

Motor Simulation during Action Word Processing in Neurosurgical Patients

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Abstract

■ The role that human motor areas play in linguistic processing is the subject of a stimulating debate. Data from nine neurosurgical patients with selective lesions of the precentral and postcentral sulcus could provide a direct answer as to whether motor area activation is necessary for action word processing. Action-related verbs (face-, hand-, and feet-related verbs plus neutral verbs) silently read were processed for (i) motor imagery by vividness ratings and (ii) frequency ratings. Although no stimulus- or task-dependent modulation was found in the RTs of healthy controls, patients showed a task × stimulus interaction resulting in a stimulus-dependent somatotopic pattern

of RTs for the imagery task. A lesion affecting a part of the cortex that represents a body part also led to slower RTs during the creation of mental images for verbs describing actions involving that same body part. By contrast, no category-related differences were seen in the frequency judgment task. This task-related dissociation suggests that the sensorimotor area is critically involved in processing action verbs only when subjects are simulating the corresponding movement. These findings have important implications for the ongoing discussion regarding the involvement of the sensorimotor cortex in linguistic processing. ■

INTRODUCTION

There is an ongoing, important debate regarding the neural processes underlying semantic representations of action words (Kemmerer & Gonzalez-Castillo, 2010). Processing sentences and words that describe body part movements and actions is known to activate, among other regions, the sensorimotor areas of the brain (Tomasino, Werner, Weiss, & Fink, 2007; Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Boulenger et al., 2006; Buccino et al., 2005; Pulvermuller, Shtyrov, & Ilmoniemi, 2005; Tettamanti et al., 2005; Hauk, Johnsrude, & Pulvermuller, 2004; Oliveri et al., 2004). Although it has been demonstrated that the motor system is activated during action word processing, some issues remain open for discussion (Willems & Hagoort, 2007).

One core question stands: Is the involvement of sensorimotor areas auxiliary, concomitant, or necessary to language processing and comprehension (Chatterjee, 2010; Jirak, Menz, Buccino, Borghi, & Binkofski, 2010). The Semantic Somatotopy Model (Pulvermuller, 2005) proposes that the relationship between action verb processing and motor area activation is semantic and that these areas are causally involved in language understanding (Pulvermuller, Hauk, Nikulin, & Ilmoniemi, 2005). According to the “em-

bodied cognition” view, sensorimotor representations are similarly accessed when an action is observed (Buccino et al., 2001) or when an action word is processed using the observation–execution matching system (Aziz-Zadeh et al., 2006). Neither view clarifies whether the involvement of the motor system is necessary to understand language or if it is only a side effect of distinct upstream processes involved in understanding language.

Indirect evidence regarding the involvement of the cortical motor area in action word meaning representation has been provided by TMS. The excitability of the left motor hand area (as determined by suprathreshold stimulation and measured by motor-evoked potentials) has been shown to be modulated during a grammatical transformation task involving action words, as compared with non-action words (Oliveri et al., 2004). Similarly, a decrease in the amplitude of motor-evoked potentials recorded from hand or foot muscles has been observed during listening to hand and foot action-related sentences, respectively (Buccino et al., 2005). Subthreshold TMS to the primary motor cortex produced faster lexical decisions in response to visually presented action words (Pulvermuller, Hauk, et al., 2005). The TMS/fMRI studies demonstrate a correlation, not causation (Hickok, 2011), and do not rule out a motor preparation or motor priming interpretation of results.

Definitive clarifications regarding the role of the motor system in language processing should come from neuropsychology (Mahon & Caramazza, 2008). Deficits in processing action-related stimuli have been reported in several

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diseases that affect the motor system. These studies raise two important issues. On one hand, the tasks used could have involved processes other than access to action-related conceptual knowledge. Considerable evidence has shown that the involvement of motor areas depends on the cognitive operations exerted upon verbs (Willems, Toni, Hagoort, & Casasanto, 2010; Papeo, Vallesi, Isaja, & Rumiati, 2009; Raposo, Moss, Stamatakis, & Tyler, 2009; Postle, McMahon, Ashton, Meredith, & de Zubicaray, 2008; Tomasino, Fink, Sparing, Dafotakis, & Weiss, 2008; Ruschemeyer, Brass, & Friederici, 2007; Tomasino et al., 2007; Willems & Hagoort, 2007). One study reporting deficits in conceptual knowledge for actions used tasks (e.g., deciding which of two depicted actions would make a louder sound, dealing cards, or shuffling cards) that involved inferential and comparative processing (Hickok, 2011) that could trigger implicit imagery as a potential problem-solving strategy. In a second study, it is not possible to establish whether the performance of patients with Parkinson's disease (Boulenger, Mechtouff, et al., 2008) was because of the specific effects of this grammatical class rather than to access to semantics per se, because their performance with other types of verb stimuli was not investigated (Mahon & Caramazza, 2008).

Another important issue is the extent and the location of the lesions. The impaired comprehension performance of 27 patients on hand-, mouth-, or foot-related stimuli does not provide conclusive evidence regarding the key role of motor areas in action word processing. This deficit was found to be associated with several regions across the left hemisphere and not solely with premotor/motor or somatosensory regions (Arevalo, Baldo, & Dronkers, 2010). Lesions correlated with deficits in lexical and conceptual knowledge of actions were not solely found in the motor areas but were also found in widely distributed regions such as the inferior frontal gyrus, the insula, the supra-marginal gyrus, the posterior middle temporal gyrus (Kemmerer, Rudrauf, Manzel, & Tranel, 2010). Despite the fact that motor neuron disease has been shown to produce deficits in verb naming and comprehension (Bak & Hodges, 2001), this condition was not restricted to the motor cortex alone (Hickok, 2011). Lastly and more directly related to the contribution of the motor cortex itself, it has been documented that the presence of right motor cortex lesions produce deficits in action word processing (Neininger & Pulvermuller, 2001, 2003). These lesions, however, extended to the temporal lobe, and the parietal lobe. Because the role of the right hemisphere in processing certain aspects of semantics is not universally accepted, the logic for examining patients with right hemisphere lesions remains unclear (Chatterjee, 2010). Taking in consideration that other neuropsychological studies show how lesions to the M1 cortex do not predictably cause deficits in action word processing (Mahon & Caramazza, 2005; Saygin, Wilson, Dronkers, & Bates, 2004; De Renzi & di Pellegrino, 1995), it follows that linguistic and action-related deficits do not always occur together in brain-damaged patients (Mahon et al., 2007; Negri et al., 2007).

