

Listening to Action-related Sentences Activates Fronto-parietal Motor Circuits

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Abstract

■ Observing actions made by others activates the cortical circuits responsible for the planning and execution of those same actions. This observation–execution matching system (mirror-neuron system) is thought to play an important role in the understanding of actions made by others. In an fMRI experiment, we tested whether this system also becomes active during the processing of action-related sentences. Participants listened to sentences describing actions performed with the mouth, the hand, or the leg. Abstract sentences of comparable syntactic structure were used as control stimuli.

The results showed that listening to action-related sentences activates a left fronto-parieto-temporal network that includes the *pars opercularis* of the inferior frontal gyrus (Broca's area), those sectors of the premotor cortex where the actions described are motorically coded, as well as the inferior parietal lobule, the intraparietal sulcus, and the posterior middle temporal gyrus. These data provide the first direct evidence that listening to sentences that describe actions engages the visuomotor circuits which subserve action execution and observation. ■

INTRODUCTION

Experiments in monkeys have shown that observing an action made by another individual activates an observation–execution matching system, named mirror-neuron system (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Electrophysiological studies (Gangitano, Mottaghy, & Pascual-Leone, 2001; Cochin, Barthelemy, Roux, & Martineau, 1999; Hari et al., 1998; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995) and imaging data (Grèzes, Costes, & Decety, 1998; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Rizzolatti, Fadiga, Matelli, et al., 1996) showed that a mirror-neuron system similar to that described in monkeys also exists in humans. It has been proposed that this system subserves the understanding of actions made by others. According to this view, observing an action evokes responses in fronto-parietal circuits which code for motor representations of the actions observed. The neural transcoding of the observed action into a corresponding motor plan allows one to understand the meaning of the action observed (Rizzolatti, Fogassi, & Gallese, 2001). Motor programs equivalent to those used in actions are

instinctively and simultaneously implemented during action observation, allowing the outcome of the observed action to be predicted (Flanagan & Johansson, 2003). This neural mechanism may underlie the capacity displayed by individuals of social groups to interpret the actions and intentions of other members of the group (Rizzolatti, Fogassi, et al., 2001; Gallese & Goldman, 1998).

Imaging studies also showed that the human mirror-neuron system consists of a series of parallel premotor–parietal circuits (Blakemore & Decety, 2001; Iacoboni et al., 1999) that show a somatotopic organization (Buccino, Binkofski, et al., 2001). The observation of mouth actions leads to an activation of the *pars opercularis* of the inferior frontal gyrus, which extends to the rostral-most sector of the ventral premotor cortex; the observation of hand actions leads to the activation of the ventral premotor cortex, partially extending to the *pars opercularis* of the inferior frontal gyrus; the observation of foot actions leads to the activation of the dorsal premotor cortex. When the actions observed involved congruent objects, a corresponding somatotopic organization was also found in the posterior parietal lobe (Buccino, Binkofski, et al., 2001). Crucially, fronto-parietal circuits are found to be activated only when the observed actions belong to the observer's motor repertoire (i.e., actions that the observer himself can execute). For instance, activations in fronto-parietal circuits are found when humans observe a dog biting,

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but not when they observe a dog barking (Buccino, Lui, et al., 2004).

Action observation is not the only condition triggering the activation of the mirror-neuron system. Recently, it has been shown that in monkey's premotor cortex there are mirror neurons (bimodal, audiovisual mirror neurons) that discharge not only when an action is seen or executed, but also when the noise related to the action is heard (Kohler et al., 2002). This new observation supports the idea that the mirror-neuron system codes action content at an abstract level and that this content can be accessed auditorily.

In humans, action-related knowledge can be retrieved not only by action observation or by hearing action sounds, but also by understanding sentences describing actions. This raises the possibility that the comprehension of actions relies on the observation–execution matching system even when the actions are described using language. Exploring this possibility amounts to addressing the relationship between the somatosensorimotor system and the symbolic/conceptual neural system governing language. Although the brain system underlying somatosensorimotor functions is well known, very little is known about the format assumed by the conceptual-level representations accessed by language. Two main theories have been proposed. The first claims that the meaning of an action, when verbally presented, is accessed using abstract and amodal units (Fodor, 2001; Pylyshyn, 1984). An alternative hypothesis suggests that understanding words semantically related to actions depends upon the motor structures involved in the execution of the very same actions (Pulvermueller, 2002; Lakoff & Johnson, 1999). Evidence in favor of the latter hypothesis has been recently provided (Hauk, Johnsrude, & Pulvermuller, 2004). According to this view, listening to action-related sentences should modulate the motor system in the same way as observing actions (Buccino, Binkofski, et al., 2001).

