	2	2	ON	200
P17	F	62	28	125	30	10	8	1	ON	200–500
P18	M	80	13	121	28	25	9	2	ON	850
P19	M	61	19	123	29	10	1.5	1.5	ON	100
P20	F	69	18	122	26	18	2.5	2	ON	200
Patient	9/20 F	64.5 (9.5)	16.6 (3.7)	110 (9.9)	28.3 (1.5)	27.7 (16.1)	5.7 (3.4)		2.3 (.8)	
Control	11/21 F	65.4 (6.1)	16.2 (1.9)	115.9 (6.6)	28.9 (.9)					

Table 2
Mean (and standard deviation) of the lexical measures for each sentence type. Log frequency values were obtained from the WebCelex database (<http://celex.mpi.nl>). All other measures retrieved from the English Lexicon Project database (<http://ellexicon.wustl.edu>), Balota et al. (2007).

Sentence type	Letters	Phonemes	Syllables	Words	LD RT	LD Acc	Mean word frequency
Literal	37.3 (5.3)	29.6 (4.5)	11.0 (1.6)	7.8 (1.2)	1614 (215)	.90 (.09)	1.6 (.4)*
Metaphoric	36.2 (6.8)	29.1 (5.8)	11.2 (2.3)	7.9 (1.2)	1661 (188)	.91 (.08)	2.0 (.3)
Idiomatic	35.0 (6.8)	27.9 (5.2)	10.4 (2.5)	7.8 (1.3)	1578 (193)	.90 (.08)	1.9 (.3)
Abstract	35.4 (6.2)	30.2 (5.2)	11.5 (2.2)	7.9 (1.2)	1672 (226)	.92 (.07)	2.1 (.3)

* Value significantly smaller compared to each of the other conditions, all $p < .05$.

Handedness Inventory (Oldfield, 1971). Participants received monetary compensation for participation in the study. The study was approved by the institutional review board of the Medical College of Wisconsin, and all participants signed an informed consent form.

2.2. Materials

The stimuli consisted of 50 nonsense sentences and 100 sensible sentences. The task required subjects to indicate, using two response keys, whether a sentence was meaningful or nonsense. We chose this task because it requires semantic processing of the sentence as a whole, which was crucial for our goal of distinguishing between literal, idiomatic, and metaphoric uses of the verb. Furthermore, the meaningful vs. nonsense judgment is orthogonal to the sentence type manipulation (i.e., can be applied equally to all sentence types without introducing bias). Nonsense sentences were grammatically well-formed but constructed such that the verb was semantically incompatible with one or both of its arguments (e.g., *The business is pinching the sunset*). The sensible sentences were equally divided into four conditions: literal action (e.g., *The woman is pinching my cheeks*), non-idiomatic metaphoric action (e.g., *The cost is pinching the consumers*), idiomatic action (e.g., *The business is pinching pennies*), and abstract (e.g., *The business is saving cash*). The 25 sentences in each of the three action-related conditions were built by combining a set of 21 action verbs—all referring to hand/arm actions—with different noun phrases. The same set of verbs was used in these three conditions, but the noun phrases were chosen so as to direct interpretation of the verb toward either a literal or a figurative meaning. In this regard, the subject in the literal action sentences was typically a person, while the subject of the figurative sentences was an entity that would not be able to literally carry out the action denoted by the verb. Sentences in the abstract condition contained verbs not related to physical actions (e.g., *warn*, *surprise*, *promote*). The idiomaticity of the idiomatic sentences as well as the non-idiomatic status of the metaphoric sentences was verified using an online idiom dictionary compiled from the *Cambridge International Dictionary of Idioms* and the *Cambridge Dictionary of American Idioms* (<http://idioms.thefreedictionary.com/>). Most idioms have limited flexibility regarding the form in which they can

appear, since specific verb-noun combinations are often required (e.g., *to spill the beans*). Due to these constraints, we opted to allow for some syntactic variation in the sentences to make them sound as natural as possible while maintaining similar sentence length.

The four conditions were matched in sentence length (number of letters, number of phonemes, number of syllables, and number of words), as well as response time (RT) and accuracy (Acc) in lexical decision for the content words in the sentence, according to the English Lexicon Project (ELP) database (Balota et al., 2007); see Table 2; all $p > .05$). The idiomatic, metaphoric, and abstract conditions were also matched for mean lemma frequency according to the WebCelex database (<http://celex.mpi.nl>; all $p > .05$). A pilot study showed that performance on the literal sentences was higher than on the other three conditions when they were all matched in lemma frequency; so in order to make performance comparable across all conditions, lower frequency nouns had to be used in the literal sentences, resulting in a significantly lower mean lemma frequency compared to the other conditions (all $p < .05$).