Many authors argue that there is a lack of compelling evidence regarding the impact that damage to the motor area has on verb processing (Fischer & Zwaan, 2008), and it could come from studies showing that "effectively removing motor structures impairs the ability to understand verbs describing body actions" (Mahon & Caramazza, 2008). Because a resection of lesions in the sensorimotor cortex is rare, so far no studies have systematically investigated language processing in patients with relatively circumscribed lesions invading the motor areas of the brain (e.g., a neurosurgical lesion). In this study, we assessed the ability of neurosurgical patients to perform different tasks during action word processing. We used the same task employed in a previous TMS study (Tomasino et al., 2008). This study demonstrated that stimulation of the hand area of the left primary motor cortex significantly facilitated responses during a motor imagery task and did not affect responses for frequency judgments (Tomasino et al., 2008).

The interaction between motor and language processes can depend on the extent to which the task requires access to the motor representations associated with words (Tomasino, Weiss, & Fink, 2010; Papeo et al., 2009; Tomasino et al., 2008). An individual who is explicitly asked to process a verb and think of performing the associated action (i.e., motor imagery) will need to access its semantic representation and the associated motor information. This is not likely to happen if the task requires estimating the subjective frequency with which the participants think they have heard or read a set of verbs (i.e., frequency judgments).

The imagery task used in this study was derived from the Movement Imagery Questionnaire (Hall & Martin, 1997). Vividness of imagery is usually referred to as either the extent to which the image matches or is similar to actual experience. The frequency judgment task reflects the average frequency with which participants think they have heard or read a set of words. In this study, the value of the rating tasks was not in the ratings per se but in the neurocognitive operations triggered by the task. There are neither "correct" nor more or less accurate responses. Therefore, RTs represent the main measures of the study. Stimuli included in the motor-related lists (face-, foot- and hand-related verbs) were matched utilizing several parameters. A rating study ruled out that other experimental variables, known to affect the time it takes to encode a verbal stimulus (e.g., the word familiarity, words imageability, and age of acquisition), did not differ significantly across our four stimulus lists. There was a 95% agreement in judging the stimuli as hand-, face-, foot-, and neutral-related verbs, and stimuli were of comparable length and verb frequency so that any increase or decrease in RTs could indeed be attributed to the different motoric component of the verbs.

A previous study from our group (Tomasino, Skrap, & Rumiati, 2011) suggested that a lesion in the precentral/postcentral regions can selectively impair motor imagery. If the sensorimotor cortex is involved in the semantic processing of action words through motor simulation,

Table 1. Patients' Clinical Details and Post Surgical Neurological Conditions

	<i>Lesion</i>	<i>Histology</i>	<i>Volume (cc)</i>	<i>Postsurgery</i>
H1	P, motor, LH	Astrocytoma	9.1	Weakness, paresthesia R side of the body
H2	P, sensorimotor, LH	Astrocytoma	3	–
H3	F, motor, Pm, LH	Oligodendroglioma	32.2	Hemiparesis (R arm and face), weakness (R arm)
H4	F, sensorimotor, LH	Astrocytoma	11.2	–
H5	F, motor, RH	Glioblastoma	2.3	Hypersensitivity (L side of the body)
HM1	F, motor, LH	Astrocytoma	1.6	Weakness (R hand, fingers)
HM2	F, pM, RH	Glioblastoma	3	–
HM3	P, motor, RH	Glioblastoma	5.6	–
HF	F, pM, RH	Oligoastrocytoma	14.7	Hemiparesis (L hand)

Tumor volume has been calculated by MRIcro as an ROI selectively drawn on T1-weighted images on the contrast-enhanced lesion area. H1–H5 = patients with a lesion affecting the hand representation; HM1–HM3 = patients with a lesion affecting the hand and the mouth representations; HF = patient with a lesion affecting the hand and the foot representations; LH = left hemisphere; RH = right hemisphere; P = Parietal; F = Frontal; pM = premotor; R = right; L = left.

we should observe task-dependent differential modulation effects on the patients' RTs on the imagery task and no effect on frequency judgments. Such a pattern of results would provide neuropsychological evidence for "context-dependent" motor responses during action word processing (Tomasino, Weiss, & Fink, 2010; Papeo et al., 2009; Raposo et al., 2009; Postle et al., 2008; Ruschemeyer et al., 2007).

METHODS

Participants

Nine neurosurgical patients (six men and three women; mean age = 41.22 years, $SD = 8.4$ years) with a tumor invading the precentral and/or postcentral area, according to their fMRI sensorimotor maps (see below), of the left ($n = 5$) or the right ($n = 4$) hemisphere were exclusively selected. Five patients presented with a lesion affecting the hand representation (hereafter H1, H2, H3, H4, and H5), three with a lesion affecting the hand and the mouth representations (hereafter HM1, HM2, and HM3), and one with a lesion affecting the hand and the foot representations (hereafter HF; see Table 1 for the description of the clinical characteristics). The neuropsychological, neuroanatomical, and experimental data were collected at least 5 months after tumor removal surgery. All patients were right-handed (Oldfield, 1971) and did not exhibit any impairment in neuropsychological functioning that would confound their performances on the experimental tasks. They all scored 36/36 on the Token Test (Spinnler & Tognoni, 1987) tapping comprehension, 15/15 on naming living entities, and 20/20 on naming non-living entities (Naming, BORB 13; Riddoch & Humphreys, 1993) and had a short-term digit span within the normal range (Spinnler & Tognoni, 2009). They all scored 20/20

on the oral praxis test, and all but one (P6, 68/72) scored 72/72 on the ideomotor apraxia test (De Renzi et al., 1980). No signs of constructional apraxia (all scored 14/14; Spinnler & Tognoni, 2009) and no signs of visuo-perceptual (all scored 25/25, BORB 8; Riddoch & Humphreys, 1993) or spatial attention deficits were detected (all scored 22/22 on Test A and Test B, Balloon Test; Edgeworth et al., 1998). At the time of testing, none of the patients had hemiparesis. However, either before or transiently after tumor removal, they suffered seizures involving the upper or lower limb or the face representation or presented with weakness or paresthesia (see Table 1). Patients provided their informed consent to participate in this study, which was approved by the institute's ethics committee.