Brain imaging may contribute to the understanding of these issues by revealing the regional activation associated with the processing of sentences describing motor actions. If language processing of action-related sentences relies, at least in part, on sensorimotor representations and not only on abstract and amodal units, then activations should be observed in areas coding for action representation. Crucially, regions containing mirror neurons, including Broca's area, should be activated by this task. Cytoarchitecturally, the monkey prefrontal area F5 (i.e., the prefrontal region where mirror neurons have originally been discovered) has been suggested to be the monkey homologue of human Brodmann's area (BA) 44 (Petrides & Pandya, 1994). BA 44 constitutes the dorso-caudal aspect of Broca's area, a brain region traditionally implicated in language processing. The human observation–execution matching system has been consistently shown to include Broca's area (Rizzolatti, Fogassi, et al., 2001). The

fact that mirror neurons in humans may be located in Broca's area opens the possibility that mirror neurons mediate action understanding not only during observation, but also during linguistic tasks (Théoret & Pascual-Leone, 2002; Rizzolatti & Arbib, 1998).

To directly address this issue, we conducted an fMRI study on 17 healthy, right-handed, native Italian speakers, while they were passively listening to sentences describing actions performed with the mouth (e.g., "Mordo la mela"; English: "I bite an apple"), with the hand (e.g., "Afferro il coltello"; "I grasp a knife"), and the leg (e.g., "Calcio il pallone"; "I kick the ball"). As a control condition, participants listened to sentences with an abstract content (e.g., "Apprezzo la sincerità"; "I appreciate sincerity").

RESULTS

Anatomo-functional Activations

We tested which brain systems are engaged by the processing of action sentences irrespective of body parts involved. The random-effect analysis selectively identified the *pars opercularis* of the left inferior frontal gyrus (Broca's area) as the only brain region conjointly activated by all action-related conditions compared to the baseline (Table 1A, Figure 1).

Next, we identified body-part-specific responses, which we suggest are engaged in forming motor representations of the actions described by the sentences (Figure 1).

Mouth sentences selectively activated the *pars opercularis* extending more rostrally, dorsally, and ventrally around the focus conjointly activated by all body parts, and the *pars triangularis* of the left inferior frontal gyrus (see Table 1B).

Hand sentences selectively activated the hand region in the left precentral gyrus, the left posterior intraparietal sulcus, the left posterior inferior temporal gyrus, the left insula, and the right middle temporal gyrus (see Table 1C).

Leg sentences selectively activated the left dorsal premotor cortex (within the superior frontal sulcus)—more dorsally and rostrally compared to the activation elicited by hand sentences—and the left inferior parietal lobule (see Table 1D).

We had hypothesized that listening to sentences describing actions would activate body-part-specific premotor–parietal circuits. Given the lack of consistent activation in the inferior parietal lobule while listening to action-related sentences (only leg sentences activated the left inferior parietal lobule and only hand sentences activated the left posterior intraparietal sulcus), we explored activations in the inferior parietal region at a lower significance threshold (random effects, $p < .005$ uncorrected). These analyses revealed corresponding activations in the left inferior parietal lobule for mouth

Table 1. Stereotactic Coordinates (x, y, z) for Significant Clusters (Random Effects, $p < .001$, Uncorrected, or $p < .005$, Uncorrected if Marked by an Asterisk) are Given in Millimeters Together with Effect Sizes ($Z = Z$ Scores)

<i>Brain Region</i>	<i>x</i>	<i>y</i>	<i>z</i>	<i>Z</i>
<i>(A) Action-related vs. Abstract (Irrespective of Body Part)</i>				
L IFG (PO)	-52	10	16	4.91
<i>(B) Mouth vs. Abstract (Masked Exclusive for Hand vs. Abstract and Leg vs. Abstract)</i>				
L IFG (PO)	-56	12	12	5.01
	-44	2	24	3.63
L IFG (PT)	-40	30	16	4.20
L IPL	-60	-34	32	3.09*
L MTG	-58	-62	0	3.16*
<i>(C) Hand vs. Abstract (Masked Exclusive for Mouth vs. Abstract and Leg vs. Abstract)</i>				
L precentral gyrus	-30	-2	56	3.81
L insula	-36	0	4	4.35
L IPL	-62	-26	36	3.36*
L anterior IPS	-46	-38	44	3.54*
L posterior IPS	-28	-68	48	3.20
L posterior ITG	-50	-58	-16	4.17
L MTG	-40	-58	4	4.11*
R MTG	40	-62	20	4.19
<i>(D) Leg vs. Abstract (Masked Exclusive for Mouth vs. Abstract and Hand vs. Abstract)</i>				
L SFS	-26	4	64	3.70
L IPL	-64	-32	28	3.89
L anterior IPS	-38	-50	56	3.76*
L posterior IPS	-28	-72	48	3.33*
L MTG	-58	-62	4	3.32*
<i>(E) Abstract vs. Action-related</i>				
R/L posterior CG	2	-56	28	5.26