2.3. Procedure

PD patients were tested immediately after examination by a neurologist, who administered the Unified Parkinson's Disease Rating Scale (UPDRS). Patients and controls were given the Mini-Mental State Examination-Second Edition (MMSE-2), the Wechsler Test of Adult Reading (WTAR), and the Edinburgh Handedness Inventory (Oldfield, 1971) at the beginning of the testing session. A laptop PC running E-prime software (version 1.2, Psychology Software Tools, Inc.) was used for stimulus presentation and response recording. Response buttons were two AbleNet Jelly Bean switches (www.ablenetinc.com) connected to a PST Serial Response Box (Psychology Software Tools, Inc.). On each trial, a sentence was presented on the screen and remained visible until the participant made a response. Participants were instructed to decide whether the sentence was meaningful, and to respond as fast and as accurately as possible by pressing one of the two response buttons with their preferred hand (all participants chose to use their

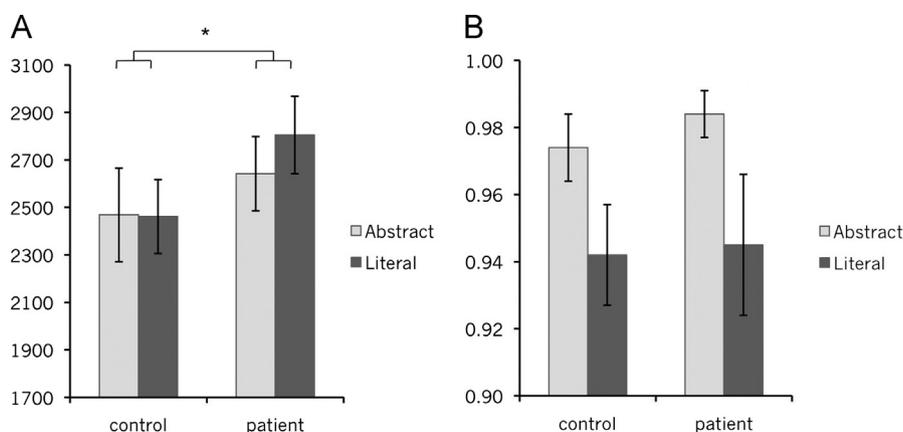


Fig. 1. Response time and accuracy for literal action and abstract sentences. * $p < .05$. (a) Response time and (b) Accuracy.

right hand). They performed six practice trials (using a separate set of sentences) before beginning the actual task.

2.4. Data analysis

Trials in which RT exceeded 6 s were discarded. This cut-off was determined by choosing a value that eliminated approximately 5% of the data, following recommendations by Ratcliff (Ratcliff, 1993). In the RT analysis, we also discarded trials that were identified as outliers for each participant according to Tukey's boxplot rule (Tukey, 1977), where outliers are defined as trials whose RT is shorter than 1.5 interquartile ranges below the first quartile or longer than 1.5 interquartile ranges above the third quartile. Only correctly answered trials were included.

As mentioned in the Introduction, our goal in this study was to test for the presence of three interactions involving Group and Sentence Type (ST): Group \times ST (abstract, literal), Group \times ST(abstract, idiomatic), and Group \times ST(abstract, metaphoric). While it is common in the psychological literature to analyze a factorial design by first testing the omnibus hypothesis (encompassing all main effects and all possible interactions between the factors manipulated in the task) with an ANOVA model, and using the result of the F -test as a "license" to test more specific hypotheses, this approach is not always the most appropriate one, particularly when the goal of the study is to test a small subset of all possible effects, with the remaining effects bearing no relevance to the study's hypotheses (Howell, 2012). In a mixed design such as this one, we can directly test the interactions of interest by using independent-samples t -tests to compare the within-group differences. Since our three contrasts of interest are *a priori*, theoretically motivated effects, their investigation with focused t -tests is justified, their results being independent of any higher-level ANOVAs that could be performed (Rosnow & Rosenthal, 1996). Thus, we defined the "net RT" for each of the action-related conditions as the RT difference between each action-related condition and the abstract condition (i.e., $\text{netRT}_{\text{Lit}} = \text{RT}_{\text{Lit}} - \text{RT}_{\text{Abs}}$; $\text{netRT}_{\text{Idi}} = \text{RT}_{\text{Idi}} - \text{RT}_{\text{Abs}}$; $\text{netRT}_{\text{Met}} = \text{RT}_{\text{Met}} - \text{RT}_{\text{Abs}}$).

We also had specific predictions about the direction of these effects—namely, that performance on action-related sentences would be relatively worse for patients than for controls. In fact, no reasonable alternative hypothesis would predict effects in the opposite direction (i.e., that PD patients would have a relative advantage over controls on the action sentences). Symbolic, non-embodied theories of semantic representation would instead predict no interactions. The directionality of the hypotheses under consideration provides a further reason to use t -tests here rather than F -tests: While t -tests can be directional (one-tailed), the F -test is inherently non-directional, again resulting in unnecessary loss of statistical power.

We tested the assumption of normality for each distribution using both the Shapiro–Wilk test and measures of skewness and kurtosis. Only one of the six net RT variables yielded a $p < .05$ in the Shapiro–Wilk test, and none of them showed significant skewness or kurtosis, so we used one-tailed t -tests to assess the differences in net RT between patients and controls for each type of action sentence.

Similarly, we defined the "net accuracy" (net Acc) for each action condition as the difference in Acc between each one and the abstract condition. All six net Acc variables showed significant departure from normality according to all three criteria, so we used the non-parametric Wilcoxon rank sum test to compare net Acc between patients and controls.

3. Results

A Wilcoxon rank sum test showed that the mean UPDRS score of the patients off medication (45.7) was not significantly different from that of the patients on medication (24.5), $W = 14$, $p = .25$. We

analyzed the two subgroups separately at first to verify whether their results were similar. Since the ON and OFF groups displayed effects in the same direction, we grouped all patients together for the main analysis.

On average, 8.4% of trials were discarded (9.3% for literal, 7.8% for idiomatic, 8.2% for metaphoric, 8.2% for abstract) in the control group, and 9.9% in the patient group (11% for literal, 8.4% for idiomatic, 8.8% for metaphoric, 11.6% for abstract).