Sensorimotor fMRI Maps: Lesion Localization

The presurgical fMRI maps acquired as part of the routine examination for performing fMRI-guided neuronavigation during surgery were used in this study to localize the patients' lesions with respect to the face/hand/foot representation (see Figures 2 and 3). High-resolution anatomical and functional images were acquired by utilizing a Siemens 1.5 T MRI whole-body scanner (Siemens Avanto, Erlangen, Germany) with a standard head coil and a custom-built head restrainer to minimize head movements. Functional images were obtained by using a single-shot EPI sequence (36 axial slices, repetition time = 3000 msec, echo time = 60 msec, field of view = 220 mm, matrix = 64×64 ; slice thickness = 5 mm, flip angle = 90° , voxel size = $3.28 \times 3.28 \times 5$ mm, four dummy images to allow the magnetization of the spins to stabilize to a steady state). 3-D images were acquired by using a T1-weighted 3-D magnetization-prepared, rapid acquisition gradient-echo (repetition time = 2300 msec, echo time = 2.86 msec, field of view = 256 mm, 176 sagittal slices of 1 mm thickness, flip angle = 20° , voxel

size = $1 \times 1 \times 1$ mm). Motor localizer tasks, which included performing mouth movements and hand and foot movements, were presented in three different runs as block designs ($n = 4$, 15 sec each for a total of 135 sec: move vs. rest for each body part movement). Upon reading the word "Move," patients were instructed to perform (i) lip protrusion, (ii) left and right hand movements (wrist extension), and (iii) left and right foot movements (moving the top of the foot toward their head).

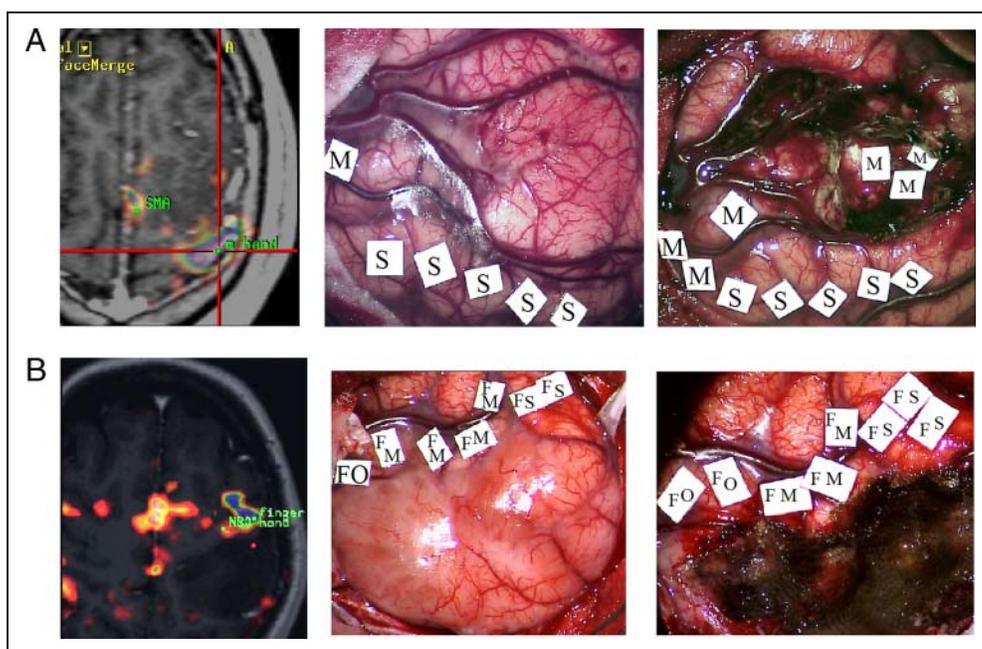
Statistical analysis was performed on UNIX workstations (Ubuntu 8.04 LTS, i386, www.ubuntu.com/) using MATLAB r2007b (The Mathworks, Inc., Natick, MA) and SPM5 (Wellcome Department of Imaging Neuroscience, London, www.fil.ion.ucl.ac.uk/spm). Dummy images were discharged before further image processing. Preprocessing included spatial realignment, segmentation producing the parameter file used for normalization, resampling to a voxel size of $2 \times 2 \times 2$ mm, and spatial smoothing with a 6-mm FWHM Gaussian kernel. We modeled the alternating epochs by utilizing a simple boxcar reference vector. A general linear model for blocked designs was applied to each voxel. This was achieved by modeling the activation and the baseline conditions for each subject and their temporal derivatives by means of reference waveforms, which corresponded to boxcar functions convolved with a hemodynamic response function (Friston, Frith, Turner, & Frackowiak, 1995; Friston, Holmes, et al., 1995). Furthermore, we included six additional regressors modeling head movement parameters obtained from the realignment procedure. We performed a whole-brain random effect analysis. Low-frequency signal drifts were filtered using a cutoff period of 128 sec. Motor and resting blocks were modeled as the regressors of main interest, which were convolved with a canonical hemodynamic response function. At the single subject level, specific

effects were assessed by applying appropriate linear contrasts to the parameter estimates of the experimental conditions resulting in t statistics for each voxel. We used a threshold of $p < .05$, corrected for multiple comparisons at the cluster level (using family-wise error), with a height threshold at the voxel level of $p < .001$, uncorrected.

Using the patients' fMRI motor maps, we could identify the tumor area activated by the action-execution task (see Figures 2 and 3). Patients were grouped as follows: H1, H2, H3, H4, and H5 had a lesion involving the hand area; HM1, HM2, and HM3 had a lesion involving the hand and the mouth area; and HF had a lesion involving the hand and the foot area. The hand movement task activated the tumor area (H1, H2, H3, H5, HM1, and HM3) in all the patients or an area above the lesion (H4) or anterior to the lesion (HF). The foot movement task activated the tumor area in HF as can be observed if the healthy foot movement-related activation is taken as reference. The lip movement task activated the tumor area in HM1 and HM3 but did not activate the lesioned hemisphere in HM2 (the healthy hemisphere was taken as reference).