L = left; R = right; IFG = inferior frontal gyrus; PO = pars opercularis; PT = pars triangularis; SFS = superior frontal sulcus; IPL = inferior parietal lobule; IPS = intraparietal sulcus; MTG = middle temporal gyrus; ITG = inferior temporal gyrus; CG = cingulate gyrus.

and hand sentences, and in the left posterior intraparietal sulcus for leg sentences (but not for mouth sentences). Furthermore, the left anterior intraparietal sulcus was found to be activated by hand and foot sentences (see Table 1B–D and Figure 2).

At this lowered statistical threshold (random effects, $p < .005$ uncorrected), activations for sentences describing actions performed by all three body parts were found in the left posterior middle temporal gyrus (Figure 2).

Finally, the activations associated with abstract sentences, when compared to action-related sentences, were clearly distinct from those subserving the action-related effects. Activations were only found in the posterior cingulate gyrus, bilaterally, a brain region that is not related to action representation (Table 1E).

Behavioral Data Collected after fMRI Data Acquisition

Once the fMRI data acquisition was completed, all participants declared being unaware of the grouping of sentences into different experimental conditions. Immediately after fMRI data acquisition, participants were also asked to recall the highest number of sentences or part of sentences they could remember. On average, they were able to recall 7.33% ($SD = 3.04$) of all the heard sentences (13.20 sentences out of a total of 180 sentences). The percentage of abstract sentences recalled was on average 6.89 ($SD = 5.71$; 4.13 out of 60 sentences), that of mouth sentences 8.17 ($SD = 5.41$; 3.27 out of 40 sentences), that of hand sentences 4.67 ($SD = 3.84$; 1.87 out of 40 sentences), and that of leg sentences 9.83 ($SD = 5.48$; 3.93 out of 40 sentences).

The three action-related conditions as a group did not differ significantly from the abstract condition, with respect to the percentage of sentences recalled [ANOVA, $p = 0.649$, $F(1,15) = 0.215$].

DISCUSSION

The main result of the present study is that, compared to syntactically equivalent sentences with an abstract content, action-related sentences were associated with the activation of a left-hemispheric fronto-parieto-temporal network. We believe that this difference in activation is most likely due to the difference in semantic content between the sentence types.

More specifically, listening to action-related sentences activated a left-lateralized fronto-parieto-temporal system, which has been shown to be activated also by action execution and observation. Our findings are thus consistent with the hypothesis that the activation of this system contributes to the understanding of the action-related content conveyed by sentences.

Within the left fronto-parieto-temporal system activated by action-related sentences, the *pars opercularis* of the left inferior frontal gyrus (Broca's area) plays a crucial role, as it is the only brain region activated independently of body parts. This suggests that during listening to action-related sentences, this portion of Broca's area codes for the actions at an abstract level. This specific

Figure 1. Activations (random effects, $p < .001$, uncorrected) are displayed on the average anatomical T1 image across participants. Action-related effects, irrespective of the different body parts, are shown in white, whereas body-part-specific effects are shown in blue (M = mouth), red (H = hand), and green (L = leg). Somatotopic activations in Broca's area and in the premotor cortex are shown in a magnified view (square box). The axial planes of the body-part-specific premotor activations are indicated by dashed lines crossing the magnified view. Dashed lines link brain activations with the corresponding stereotactic coordinates, with axial, coronal, and sagittal section views, and with histograms indicating BOLD signal change percentage (amplitude of the hemodynamic response curve) for the action-related conditions compared to the abstract condition (A = abstract). Standard errors are indicated by bars and significant effects by asterisks.