3.1. Literal action

Relative to the control condition (abstract), net RT in the literal condition was 161 ms in the PD group (n.s.) and -7 ms in the control group (n.s.), and the difference of 168 ms was significant, $t(39) = 1.88$, $p = .034$, one-tailed (Fig. 1A and Table 3). That is, the advantage that the control participants have in using their motor systems to understand the literal action sentences is reduced by 125 msec for the PD patients. Net Acc did not differ between controls and patients ($W = 191.5$, $p = .68$, one-tailed), but in both groups there was a non-significant trend toward lower accuracy for literal sentences (Fig. 1B and Table 3).

The fact that both groups showed a trend toward lower accuracy for literal than for abstract sentences raises the possibility that the observed difference in net RT between controls and patients could be due, in principle, to a trade-off between speed and accuracy. In other words, if our set of literal sentences was overall harder to process than our abstract sentences, this difference in difficulty could have been amplified in the patient group (owing to non-specific cognitive impairments), and manifest itself in the form of slower RT for literal sentences. To investigate this possibility, we re-analyzed the data after removing the sentences in the literal condition that received correct responses from less than 90% of the control participants (five sentences). This resulted in the literal and abstract conditions having identical Acc in the control group (.97), and similar Acc in the PD group (.97 and .98, respectively). This new analysis showed essentially the same difference in net RT between PD patients and controls as the original analysis, $t(39) = 1.73$, $p = .046$, one-tailed, which confirms that the increase in net RT for PD patients is not due to a difference in overall difficulty between the two sentence types, but rather due to differences in their action-semantic content.

3.2. Idiomatic action

For idiomatic sentences, net RT was -116 ms in the PD group (n.s.) and -286 ms in the control group ($p < .005$), and the difference of 170 ms was significant, $t(39) = 1.71$, $p = .047$, one-tailed (Fig. 2A and Table 3). That is, the advantage that controls have in using

their motor system to process the idiomatic action sentences is reduced by 170 ms for PD patients. Mean Acc did not differ between idiomatic and abstract sentences for either group (Fig. 2B and Table 3), resulting in similar net Acc in the two groups, $W=199.5$, $p=.62$, one-tailed.

3.3. Metaphoric action

Net RT for metaphoric action sentences was 134 ms for PD patients ($p<.005$), and 104 ms for controls (n.s.), but the difference of 30 ms did not reach significance, $t(39)=.41$, $p=.34$, one-tailed (Fig. 3A and Table 3). Mean accuracy was similar for metaphoric and abstract sentences in the control group (net Acc=.004), while patients showed a non-significant trend toward lower Acc for metaphoric sentences (net Acc=-.021) (Fig. 3B and Table 3), reflecting a moderate trend toward lower net Acc for patients relative to controls, $W=261$, $p=.08$.

4. Discussion

The goal of this study was to evaluate whether a disorder of the motor system (PD) is associated with specific impairments in the semantic processing of action-related sentences. Assessing semantic language processing in the context of sentence comprehension has the advantage of greater ecological validity over paradigms involving isolated words and pictures. In addition, sentence comprehension typically requires deeper levels of processing than picture naming or word recognition. Furthermore, focusing on sentence comprehension allowed us to investigate the role of the motor system in the processing of figurative language.

Compared to healthy controls, PD patients showed longer net RTs for Literal and for Idiomatic action sentences. This effect was absent in the Metaphoric action condition, but the accuracy analysis revealed a trend toward lower net Acc in the patient than in the control group. This pattern of results provides empirical support to the claim that the motor system plays a functional role in the semantic processing of action-related language. The task

Table 3
Statistics for the within-group contrasts between each of the action conditions and the abstract condition. *T*-tests were used for RT comparisons, Wilcoxon signed-rank tests were used for Acc comparisons. Critical α corrected for multiple comparisons with Bonferroni correction: $.05/6=.0083$. Bold font indicates significance.

Group	IV	Lit>Abs	Idi>Abs	Met>Abs
PD patient	RT	$t(19)=2.75$, $p=.013$	$t(19)=2.22$, $p=.039$	$t(19)=3.83$, $p=.001$
	Acc	$V=12$, $p=.061$	$V=9$, $p=.875$	$V=13.5$, $p=.164$
Control	RT	$t(20)=.10$, $p=.918$	$t(20)=3.44$, $p=.003$	$t(20)=1.62$, $p=.121$
	Acc	$V=34$, $p=.043$	$V=19.5$, $p=.439$	$V=37.5$, $p=.716$

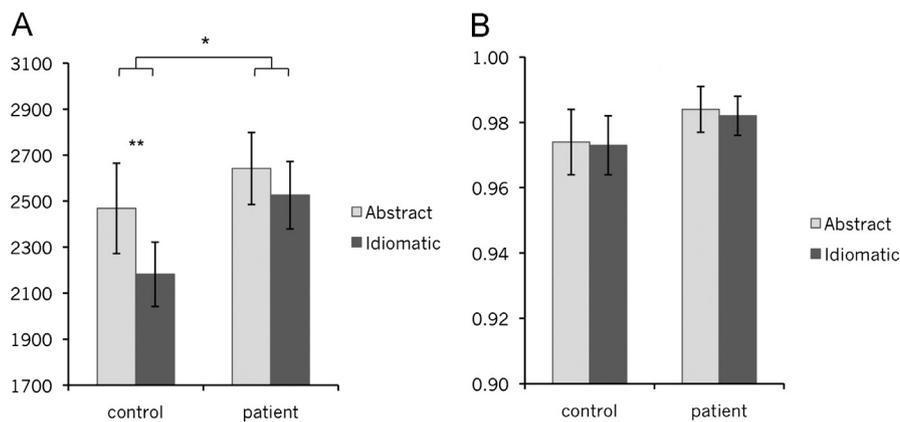


Fig. 2. Response time and accuracy for idiomatic action and abstract sentences. * $p<.05$; ** within-group comparison significant at $p<.005$. (a) Response time and (b) Accuracy.