Lesion localization was also performed by a neurosurgeon who was blind to the purpose of the study. All the lesions were relatively circumscribed to the precentral and/or post-central area (see the lesion volume and histology in Table 1). In addition, the neurosurgeon determined the extent and site of the lesion with respect to the sensorimotor representation during an awake craniotomy while performing direct cortical stimulation mapping of the sensorimotor homunculus. Direct cortical stimulation of the primary motor area induced a motor response of the contralateral hemibody allowing for reconstruction of Penfield's homunculus before removing the lesion (see Figure 1 for an example of two cases included in this study; the tags indicate a spared

Figure 1. Two representative cases (A) and (B). The left side shows the fMRI activation related to hand movements, the exposed cortex before craniotomy is shown in the central section, and the right side shows the surgical cavity after lesion removal. The tags indicate the presence of motor function in the area near the lesion in terms of body part movements evoked by the stimulation. M = motor; S = sensory; FM = finger, motor; FS = finger, sensory; F = foot.



[motor] function in the area near the lesion in terms of body part movements evoked by the stimulation). Complete neurosurgical resections were carried out, stopping when the cortical stimulation evoked a body part movement.

Design and Procedure

We used two tasks (motor imagery and frequency judgment) counterbalanced across subjects and four types of stimulus (face-, foot-, hand-related and neutral verbs). Identical verb stimuli ($n = 144$) were randomly presented in the two tasks, so that any differences in performance could be related to the cognitive operation required and not to the stimulus list (resulting in 288 trials, 36 trials for each verb category). Verbs were presented for 1900 msec and were followed by a fixation cross lasting 450 msec. Throughout the experiment, subjects sat in a comfortable armchair in front of a computer screen at a distance of 57 cm. Stimuli were presented on a white background of a 19-in. LCD monitor by Presentation software (version 9.90; Neurobehavioral Systems, Inc., Albany, CA), which was also used for response recording. Subjects were instructed to keep their hands still and as relaxed as possible. They responded by pressing one of seven keys on a keyboard with the left hand. All participants were right-handed; therefore, left hand responses were chosen in an effort to minimize interference between motor response preparation and execution. Our action verbs relating to hand movements should rigger mainly right (dominant)-hand motor imagery.

Stimuli

One hundred forty-four (144) Italian action verbs relating to hand ($n = 36$, e.g., “to grasp”), face ($n = 36$, e.g., “to chew”), and foot movements ($n = 36$, e.g., “to kick”), as well as neutral verbs ($n = 36$, e.g., “to suffer”), were selected and presented in their infinitive form. The final choice of stimuli was based on a pilot study of 20 normal adults with a 95% agreement in judging the stimuli as hand-, face-, foot-related and neutral verbs. Stimuli were of comparable length ($p > .05$, *ns*; see Table 2), and their frequency (Laudanna, Thornton, Brown, Burani, & Marconi, 1995) was equal across conditions ($p > .05$, *ns*; see Table 2).

Stimulus Norming Study

We performed a rating study to verify whether other experimental variables known to affect the time it takes to encode a verbal stimulus differed across our four stimulus lists. Fifteen healthy participants, all being native speakers of Italian with comparable levels of education, all monolinguals, with normal or corrected-to-normal vision, with no history of neurological illness, psychiatric disease, or drug abuse, judged each verb stimulus. Following the instructions of Barca, Burani, and Arduino (2002), they rated the stimuli on several dimensions. Participants judged word familiarity, that is, how well each word is known, on a scale ranging from 1 to 7, where “1” = *very little known* and “7” = *very well known*, and the words imageability, that is, how quickly and easily each word

Table 2. Summary of Psycholinguistic Variables for All the Verb Categories

	Verbs				Significant Effects
	Face	Feet	Hands	Neutral	
Number of items	36	36	36	36	–
Length	8.9 ± 2.3	9.1 ± 2.04	9.1 ± 2.1	8.5 ± 1.6	<i>ns</i>
Frequency	42 ± 140.5	61.4 ± 163.8	40.8 ± 97.3	76.4 ± 105.6	<i>ns</i>
Agreement	95	96	96	95	<i>ns</i>
Familiarity	6.7 ± 0.5	6.8 ± 0.1	6.8 ± 0.1	6.7 ± 0.2	<i>ns</i>
Imageability	6.5 ± 0.6	6.7 ± 0.2	6.7 ± 0.1	5.5 ± 0.7	face, feet, hand > neutral, $p < .001$
AoA	2.9 ± 1.5	3.1 ± 1.2	2.8 ± 0.9	4.1 ± 1.3	face, feet, hand > neutral, $p < .01$
Mean RTs: frequency judgment	1294 ± 147	1301 ± 148	1301 ± 146	1328 ± 175	Stimulus: face, feet, hand > neutral, $p < .01$
Mean RTs: imagery	1288 ± 139	1303 ± 160	1290 ± 160	1351 ± 159	

AoA = age of acquisition, with means representing the following scale: 2 = 3–4 years, 3 = 5–6 years, 4 = 7–8 years, 5 = 9–10 years, 6 = 11–12 years. RTs in msec and *SDs* from the norming task study. Imageability: face versus neutral $t(35) = 7.019$, foot versus neutral $t(35) = 9.018$, hand versus neutral $t(35) = 9.955$, all $ps < .001$; AoA: face versus neutral $t(35) = -3.53$, $p < .005$, foot versus neutral $t(35) = -3.044$, $p < .01$, hand versus neutral $t(35) = -5.47$, $p < .001$; main effect of stimulus: neutral versus face ($t(24) = -4.53$, $p < .001$), foot ($t(24) = -3.8$, $p < .005$), and hand ($t(24) = -3.7$, $p < .005$).

arouses mental images, on a scale ranging from 1 to 7, where “1” = *bardly imageable* and “7” = *highly imageable*. In addition, they estimated at which age they thought they first learned each word, on a scale ranging from 1 to 7, where “1” = 0–2 years, “2” = 3–4 years, “3” = 5–6 years, “4” = 7–8 years, “5” = 9–10 years, “6” = 11–12 years, and “7” = 13–14 years. The four verb types did not significantly differ for familiarity [$F(3, 105) = .83, p > .05, ns$; see Table 2]. The motor-related verbs did not differ in terms of imaginability (all $ps > .05$) or age of acquisition (all $ps > .05$). But each motor category elicited more vivid mental images than neutral verbs [$F(3, 105) = 47.47, p < .001$; see Table 2] and was acquired earlier than neutral verbs [$F(3, 105) = 7.56, p < .001$; see Table 2]. Importantly, our pilot study showed that the stimuli composing the motor-related lists (face, foot, and hand related) were similar so that any increase or decrease in RTs can be attributed to the different motoric component of the verbs.