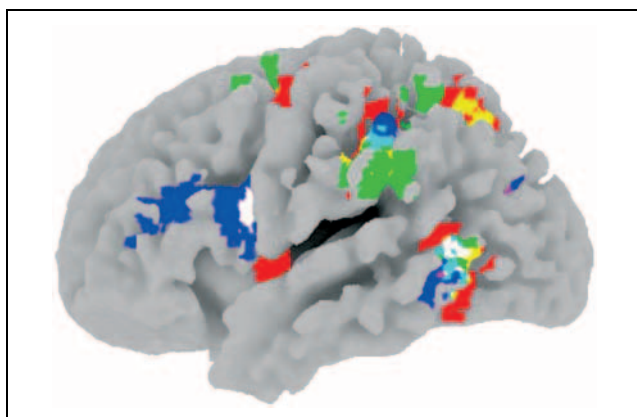
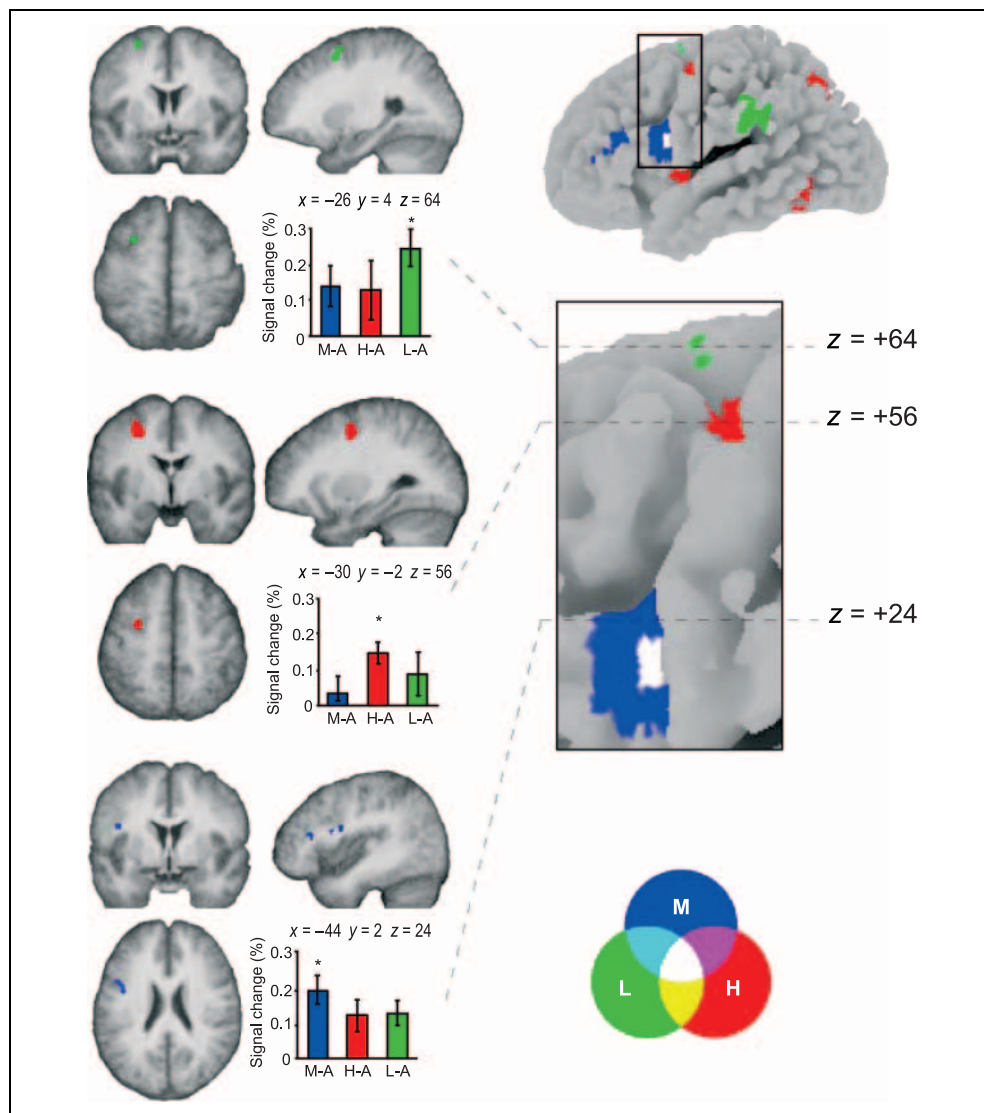


Figure 2. A lateral view of the average anatomical T1 image showing the activations in left inferior parietal and left middle temporal regions found at a lowered statistical threshold, in agreement with the experimental a priori hypothesis ($p < .005$, uncorrected; see Figure 1 for color codes).