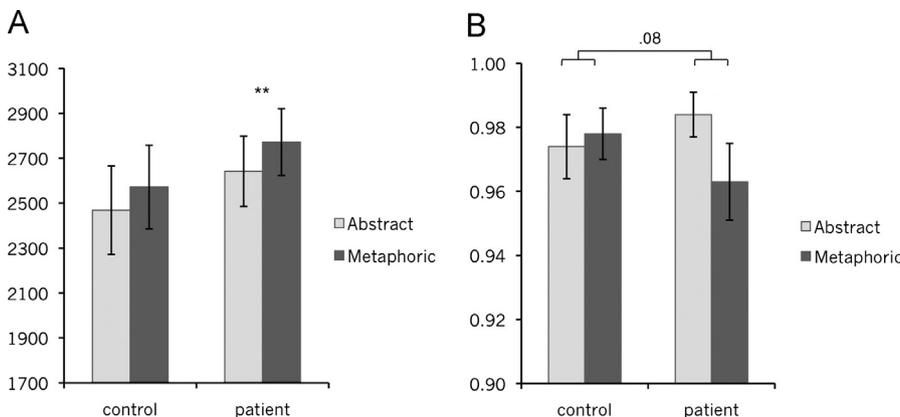


Fig. 3. Response time and accuracy for metaphoric action and abstract sentences. ** within-group comparison significant at $p<.005$.

relied on conceptual processing in that it did not involve pictures or video clips, and contained no instruction or requirement to perform mental imagery. To our knowledge, this is the first demonstration that a pathological condition affecting primarily the motor system is associated with a specific impairment in the comprehension of action-related sentences. Furthermore, our results suggest that even the figurative senses of action verbs are dependent on motor representations.

Our results are consistent with previous studies that evaluated processing of action concepts in PD. Bertella et al. (2002) and Cotelli et al. (2007) showed that PD patients perform worse in action naming than in object naming, and Herrera, Rodríguez-Ferreiro, and Cuetos (2012) found that the prevalence of motor-related semantic content affected the performance of PD patients (but not of healthy controls) on action naming. Boulenger et al. (2008) found that the effect of masked priming on a lexical decision task was smaller for action verbs than for concrete nouns when PD patients were off medication, but not when they were under dopaminergic drug treatment. Finally, Fernandino et al. (2012), found that PD patients were specifically impaired in processing action verbs (relative to abstract verbs) as assessed by a lexical decision and by a semantic similarity judgment task. The present findings show that impaired processing of action-related concepts in PD also extends to sentence comprehension, including figurative language.

Although both groups showed somewhat higher error rates for literal action than for abstract sentences, it is unlikely that the group difference in net RT for the literal condition was driven by difficulty as reflected in Acc, because the same interaction was found when the analysis was done on a subset of the stimuli where Acc was matched between conditions.

The fact that PD patients displayed specific impairments in the processing of action-related metaphoric and idiomatic sentences indicates that the motor system makes functional contributions to the processing of the non-literal senses of action verbs. These results are consistent with current theories postulating that abstract and figurative language is processed in terms of embodied representations (Feldman & Narayanan, 2004; Gallese & Lakoff, 2005).

Our finding that controls responded equally fast to abstract and literal action sentences seems to contrast with the results of Glenberg et al. (2008b), who found that participants were faster when judging concrete sentences than when judging abstract sentences. In general, when concrete and abstract sentences are matched in length and mean word frequency, responses tend to be faster for the concrete ones. In the current study, however, we sought to match literal and abstract sentences in terms of difficulty (see Materials, above), so we used lower frequency nouns for literal sentences.

As pointed out in the Introduction, the neuroimaging results examining motor activation for processing figurative action language are mixed. Boulenger et al. (2009) and Desai et al. (2011) observed activation of primary motor and/or premotor cortex for figurative action sentences, while Raposo et al. (2009) and Aziz-Zadeh et al. (2006) did not. In an fMRI study, using stimuli and task similar to those used here, Desai, Conant, Binder, Park, and Seidenberg (submitted) found secondary motor activation for action metaphors but not action idioms. One possibility is that in that fMRI study, a brief initial activation of the motor cortex to action idioms was not detected, while sustained activation for literal and metaphoric sentences was, due to the slow nature of the BOLD response. A second possibility is that PD patients showed poorer performance in action-related, figurative language comprehension not due to a specific impairment in action semantics, but due to an impairment in processing figurative language in general. Relative to literal language, figurative language may rely to a larger extent on executive function, and there is evidence that PD affects executive abilities in addition to motoric functions

(Koerts, Leenders, & Brouwer, 2009; Monetta & Pell, 2007; Owen, 2004; Zgaljardic, Borod, Foldi, & Mattis, 2003). Because this study did not include figurative sentences that were not action related, this possibility remains to be examined in future studies.