Experimental Task

Task instructions (8 sec) that guided the two cognitive operations (exerted upon stimuli in a top-down fashion) were “Silently read the verb” and (i) “Imagine yourself performing the action, feeling the sensations you would feel if you were performing the movement. Rate the ease and the kinesthetic vividness in forming the mental image on a scale from 1 (*very hard to feel*) to 7 (*as real movement*) [Imagery task]” and (ii) “Is this a word that you hear often? Judge how often you hear this word on a scale from 1 (*never*) to 7 (*always*) [Frequency Judgment].” Before the experiment, participants were asked “to give a very intuitive and direct answer in both tasks.”

Task Norming Study

Twenty-five right-handed (Edinburgh Inventory Test) healthy subjects (11 women; mean age = 30.88 years, $SD = 11.7$ years), different from those who participated in the above-mentioned rating study, gave their informed consent to participate in the study. They were asked to perform the imagery and frequency judgment tasks. We removed the middle (4) “I don’t know” judgments (4.36% of the overall data points) from the analysis because these judgments could skew the data. In addition, outliers were removed by excluding any trials in which the participant’s RTs were two standard deviations above or below the mean RTs for the condition in which the trial occurred (Ratcliff, 1993).

SPSS for Windows (version 12.0) was used. A repeated measure ANOVA with “task” (imagery and frequency judgment) and “stimulus type” (face, foot, hand, neutral) as factors was performed on the subjects’ RTs. The results showed that stimuli comprising the face, foot, and hand lists are similarly processed in terms of RTs. Any increase or decrease in RTs is indeed attributable to the patients’

difficulty in processing the different motoric component of the verbs. The only significant main effect we found was the type of stimulus $F(3, 72) = 10.47, p < .001$, with action verbs not differing between each other (all $ps > .05, ns$; see Table 2) and significantly longer RTs for neutral versus action verbs (see Table 2; all $ps < .01$).

Statistical Analyses

For each patient, RTs were analyzed by an ANOVA, with Type of Stimulus and Task as factors. Outliers were removed by excluding any trials in which the participants’ RTs were two standard deviations above or below the mean RTs for the condition in which the trial occurred (Ratcliff, 1993). The middle (4) “I don’t know” judgments (1.8% of the whole data set) were removed from the analysis. Significance was set at $p < .05$. Using the Sidak adjustment, post hoc multiple comparisons were used.

RESULTS

For the control participants, RTs on both the frequency judgment and imagery tasks were not affected by the stimulus category. However, we observed numerous Task \times Stimulus category interactions in a series of analyses involving individual patients (H1: $F(3, 253) = 2.69, p < .05$; H2: $F(3, 260) = 2.7, p < .05$; H3: $F(3, 253) = 3.09, p < .05$; H4: $F(3, 235) = 3.015, p < .05$; H5: $F(3, 266) = 12.4, p < .001$; HM1: $F(3, 209) = 4.01, p < .01$; HM2: $F(3, 255) = 3.04, p < .05$; HM3: $F(3, 299) = 2.67, p < .05$; HF: $F(3, 316) = 2.74, p < .05$; see Figures 2 and 3). This interaction was driven by the imagery task and resulted in a stimulus-dependent somatotopic pattern of RTs for the imagery task only (see below).

Frequency Judgment Tasks

Post hoc pairwise comparisons performed for both the imagery and the frequency judgment tasks showed no significant differences between the stimuli for the frequency judgment task. Patients’ processing times were comparable to controls (see Figures 2 and 3). For all the patients, the RTs for frequency judgments on face-related verbs were not significantly different from RTs for all the other categories (face- vs. foot-related verbs, face- vs. hand-related verbs, face-related vs. neutral verbs, all $ps > .05, ns$). Similarly, the RTs for frequency judgments on foot-related verbs (foot- vs. hand-related verbs, foot-related vs. neutral verbs, all $ps > .05, ns$) and hand-related verbs (hand-related vs. neutral verbs, $p > .05, ns$) were not significantly different either. Patient H5 was the only exception, showing significantly higher RTs for frequency judgments on foot- vs. hand-related and for neutral vs. hand-related verbs (both $ps < .05$).