coding might be related to the role played by the verb in the sentences. Indeed, the location of the body-part-independent activation is consistent with previous studies showing the involvement of this area in verb processing (Tranel, Adolphs, Damasio, & Damasio, 2001; Pulvermuller, Lutzenberger, & Preissl, 1999; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995). The activation of the *pars opercularis* in the present study may be interpreted as due either to the specific role of verbs as determinants of the syntactic structure of a sentence or to the semantic content of verbs, or both. As to the first interpretation, evidence in favor of a role of Broca's area in syntactic processing at the sentence level has been recently provided by brain imaging and electrophysiological studies (Tettamanti et al., 2002; Moro et al., 2001; Shapiro, Pascual-Leone, Mottaghy, Gangitano, & Caramazza, 2001). As to the second interpretation, evidence has been more elusive. The findings reported here may provide a significant advancement. Given that the syn-

tactic structure of action-related sentences was invariant with respect to that of the abstract sentences, and that the only distinguishing factor between the two types of sentences was their semantic content, we conclude that, in the present experiment, the *pars opercularis* of Broca's area played a role in the access to abstract action representations, rather than in syntactic processing.

Although this explanation accounts well for the conjoint activation of Broca's area by all the three effectors, the additional activation in the *pars opercularis* during the processing of mouth-related sentences and its extension into the *pars triangularis* does not fit a linguistic explanation. It is well known that mouth motor actions are richly represented in the inferior frontal gyrus, and that articulatory deficits follow lesions to this brain area (Tonkonogy & Goodglass, 1981). It is therefore likely that the activation induced specifically by mouth-related sentences codes for the motor representations of mouth actions.

Congruent with this motor account of the mouth-specific opercular activation is the finding of three activation foci in the premotor cortex specifically related to mouth, hand, and leg action-related sentences, respectively. These three activations in the left premotor cortex were somatotopically organized: The mouth activation was more ventral (dorsal-most aspect of the *pars opercularis*), the hand activation was in a medio-dorsal location (hand region in the left precentral gyrus), and the leg activation lay even more dorsally (within the superior frontal sulcus). This somatotopic organization corresponds only in part to the one observed by Buccino, Binkofski, et al. (2001) in volunteers watching video-clips of object-related mouth, hand, and foot movements. Although our results closely correspond to those of Buccino and colleagues with respect to the conjoint activation of Broca's area and with respect to the activations in the premotor cortex for mouth and leg, we found the hand activation to be localized more medio-dorsally within the premotor cortex (present study: $x = -30$; $y = -2$; $z = +56$; Buccino et al.: $x = -56$; $y = -6$; $z = +48$ [after conversion of the Buccino et al.'s coordinates from Talairach to MNI stereotactic space; see www.mrc-cbu.cam.ac.uk/Imaging/ for the transformation algorithms]). This discrepancy could be due to the different tasks used in the two experiments or to anatomic-functional variability in the healthy population. Noteworthy, the stereotactic location of the hand-specific activation found in the present study is consistent with that of other studies that have investigated hand/arm premotor representations (e.g., Krams, Rushworth, Deiber, Frackowiak, & Passingham, 1998; Fink, Frackowiak, Pietrzyk, & Passingham, 1997). Fink and colleagues found activations in the premotor cortex during finger movements at locations very close to that found in the present study during listening to hand-related actions (extensions $x = -28/-37$; $y = -1/-14$; $z = +46/+68$). The

findings of Fink and colleagues are also consistent with the present data, in that leg movements were associated with more dorsally located premotor activations (extensions $x = -26/-39$; $y = -5/-13$; $z = +47/+71$).

In sum, in the frontal lobe there is an activation that appears to be related to the semantic aspects of the presented linguistic material, at an abstract, body-part-independent level. Other activations are clearly related to the motor representation of the action described in the heard sentences. These motor representations are somatotopically organized and partially coincide with those active during action observation.

This bipartition of frontal lobe functions participating in language processing also receives support from a study on silent lip-reading, a task requiring the extraction of articulatory mouth movements by means of an integration of visual, phonological, and motor information (Paulesu et al., 2003). Silent lip-reading was associated with activations covering the dorsal sector of the *pars opercularis* in the left inferior frontal gyrus and the ventral portion of the left precentral gyrus (with stereotactic coordinates closely matching those selectively activated by mouth-related sentences in the present study). These activations were seen whether or not lip movements conveyed lexical-semantic information and were therefore interpreted as being related to motor articulatory representations. Conversely, lip movements conveying lexical information (as opposed to nonlexical lip movements) elicited additional activations covering the *pars triangularis* and a rostral sector of the *pars opercularis* in the left inferior frontal gyrus. These activations were presumably related to lexical-semantic representations.