It is also unclear why the PD processing deficit shown in the metaphorical condition was observed in net Acc rather than net RT, unlike the two other action conditions. This could indicate that PD patients employed a different strategy when processing metaphorical sentences, possibly due to increased perceived difficulty. This qualitative difference in the pattern of results makes it difficult to directly compare the magnitude of the deficit in this condition with that of the literal and idiomatic conditions. Further studies are needed to clarify this issue.

5. Conclusions

The degree to which sensory and motor systems contribute to the semantic processing of language is currently an issue of active research and lively debate in cognitive neuroscience. While most researchers now accept that the motor system is somehow activated during action language processing, there is less agreement about whether it plays a causal, functional role in the process. The results reported here show that PD patients display specific deficits in the comprehension of sentences involving action verbs, compared to sentences involving abstract verbs, supporting the view that the motor system makes a functional contribution to action language semantics. The fact that PD patients also displayed deficits on idiomatic and metaphoric action sentences lends tentative support to theories proposing that figurative language is also grounded in embodied representations. Further investigation is required to determine the extent to which sensory-motor systems contribute to the processing of different kinds of figurative constructions, and to elucidate the mechanisms through which they do so.

Acknowledgments

We thank Vicki Conte for her invaluable help with patient recruitment, and the patients and their families for participation. We also thank Arthur Glenberg and an anonymous reviewer for comments on an earlier draft of this article, and Megan Rozman for assisting with data collection. This work was funded by the Grant NIH R01 DC010783 (RD).

Appendix A. Sensible sentences used in the study

Abstract sentences

The violent film changed all of his ideas.
 The safety issue was debated again in training.
 His prison time atoned for the sins.
 The auto industry warned the new customers.
 The congress funded a proposal on that issue.
 That question surprised him very much.
 The defense was critical of the argument.
 The country wanted the plan for a nuclear program.
 The ownership ended all the restrictions for workers.
 The whole town exploited the kids.
 Her tragic story upset me a lot.
 The bank ignored the pleas from her.
 The regime hid the evidence for many years.
 The magazine article just described some aspects of this issue.
 The bank is saving money from the start.

The team offense performed very well.
 The business is saving cash.
 The regime promoted him to the top.
 The speech stimulated her interest in him.
 The congress is causing a big trade deficit again.
 The new company wanted the cash in the plan.
 The bank wanted the numbers out of the report.
 The city is attending to all the big crime problems.
 The war caused food shortages in some fields.
 The new firm upset the rivals with a great product.

Literal sentences

The repairman bent the cable for her.
 The golfer seized the club with a strong grip.
 The chef in the kitchen stirred the soup.
 The female subjects pressed the correct button.
 The janitor swept all the dirt away.
 Her strong husband tore off the door.
 His favorite student wiped the blackboard clean.
 The woman picked up the eraser for her child.
 The grandmother is pinching my cheeks.
 The summer student raised his hand for permission to speak.
 The sailor pulled the rope around the mast.
 The serviceman always pushed the green button.
 His company's president shook his fist in the air.
 The little schoolboy is shaking with fear.
 The firefighter is pouring water around the building.
 The toddler picked raisins out of the cookie.
 The carpenter raised the painting to eye level.
 That gentleman tickled my armpit.
 The teenage tourist just scratched his name on that tree.
 The worker swept the leaves under the tree.
 The craftsman lifted the pebble from the ground.
 That superhero caught the speeding bullet.
 The lengthy spike was hammered into the ground.
 The apprentice must grab the torch by the handle.
 The shoplifter finally turned the key in the lock.

Idiomatic sentences

That question caught him off guard.
 The bank bent the rules for her.
 The bank pulled the plug on the deal.
 The firm picked up the tab for the lunch.
 The government is pouring money down the drain.
 The new firm raised the bar with a great product.
 That movie tickled my fancy.
 The magazine article just scratched the surface of this issue.
 The regime swept the evidence under the rug.
 The speech swept her off her feet.
 Her tragic story tore my heart out.
 His prison time wiped the slate clean.
 His son's death shook the foundations of his faith.
 The army must grab the bull by the horns.
 The business is pinching pennies.
 The nation finally turned the corner in the crisis.
 The whole city is shaking in its boots.
 The automobile industry pressed the panic button.
 The company seized the day with a great product.
 The country lifted the veil on its nuclear program.
 The news of the attacks stirred his blood.
 The safety issue was hammered home in training.

The war raised the specter of food shortages.
 The defense picked holes in the argument.
 The organization always pushed the right buttons.

Metaphoric sentences

The congress pulled their support for the plan.
 The discovery lifted this nation out of poverty.
 The media bent her story a lot.
 Her tragic death tore my dream to pieces.
 His son's death shook him and his whole family.
 The big show caught the crowd's attention.
 The committee finally turned its thinking towards education.
 The news of the attacks stirred his emotion.
 The team swept the tournament with ease.
 The weak army was hammered again in battle.
 The senate picked out some good ideas.
 The new firm raised many new questions about his past.
 The war raised the price of wheat and rice.
 The big army pressed the enemy back.
 That film tickled my imagination.
 The firm is pouring cash into a huge project.
 The panel picked up the discussion after the break.
 The demand always pushed the prices up.
 The bad decision is shaking the investor confidence.
 The coalition swept the election across the state.
 The crime seized the minds of the local public.
 His prison time wiped the sin away.
 The city council just scratched the big and costly project.
 The army must grab the chance they have got.
 The cost is pinching the consumers.