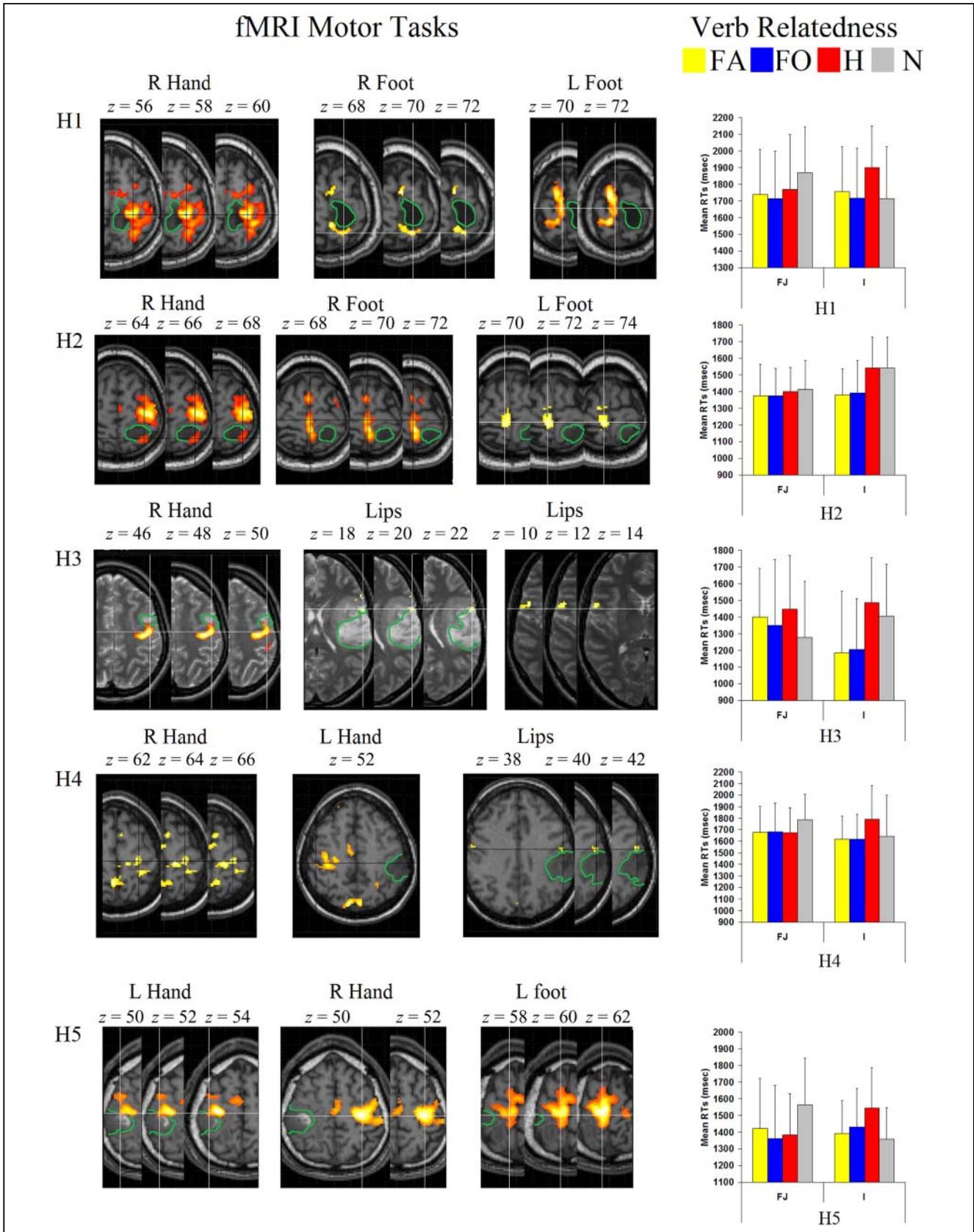


Figure 2. Relative increases in neural activity associated with the hand movement task (H1, H2, H3, H4, and H5) are localized within the lesioned area (green). Radiological convention is adopted. The mean RTs are higher for hand-related verbs. The patients' mean RTs (msec) for the two tasks are shown on the right side of the panel. Error bars indicate standard deviations (*SD*). I = imagery task; FJ = frequency judgment task; FA = face related; FO = foot related; H = hand related; N = neutral verbs.

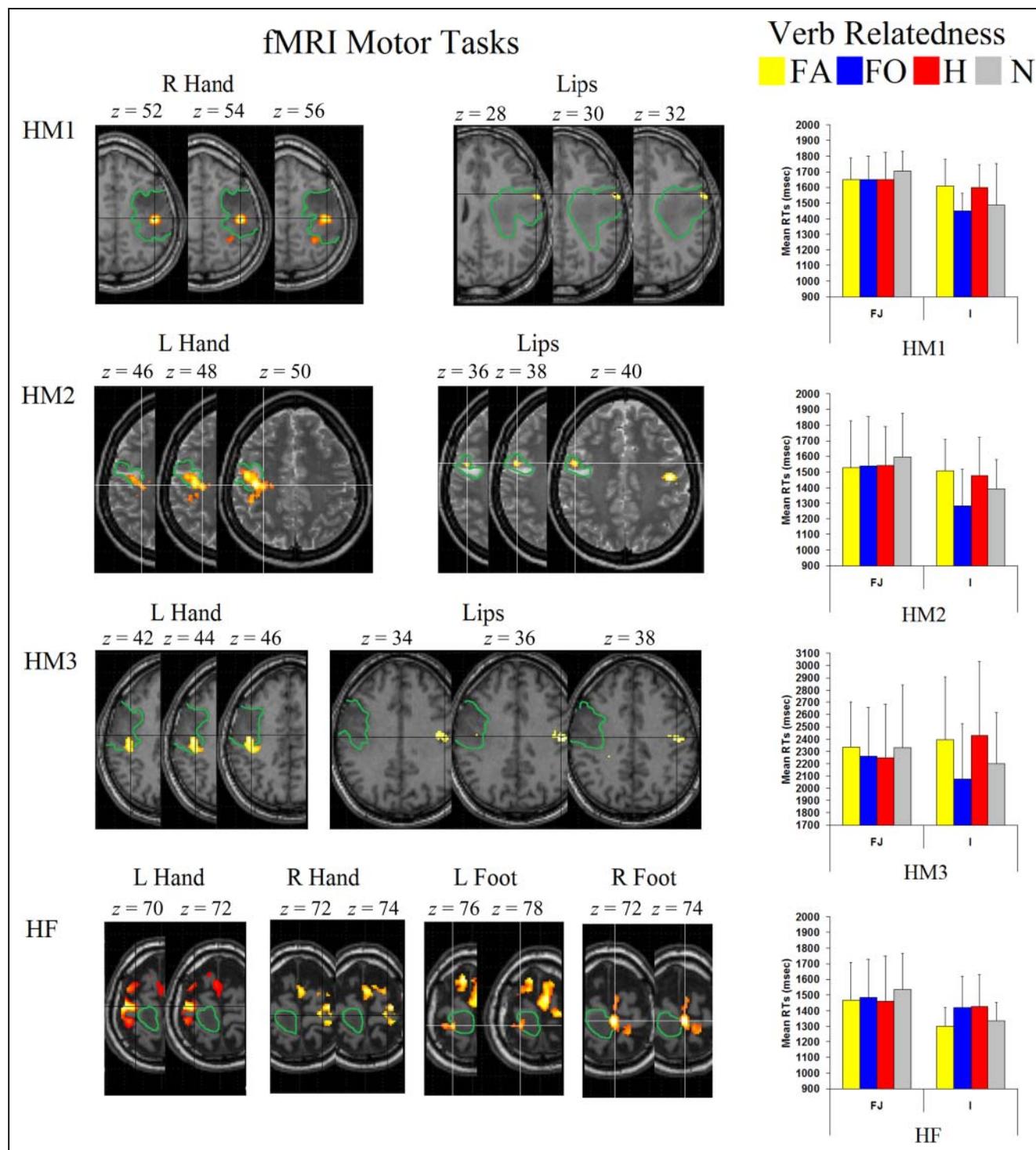


Figure 3. Relative increases in neural activity associated with hand and mouth movement tasks (in HM1, HM2, and HM3) and with hand and foot movement tasks (in HF) are localized within the lesioned area (green). Radiological convention is adopted. The mean RTs are higher for hand- and face- (HM1, HM2, and HM3) or for hand- and foot-related verbs (HF). The patients' mean RTs (msec) for the two tasks are shown on the right. Error bars indicate standard deviations (*SD*). I = imagery task; FJ = frequency judgment task; FA = face related; FO = foot related; H = hand related; N = neutral verbs.