Increasing evidence shows that the posterior parietal lobe is part of the observation-execution matching system both in monkeys and humans (Gallese, Fogassi, Fadiga, & Rizzolatti, 2002). Our data showed distinct, although partially overlapping activations in the left inferior parietal lobule for sentences describing mouth, hand, and leg actions. Inferior parietal areas have been shown to be engaged by observing actions, only if the actions are performed towards a goal or an object (Buccino, Binkofski, et al., 2001). This is in agreement with the syntactic structure of the sentences used here, in which the objects of the actions were always specified.

In monkeys, the inferior parietal lobule receives its major visual input from the dorsal stream, and in particular, from area MT/V5 (Ungerleider & Haxby, 1994). We found activations in the left posterior middle temporal gyrus for mouth, hand, and leg sentences at $p < .005$, uncorrected. These activations fall within or close to area MT/V5 (Dukelow et al, 2001; Tootell et al, 1995; Watson et al, 1993) and are most likely related to the representation of the movement content of the actions described by sentences. The occipito-temporal cortex, including area MT/V5 and the adjacent region, has previously been found to be bilaterally activated

when subjects named pictures of actions of variable nature (such as “stir” or “paint”) (Damasio et al., 2001). The activation of the MT/V5 region observed in the present experiment, where subjects passively listened to action-related sentences, differed with respect to the previously mentioned study, where the retrieval of action words was investigated, in that here it was lateralized to the left hemisphere. This suggests that the access to action representations per se (i.e., lacking any requirements of word retrieval) is left lateralized. This distinction is indeed supported by a study that investigated the access to action knowledge through pictures and through visually presented verbs. Activations were found, in the former case, bilaterally within or close to area MT/V5, whereas in the latter case, in the left posterior aspect of the middle and superior temporal gyri (Kable, Lease-Spellmeyer, & Chatterjee, 2002).

Listening to hand-related sentences also activated part of the insula. Given the scanty information on the role of this region in motor control, it is difficult to give a satisfactory explanation for this activation. Note however that the posterior insula, defined as the posterior part of dysgranular plus the granular insular sectors, has reciprocal connections with somatosensory and motor areas (Mesulam & Mufson, 1982).

Taken together, our findings are consistent with the hypothesis that understanding sentences conveying an action-related content requires the contribution of sensorimotor circuits, partially overlapping with those active during the execution and observation of the same actions. Our data only allow us to draw conclusions about understanding sentences describing actions belonging to the human motor repertoire, namely, actions that humans can themselves execute. The extent to which the present account can be extended to include the understanding of sentences involving verbs such as “swarm” or “fly” is currently unknown.

An alternative interpretation of the present findings is that the activation of sensorimotor circuits might be due to the fact that participants were simply engaged in motor imagery of the actions described by the sentences. In a narrow sense, motor imagery entails the voluntary evocation, or rehearsal, of a motor task after explicit instructions, and it has been implicated in a variety of behavioral tasks (Grèzes & Decety, 2001). In other words, it is a voluntary task that requires effort (Jeannerod, 1997). Voluntary motor imagery is characterized by the activation of primary motor, premotor, and mesial motor areas (Ehrsson, Geyer, & Naito, 2003; Gerardin et al., 2000; Grafton et al., 1996; Stephan et al., 1995; Tyaszka, Grafton, Chew, Woods, & Colletti, 1994). Subcortical structures, such as the basal ganglia and the cerebellum, have also been found to be activated by voluntary motor imagery tasks (e.g., Decety et al., 1994). The lack of activation of primary motor, mesial motor, and subcortical areas in the present study, along

with the absence of any requirements to voluntarily engage in motor imagery, allows one to exclude the possibility that our results may be ascribed, even in part, to motor imagery, as previously defined. If the participants actually imagined the actions they heard, this would suggest that passively listening to action-related sentences automatically evokes involuntary mental states with an action content (which can be considered to correspond to the S-states proposed by Jeannerod, 2001; on automatic simulation, see also Gallese, 2003). These mental states may be considered an obligatory side effect accompanying action-related sentence processing. The necessary role of these mental states in language understanding should be a matter of further investigation.

In conclusion, our results show that listening to sentences describing actions performed by different effectors activates a left-lateralized fronto-parieto-temporal system that largely overlap with the one activated during action execution and action observation. In this domain, language does not appear to be detached from the evolutionary ancient sensorimotor system, but rather strictly linked to it.