References

- 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. <http://dx.doi.org/10.1016/j.cub.2006.07.060>.
- Bak, T. H., O'Donovan, D. G., Xuereb, J. H., Boniface, S., & Hodges, J. R. (2001). Selective impairment of verb processing associated with pathological changes in Brodmann areas 44 and 45 in the motor neurone disease–dementia–aphasia syndrome. *Brain*, 124(Pt 1), 103–120.
- Bak, T. H., Yancopoulos, D., Nestor, P. J., Xuereb, J. H., Spillantini, M. G., Pulvermüller, F., et al. (2006). Clinical, imaging and pathological correlates of a hereditary deficit in verb and action processing. *Brain*, 129(Pt 2), 321–332. <http://dx.doi.org/10.1093/brain/awh701>.
- Balota, D. A., Yap, M. J., Cortese, M. J., Hutchison, K. A., Kessler, B., Loftis, B., et al. (2007). The English Lexicon Project. *Behavior Research Methods*, 39(3), 445–459.
- Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences*, 22, 577–660.
- Bertella, L., Albani, G., Greco, E., Priano, L., Mauro, A., Marchi, S., et al. (2002). Noun verb dissociation in Parkinson's disease. *Brain and Cognition*, 48(2–3), 277–280.
- Binder, J. R., & Desai, R. H. (2011). The neurobiology of semantic memory. *Trends in Cognitive Sciences*, 15(11), 527–536. <http://dx.doi.org/10.1016/j.tics.2011.10.001>.
- Boulenger, V., Hauk, O., & Pulvermüller, F. (2009). Grasping ideas with the motor system: semantic somatotopy in idiom comprehension. *Cerebral Cortex*, 19(8), 1905–1914. <http://dx.doi.org/10.1093/cercor/bhn217>.
- Boulenger, V., Mechtouff, L., Thobois, S., Broussolle, E., Jeannerod, M., & Nazir, T. A. (2008). Word processing in Parkinson's disease is impaired for action verbs but not for concrete nouns. *Neuropsychologia*, 46(2), 743–756. <http://dx.doi.org/10.1016/j.neuropsychologia.2007.10.007>.
- Boulenger, V., Shtyrov, Y., & Pulvermüller, F. (2012). When do you grasp the idea? MEG evidence for instantaneous idiom understanding. *NeuroImage*, 59(4), 3502–3513. <http://dx.doi.org/10.1016/j.neuroimage.2011.11.011>.
- Bowlde, B. F., & Gentner, D. (2005). The career of metaphor. *Psychological Review*, 112(1), 193–216. <http://dx.doi.org/10.1037/0033-295X.112.1.193>.
- 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. <http://dx.doi.org/10.1016/j.cogbrainres.2005.02.020>.