Imagery Task

Post hoc pairwise comparisons showed that the interaction was driven by the imagery task. There were one or more

specific verb types that were occasionally associated with longer imagery processing times (resulting in a cost in RTs). For H1, H2, H3, H4 and H5, this occurred for imagery of hand movements (hand- vs. face-related verbs, all

$p < .05$, with hand-related > face-related verbs; hand- vs. foot-related verbs, for H1, H2, H3, H4, $p < .05$, with hand-related > foot-related verbs; hand-related vs. neutral verbs, for H1, H4, H5, $p < .05$, with hand-related > neutral verbs).

By contrast, the interaction was driven by imagery for hand and imagery for face movements (face- vs. foot-related verbs, all $p < .05$, with face-related > foot-related verbs, and hand- vs. foot-related verbs, all $p < .05$, with hand-related > foot-related verbs) for HM1, HM2, and HM3.

As for HF, a different pattern was found. This interaction was driven by imagery for foot movements and imagery for hand movements (hand- vs. face-related, $p < .05$, with hand- > face-related verbs, and foot- vs. face-related, $p < .05$, with foot-related < face-related verbs).

Somatotopic Effects

The fMRI motor maps of single patients provided explanation as to why an increase in imagery times is sometimes because of a face-related verb and at other times of a hand-related verb and how specific the deficits really are. For example, HM1 showed a difference between motor imagery of hand and foot actions, which is interpreted as a cost. However, the same difference was found for face and foot imagery. For this patient, hand-related and face-related fMRI activation falls within the lesioned site. H1, H2, H3, H4, and H5 showed a significant increase in RTs for hand-related verbs (vs. the other categories). Accordingly, their hand-related fMRI activation fell within the lesioned site.

HM1, HM2, and HM3 were significantly slower for imagery of hand- and mouth-related movements. Accordingly, their hand and mouth representations fell within the lesioned area.

Finally, HF showed a significant increase in RTs for hand- and foot-related verbs (vs. the other categories). The patient's hand- and foot-related fMRI activation fell within the lesioned site (see Figures 2 and 3).

Main Effects

Overall, patients were slower than controls. The majority of the patients had comparable RTs for both tasks (H1, H3, H4, H5, HM2, HM3, $p > .05$, *ns*), some were slower in the frequency judgment than in the imagery task (HM1: $F(1, 209) = 29.5$, $p < .001$ and HF: $F(1, 288) = 21.67$, $p < .001$), and one showed the reverse pattern (H2: $F(1, 260) = 11.35$, $p < .001$). Some patients showed a significant type of stimulus effect (H2: $F(3, 260) = 6.08$, $p < .001$; H3: $F(3, 253) = 3.29$, $p < .05$; HM2: $F(3, 255) = 17.8$, $p < .001$), which was driven by the imagery task as found in the task by stimulus interaction discussed above.

DISCUSSION

This study was designed to further explore the nature of the interaction between the motor system and linguistic

processing. Embodied accounts of language processing suggest that sensorimotor areas are also involved in the processing and representation of word meaning. Some theories suggest that sensorimotor areas are an integral part of lexical-semantic representations (Pulvermuller, 2005; Pulvermuller, Hauk, et al., 2005; Pulvermuller, Shtyrov, et al., 2005). Others suggest that lexical-semantic meaning is derived from internal simulations of word referents (Barsalou, 2008). Whether motor activations reflect automatic, invariant effects or are flexible and context-dependent remains unclear (van Dam, Rueschemeyer, & Bekkering, 2010). A number of studies have shown that motor activation is not automatic (e.g., Tomasino, Weiss, & Fink, 2010; Papeo et al., 2009; Raposo et al., 2009; Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005). According to this view, motor imagery simply accompanies lexical-semantic processing after a word has been effectively accessed (van Dam et al., 2010). We compared top-down cognitive operations exerted on action verbs in neurosurgical patients with lesions invading the precentral and postcentral gyrus. The frequency judgments and the imagery tasks served as a control for the cognitive set and the operations performed with verbs after/during the silent reading. The common processing steps predominantly reflected reading, language processing, response selection, and motor output-related processes.

Imagery vividness ratings are used as indicators of the similarity between imagery and perception (Finke, 1989) because vividness has been referred to as the extent to which the image matches or is similar to actual experience. In our study, participants closely followed task instructions (i.e., they were asked to describe their first impression and provide a very intuitive and direct answer), as evidenced by their quite short mean response times. The processing steps predominantly reflect the ease of mental image generation (Chiarello, Shears, & Lund, 1999). However, it is also possible that the semantic features of each word are initially examined for the frequency of sensory motor attributes, either to examine the nature of the features themselves or to attempt to generate an image (Chiarello et al., 1999).

The task norming study revealed significantly longer RTs for neutral verbs compared with the other action related verb categories, namely a concreteness effect (Grossman et al., 2002; Luzzatti et al., 2002; Plaut & Shallice, 1993; Paivio, 1971). Importantly, our motor-related verbs did not differ for time processing. Any increase or decrease in RTs between them could be attributed to the different motoric component of the verbs and the ability of patients to process that particular action-related verb category.