METHODS

Subjects

Seventeen right-handed (Oldfield, 1971) volunteer subjects (12 women and 5 men; mean age 25.3 years, range 19–36 years) of comparable education level participated in the study. They were all native monolingual speakers of Italian. None of the subjects had a history of neurological or psychiatric disorders. Participants gave written consent to participating in the study after receiving an explanation of the procedures. The study was approved by the local Ethics Committee.

Stimuli

Sentences were created by matching a transitive verb in the first-person singular to a syntactically and semantically congruent object complement. Each verb was paired with different objects each time. Subjects heard a total of 40 sentences per experimental condition (mouth, hand, leg), plus 120 baseline (abstract) sentences.¹ Verb frequency was balanced across conditions, on the basis of the available frequency norms of Italian (De Mauro, 1997; De Mauro, Mancini, Vedovelli, & Voghera, 1993). The final choice of stimuli was based on a norm for comprehensibility on 20 normal adults. Sentences were digitally recorded by a native speaker of Italian and edited using D-Sound Pro (www.d-soundpro.com). Average stimulus length was ~2.5 sec. Subjects heard all auditory stimuli via MRI-compatible headphones connected to a personal computer.

Data Acquisition and Experimental Design

We used a 1.5-T whole-body scanner (General Electric Medical Systems, Milwaukee, WI) equipped with a standard quadrature head coil. Functional whole-brain imaging was conducted using a T2*-weighted gradient-echo, echo-planar pulse sequence (TR = 4000 msec, TE = 60 msec). Thirty contiguous slices, parallel to the AC–PC line and covering the whole brain, except in a few cases in which the inferior portion of the cerebellum was not included, were acquired with a field-of-view of 280 × 280 mm, a slice thickness of 4 mm, and an in-plane resolution of 4.38 × 4.38 mm. A series of 125 sequential volumes were acquired for each scanning sequence.

Scanning sequences consisted of 24 epochs. Epochs of sentences referring to a single body part alternated regularly with epochs of abstract sentences (e.g., [mouth–abstract–hand–abstract–leg–abstract]_{*n*=4}). Each subject underwent two such scanning sequences. The presentation order of the experimental conditions was balanced across subjects. Each epoch lasted for 20 sec and consisted of 5 stimuli. Stimuli were presented at a frequency of one stimulus every 4 sec. The presentation of each sentence was followed by a varying period of silence, such that the duration of sentence presentation and the subsequent silence period together lasted for 4 sec.

Data Analysis

Data processing and statistical analysis were performed with SPM99 (www.fil.ion.ucl.ac.uk). The entire volume set for each subject was realigned to the first volume of the first sequence. The brain images obtained were then normalized to the Montreal Neurological Institute (MNI) standard space to allow for group analysis. Prior to statistical analysis, all images were smoothed using an isotropic gaussian kernel (full width at half maximum = 8 mm). High-pass filtering was used to remove artifactual contribution to the BOLD signal. Global differences in fMRI signal were compensated using proportional scaling. Data were then fitted at every voxel using a linear combination of the effects of interest calculated on least-square values. Each condition involving actions by an effector (mouth, hand, or leg) was compared by paired Student's *t* test with the associated control condition at the single-subject level, yielding for each subject one image consisting of the voxelwise difference between the parameter estimates (Friston et al., 1995). Single-subject statistics were also computed for the main effect (i.e., [(mouth + hand + leg) – abstract]), and as a control, for the baseline effect (i.e., [abstract – (mouth + hand + leg)]).

All reported cluster-level statistics were then computed as second-level random-effects group analyses, using a one-sample Student's *t* test model ($n = 17$). The results of random-effects group analyses can be generalized at the population level (Frison & Pocock, 1992).

First, we reasoned that those brain regions that were significantly more activated in the action-related conditions compared to the abstract condition (irrespective of the different body parts, i.e., mouth, hand, foot), were engaged in processing the action-related content of the sentences at an abstract level, that is, at a separate level than transcoding the actions heard into a correspondent body-part-specific motor plan. In order to identify such body-part-independent areas, a second-level one-sample Student's *t* model was used, in which the main effect (i.e., [(mouth + hand + leg) – abstract]) was inclusively masked by the three body-part-specific simple main effects ([mouth – abstract]; [hand – abstract]; [leg – abstract]). This is a conservative analysis for nonorthogonal contrasts, which allows the identification of voxels that are conjointly activated by all body-part conditions, at the specified statistical threshold.