- Buxbaum, L. J., & Saffran, E. M. (2002). Knowledge of object manipulation and object function: dissociations in apraxic and nonapraxic subjects. *Brain and Language*, 82(2), 179–199.
- Cacciari, C., Bolognini, N., Senna, I., Pellicciari, M. C., Miniussi, C., & Papagno, C. (2011). Literal, fictive and metaphorical motion sentences preserve the motion component of the verb: a TMS study. *Brain and Language*, 119(3), 149–157, <http://dx.doi.org/10.1016/j.bandl.2011.05.004>.
- Chatterjee, A. (2010). Disembodying cognition. *Language and Cognition*, 2(1), 79–116, <http://dx.doi.org/10.1515/LANGCOG.2010.004>.
- Chen, E., Widick, P., & Chatterjee, A. (2008). Functional–anatomical organization of predicate metaphor processing. *Brain and Language*, 107(3), 194–202, <http://dx.doi.org/10.1016/j.bandl.2008.06.007>.
- Cotelli, M., Borroni, B., Manenti, R., Zanetti, M., Arévalo, A., Cappa, S. F., et al. (2007). Action and object naming in Parkinson's disease without dementia. *European Journal of Neurology*, 14(6), 632–637, <http://dx.doi.org/10.1111/j.1468-1331.2007.01797.x>.
- Damasio, A. R. (1989). Time-locked multiregional retroactivation: a systems-level proposal for the neural substrates of recall and recognition. *Cognition*, 33(1–2), 25–62.
- Dauer, W., & Przedborski, S. (2003). Parkinson's disease: mechanisms and models. *Neuron*, 39(6), 889–909.
- Desai, R. H., Binder, J. R., Conant, L. L., Mano, Q. R., & Seidenberg, M. S. (2011). The neural career of sensory–motor metaphors. *Journal of Cognitive Neuroscience*, 23(9), 2376–2386, <http://dx.doi.org/10.1162/jocn.2010.21596>.
- Desai, R. H., Binder, J. R., Conant, L. L., & Seidenberg, M. S. (2010). Activation of sensory–motor areas in sentence comprehension. *Cerebral Cortex*, 20(2), 468–478, <http://dx.doi.org/10.1093/cercor/bhp115>.
- Desai, R. H., Conant, L. L., Binder, J. R., Park, H., & Seidenberg, M. S. A piece of the action: modulation of sensory–motor regions by action idioms and metaphors, submitted for publication.
- Feldman, J., & Narayanan, S. (2004). Embodied meaning in a neural theory of language. *Brain and Language*, 89(2), 385–392, [http://dx.doi.org/10.1016/S0093-934X\(03\)00355-9](http://dx.doi.org/10.1016/S0093-934X(03)00355-9).
- Fernandino, L., Conant, L. L., Binder, J. R., Blindauer, K., Hiner, B., Spangler, K., et al. (2012). Parkinson's disease disrupts both automatic and controlled processing of action verbs. *Brain and Language*, 1–10, <http://dx.doi.org/10.1016/j.bandl.2012.07.008>.
- Gallese, V., & Lakoff, G. (2005). The brain's concepts: the role of the sensory–motor system in conceptual knowledge. *Cognitive Neuropsychology*, 22(3–4), 455–479, <http://dx.doi.org/10.1080/0264329042000310>.
- Gibbs, R. (2006). Metaphor interpretation as embodied simulation. *Mind and Language*, 21(3), 434–458.
- Glenberg, A. M., & Kaschak, M. P. (2002). Grounding language in action. *Psychonomic Bulletin & Review*, 9(3), 558–565.
- Glenberg, A. M., & Robertson, D. (2000). Symbol grounding and meaning: a comparison of high-dimensional and embodied theories of meaning. *Journal of Memory and Language*, 43(3), 379–401.
- Glenberg, A. M., Sato, M., & Cattaneo, L. (2008a). Use-induced motor plasticity affects the processing of abstract and concrete language. *Current Biology*, 18(7), R290–R291, <http://dx.doi.org/10.1016/j.cub.2008.02.036>.
- 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, <http://dx.doi.org/10.1080/17470210701625550>.
- Grossman, M., Anderson, C., Khan, A., Avants, B., Elman, L., & McCluskey, L. (2008). Impaired action knowledge in amyotrophic lateral sclerosis. *Neurology*, 71(18), 1396–1401, <http://dx.doi.org/10.1212/01.wnl.0000319701.50168.8c>.
- Hauk, O., Johnsrude, I., & Pulvermüller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, 41(2), 301–307.
- Hauk, O., & Pulvermüller, F. (2004). Neurophysiological distinction of action words in the fronto-central cortex. *Human Brain Mapping*, 21(3), 191–201, <http://dx.doi.org/10.1002/hbm.10157>.
- Herrera, E., Rodríguez-Ferreiro, J., & Cuetos, F. (2012). The effect of motion content in action naming by Parkinson's disease patients. *Cortex*, 48(7), 900–904, <http://dx.doi.org/10.1016/j.cortex.2010.12.007>.
- Howell, D. C. (2012). *Statistical methods for psychology* (8th ed.). Wadsworth Publishing Company.
- Ibáñez, A., Cardona, J. F., Santos Dos, Y. V., Blenkmann, A., Aravena, P., Roca, M., et al. (2012). Motor–language coupling: direct evidence from early Parkinson's disease and intracranial cortical recordings. *Cortex*, <http://dx.doi.org/10.1016/j.cortex.2012.02.014>.
- Jahanshahi, M., Jenkins, I. H., Brown, R. G., Marsden, C. D., Passingham, R. E., & Brooks, D. J. (1995). Self-initiated versus externally triggered movements. I. An investigation using measurement of regional cerebral blood flow with PET and movement-related potentials in normal and Parkinson's disease subjects. *Brain*, 118(Pt 4), 913–933.
- Jenkins, I. H., Fernandez, W., Playford, E. D., Lees, A. J., Frackowiak, R. S. J., Passingham, R. E., et al. (1992). Impaired activation of the supplementary motor area in Parkinson's disease is reversed when akinesia is treated with apomorphine. *Annals of Neurology*, 32(6), 749–757, <http://dx.doi.org/10.1002/ana.410320608>.
- Kemmerer, D., & Gonzalez-Castillo, J. (2010). The Two-Level Theory of verb meaning: an approach to integrating the semantics of action with the mirror neuron system. *Brain and Language*, 112(1), 54–76, <http://dx.doi.org/10.1016/j.bandl.2008.09.010>.
- Koerts, J., Leenders, K. L., & Brouwer, W. H. (2009). Cognitive dysfunction in non-demented Parkinson's disease patients: controlled and automatic behavior. *Cortex*, 45(8), 922–929, <http://dx.doi.org/10.1016/j.cortex.2009.02.014>.