Stimulus by Task-dependent Modulation of Reaction Times during Action Verb Processing

This study analyzed mean RTs to assess whether processing times of action verbs, during motor imagery or frequency judgment tasks, changed as an effect of a lesion in

the precentral and postcentral cortices. This was confirmed by the significant Task \times Stimulus interaction. Our patients showed a stimulus-dependent somatotopic pattern of RTs for the imagery task, which is consistent with previous studies showing a somatotopically organized pattern of responses in the motor and premotor cortex for action-related verbs and sentences (Aziz-Zadeh et al., 2006; Tettamanti et al., 2005; Hauk et al., 2004). A lesion affecting a part of the cortex, which represents a body part, also leads to slower RTs during the creation of a mental image for verbs describing actions involving that same body part. Patients with lesions involving the hand representation were slower in the creation of a mental image for hand actions, and patients with lesions involving the hand and face representation in the sensorimotor and premotor cortices (hand and face) were slower in the creation of a mental image for hand and face actions, as evidenced by their fMRI maps. No differences in the action category were found during the frequency judgment task carried out using the same verbs.

Despite the criticisms raised against the somatotopically distributed activations reported in many studies (Fernandino & Iacoboni, 2010), the fMRI motor maps used in this study are essential in locating the patients' lesions with respect to the different body part representations within the sensorimotor homunculus and to relate these findings to the patients' performances.

The differential modulation of RTs for each patient, for a particular category of action verbs describing a body part movement, was dependent on the type of task. The increase in RTs was seen during motor imagery only. These results provide neuropsychological evidence for a top-down activation of the motor system according to the type of cognitive operation exerted upon the stimuli (Kemmerer et al., 2010; Papeo et al., 2009; Raposo et al., 2009; Tomasino et al., 2007, 2008). A direct functional connection between language and the motor system would predict that reading a verb, for example, "write," activates the motor areas of the brain independent of the operation and attention (Pulvermuller, Shtyrov, et al., 2005). A previous fMRI study (Raposo et al., 2009) suggested that "motor representations are only engaged under specific conditions and ... their effects are variable and context-dependent," (p. 394) because they found that action words activated motor regions only when they occurred in isolation or in sentences that emphasize body movements. As with our study, which was not focused on motor properties (Raposo et al., 2009), we did not observe any association between motor activity and action word processing. According to cognitive theories of semantic flexibility, the degree to which alternative senses and particularly relevant features are processed when a word is heard is dependent upon the nature of the semantic context (Elman, 2004, 2009). As such, motor imagery could have a role in causing motor area activation during action-related verb processing. In a previous study (Tomasino et al., 2007), we reported motor cortical activity when participants imagined the situation described in an action phrase, but not when

they performed a secondary letter detection task designed to prevent spontaneous imagery strategies. Although previous studies of action verb processing ruled out the influence of imagery by administering a comprehension task followed by action execution (Hauk et al., 2004) or observation tasks (Aziz-Zadeh et al., 2006), one cannot exclude that participants adopted implicit imagery strategies during the linguistic task. According to this view, the modulation of motor activation during action-related word understanding depends on whether subjects simulate the movement the words are referring to during reading. In particular, in the absence of specific cognitive demands as in a passive listening task or a silent reading task (Hauk et al., 2004), subjects might imagine themselves performing the action, which in turn could activate motor areas (Tomasino et al., 2008). As such, van Dam et al. (2010) compared modulation of the BOLD response elicited by verbs denoting a general motor program (e.g., to clean) and verbs denoting a more specific motor program (e.g., to wipe). Findings concluded that the bilateral inferior parietal lobule, known to represent action plans and goals, was sensitive to the specificity of motor programs associated with the action verbs, thus reflecting differences in the ability to imagine verbs with more versus less detailed action information. This study found no differential activation in the sensorimotor cortex. Because the processing of action-related verbs triggers a cognitive set of implicit movement preparation, motor intention, and motor simulation, evidence that the motor system activation, during action-related verb processing is modulated by the task context, supports the notion that this motor system activation is a corollary phenomenon (see also Boulenger, Silber, et al., 2008; Oliveri et al., 2004). Therefore, our data support the idea of an indirect connection between the motor and language systems via sensorimotor representations. A similar capacity of the observation-execution-matching system (e.g., Buccino et al., 2001; Gallese & Goldman, 1998) and motor simulation (Porro et al., 1996) to activate sensorimotor representations (Jeannerod, 1995) may point to a common framework explaining motor activations during action-related word processing. Within this framework, the processing of action-related words may (indirectly) activate sensorimotor representations and, thus, the motor cortex, either via the observation-execution-matching system (e.g., Aziz-Zadeh et al., 2006; Buccino et al., 2005; Tettamanti et al., 2005) or by (implicitly or explicitly) triggering mental simulation (e.g., Tomasino et al., 2007; Glenberg & Kaschak, 2002). A previous study found that the activity was differentially decreased by action verbs presented as negative imperatives for the premotor and the primary motor cortex of both hemispheres (Tomasino et al.). This suggests that motor simulation (or motor planning), rather than semantic processing per se, may underlie the previously observed motor system activation related to action verb processing and that negative imperatives may inhibit motor simulation or motor planning processes. The embodied view implies that brain areas related to action and language can no longer

be seen as independent, but rather, working in concert (Jirak et al., 2010). It has been argued that the fast motor activation, its automaticity, and the somatotopic organization undermines (Jirak et al., 2010) the hypothesis that information is first converted into an abstract format and then influences the motor system (see Mahon & Caramazza, 2008). At variance with the hypothesis that the motor system is activated in a direct and straightforward manner (Jirak et al., 2010), the task-related dissociation we found in the performance of our patients rather indicates that processing of an action word through the motor route (as elicited by the mental simulation task) or through the linguistic route (as elicited by the frequency judgments) is independent and that the link between action and language is represented by motor imagery. In this respect, the reported interactions between action word processing and action execution (Boulenger et al., 2006; Zwaan & Taylor, 2006; Buccino et al., 2005; Glenberg & Kaschak, 2002) might be seen as a byproduct of action-related words (indirectly) activating sensorimotor representations via mental simulation or action preparation (see also Frak, Nazir, Goyette, Cohen, & Jeannerod, 2010).

The view that motor area activation during action word processing may reflect the by-product of imagery of an action (e.g., Jeannerod, 2001) is consistent with the idea that automatic/implicit or strategic motor imagery could emerge following identification of the action concept, and not part of the representation of the action word per se (Willems & Hagoort, 2007). This suggests the possibility that M1 is not an integral part of the network for action word representation but is recruited only to accomplish tasks that critically require the retrieval of sensorimotor attributes associated with words.

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