- Lakoff, G. (1999). *Philosophy in the flesh*. Basic Books.
- Lakoff, G., & Johnson, M. (2003). *Metaphors we live by* (2nd ed.). University Of Chicago Press.
- 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, Paris*, 102(1–3), 59–70, <http://dx.doi.org/10.1016/j.jphysparis.2008.03.004>.
- Meteyard, L., Cuadrado, S. R., Bahrami, B., & Vigliocco, G. (2012). Coming of age: a review of embodiment and the neuroscience of semantics. *Cortex*, 48(7), 788–804, <http://dx.doi.org/10.1016/j.cortex.2010.11.002>.
- Monetta, L., & Pell, M. D. (2007). Effects of verbal working memory deficits on metaphor comprehension in patients with Parkinson's disease. *Brain and Language*, 101(1), 80–89, <http://dx.doi.org/10.1016/j.bandl.2006.06.007>.
- Neininger, B., & Pulvermüller, F. (2003). Word-category specific deficits after lesions in the right hemisphere. *Neuropsychologia*, 41(1), 53–70.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113.
- Oliveri, M., Finocchiaro, C., Shapiro, K., Gangitano, M., Caramazza, A., & Pascual-Leone, A. (2004). All talk and no action: a transcranial magnetic stimulation study of motor cortex activation during action word production. *Journal of Cognitive Neuroscience*, 16(3), 374–381, <http://dx.doi.org/10.1162/089892904322926719>.
- Owen, A. M. (2004). Cognitive dysfunction in Parkinson's disease: the role of frontostriatal circuitry. *The Neuroscientist*, 10(6), 525–537, <http://dx.doi.org/10.1177/1073858404266776>.
- Papeo, L., Vallesi, A., Isaja, A., & Rumiati, R. I. (2009). Effects of TMS on different stages of motor and non-motor verb processing in the primary motor cortex. *PLoS ONE*, 4(2), e4508, <http://dx.doi.org/10.1371/journal.pone.0004508>.
- Pasquereau, B., & Turner, R. S. (2011). Primary motor cortex of the parkinsonian monkey: differential effects on the spontaneous activity of pyramidal tract-type neurons. *Cerebral Cortex*, 21(6), 1362–1378, <http://dx.doi.org/10.1093/cercor/bhq217>.
- Pulvermüller, F. (2005). Brain mechanisms linking language and action. *Nature Reviews Neuroscience*, 6(7), 576–582, <http://dx.doi.org/10.1038/nrn1706>.
- Pulvermüller, F., Hauk, O., Nikulin, V. V., & Ilmoniemi, R. J. (2005a). Functional links between motor and language systems. *European Journal of Neuroscience*, 21(3), 793–797, <http://dx.doi.org/10.1111/j.1460-9568.2005.03900.x>.
- Pulvermüller, F., Shtyrov, Y., & Ilmoniemi, R. (2005b). Brain signatures of meaning access in action word recognition. *Journal of Cognitive Neuroscience*, 17(6), 884–892, <http://dx.doi.org/10.1162/0898929054021111>.
- 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, <http://dx.doi.org/10.1016/j.neuropsychologia.2008.09.017>.
- Rascol, O., Sabatini, U., Chollet, F., Celsis, P., Montastruc, J. L., Marc-Vergnes, J. P., et al. (1992). Supplementary and primary sensory motor area activity in Parkinson's disease. Regional cerebral blood flow changes during finger movements and effects of apomorphine. *Archives of Neurology*, 49(2), 144–148.
- Ratcliff, R. (1993). Methods for dealing with reaction time outliers. *Psychological Bulletin*, 114(3), 510–532.
- Rosnow, R. L., & Rosenthal, R. (1996). Computing contrasts, effect sizes, and counternulls on other people's published data: general procedures for research consumers. *Psychological Methods*, 1(4), 331–340.
- Saygin, A. P., McCullough, S., Alac, M., & Emmorey, K. (2010). Modulation of BOLD response in motion-sensitive lateral temporal cortex by real and fictive motion sentences. *Journal of Cognitive Neuroscience*, 22(11), 2480–2490, <http://dx.doi.org/10.1162/jocn.2009.21388>.
- Scorilli, C., & Borghi, A. M. (2007). Sentence comprehension and action: effector specific modulation of the motor system. *Brain Research*, 1130(1), 119–124, <http://dx.doi.org/10.1016/j.brainres.2006.10.033>.
- Suppa, A., Iezzi, E., Conte, A., Belvisi, D., Marsili, L., Modugno, N., et al. (2010). Dopamine influences primary motor cortex plasticity and dorsal premotor-to-motor connectivity in Parkinson's disease. *Cerebral Cortex*, 20(9), 2224–2233, <http://dx.doi.org/10.1093/cercor/bhp288>.
- Tukey, J. W. (1977). *Exploratory data analysis* (1st ed.). Addison Wesley.
- van Elk, M., van Schie, H. T., Zwaan, R. A., & Bekkering, H. (2010). The functional role of motor activation in language processing: motor cortical oscillations support lexical-semantic retrieval. *NeuroImage*, 50(2), 665–677, <http://dx.doi.org/10.1016/j.neuroimage.2009.12.123>.
- Wallentin, M., Lund, T. E., Ostergaard, S., Ostergaard, L., & Roepstorff, A. (2005). Motion verb sentences activate left posterior middle temporal cortex despite static context. *Neuroreport*, 16(6), 649–652.
- Willems, R. M., Labruna, L., D'Esposito, M., Ivry, R., & Casasanto, D. (2011). A functional role for the motor system in language understanding: evidence from theta-burst transcranial magnetic stimulation. *Psychological Science*, 22(7), 849–854, <http://dx.doi.org/10.1177/0956797611412387>.
- Wu, T., Long, X., Wang, L., Hallett, M., Zang, Y., Li, K., et al. (2011). Functional connectivity of cortical motor areas in the resting state in Parkinson's disease. *Human Brain Mapping*, 32(9), 1443–1457, <http://dx.doi.org/10.1002/hbm.21118>.
- Zgaljardic, D. J., Borod, J. C., Foldi, N. S., & Mattis, P. (2003). A review of the cognitive and behavioral sequelae of Parkinson's disease: relationship to frontostriatal circuitry. *Cognitive and Behavioral Neurology*, 16(4), 193–210.
- Zwaan, R. A., & Taylor, L. J. (2006). Seeing, acting, understanding: motor resonance in language comprehension. *Journal of Experimental Psychology: General*, 135(1), 1–11.