Second, we reasoned that those brain regions that were specifically activated by only one of the three body-part conditions, and not by the other two, were presumably engaged in transcoding the action-related content of the sentences heard into a correspondent body-part-specific motor plan. In other words, these regions should be engaged in information processing at a motor level. In order to identify such body-part-specific effects, a second-level one-sample Student's *t* model was used, in which the simple main effect of interest (e.g., [mouth – abstract]) was exclusively masked by the other two simple main effects (in the present example, [hand – abstract] and [leg – abstract]). This type of analysis allows one to exclude that the brain regions significantly activated by one particular body part are also activated by the other two body parts.

All the reported activations for these two types of analysis survived an uncorrected cluster-level ($k > 30$) significance threshold of $p < .001$ (except where noted, where the significance threshold was lowered to $p < .005$, uncorrected due to a neuroanatomically constrained a priori hypothesis). The use of an uncorrected significance threshold was motivated by the use of random-effect analyses, which tend to be conservative, and by the neuroanatomically constrained a priori hypotheses (activation of the execution/observation matching system).

For anatomical localization and visualization of brain activations, an average 3-D anatomical T1 weighted brain image of the 17 participants ($0.98 \times 0.98 \times 1.5$ mm resolution), priorly normalized to the MNI standard space with SPM99, was automatically segmented with SureFit 4.38 software (Van Essen et al., 2001), after resampling to a $1.0 \times 1.0 \times 1.0$ mm resolution, to obtain a cortical surface 3-D reconstruction with tissue-specific image values for the sulcal versus gyral cortex. Cortical reconstructions were further processed with Caret 4.6 software (Van Essen et al., 2001). Caret 4.6 was also used to map brain activations obtained with SPM99 onto cortical surface maps.

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The data reported in this experiment have been deposited in the fMRI Data Center (<http://www.fmridc.org>). The accession number is 2-2004-117A4.

Note

1. The complete list of sentences can be obtained by e-mail from M. T. (tettamanti.marco@hsr.it).

REFERENCES

- Blakemore, S. J., & Decety, J. (2001). From the perception of action to the understanding of intention. *Nature Reviews: Neuroscience*, *2*, 561–567.
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R. J., Zilles, K., Rizzolatti, G., & Freund, H.-J. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience*, *13*, 400–404.
- Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., Porro, C. A., & Rizzolatti, G. (2004). Neural circuits involved in the recognition of actions performed by nonconspecifics: An FMRI study. *Journal of Cognitive Neuroscience*, *16*, 114–126.
- Cochin, S., Barthelemy, C., Roux, S., & Martineau, J. (1999). Observation and execution of movement: Similarities demonstrated by quantified electroencephalography. *European Journal of Neuroscience*, *11*, 1839–1842.
- Damasio, H., Grabowski, T. J., Tranel, D., Ponto, L. L., Hichwa, R. D., & Damasio, A. R. (2001). Neural correlates of naming actions and of naming spatial relations. *Neuroimage*, *13*, 1053–1064.
- Decety, J., Perani, D., Jeannerod, M., Bettinardi, V., Tadary, B., Woods, R., Mazziotta, J. C., & Fazio, F. (1994). Mapping motor representations with positron emission tomography. *Nature*, *371*, 600–602.
- De Mauro, T. (1997). *Guida all' uso delle parole*. Roma: Editori Riuniti.
- De Mauro, T., Mancini, F., Vedovelli, M., & Voghera, M. (1993). *Lessico di frequenza dell' italiano parlato*. Roma: Etaslibri.
- Dukelow, S. P., DeSouza, J. F., Culham, J. C., van den Berg, A. V., Menon, R. S., & Vilis, T. (2001). Distinguishing subregions of the human MT+ complex using visual fields and pursuit eye movements. *Journal of Neurophysiology*, *86*, 1991–2000.
- Ehrsson, H. H., Geyer, S., & Naito, E. (2003). Imagery of voluntary movement of fingers, toes, and tongue activates corresponding body-part-specific motor representations. *Journal of Neurophysiology*, *90*, 3304–3316.
- Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology*, *73*, 2608–2611.
- Fink, G. R., Frackowiak, R. S., Pietrzyk, U., & Passingham, R. E. (1997). Multiple nonprimary motor areas in the human cortex. *Journal of Neurophysiology*, *77*, 2164–2174.
- Flanagan, J. R., & Johansson, R. S. (2003). Action plans used in action observation. *Nature*, *424*, 769–771.
- Fodor, J. (2001). *The mind doesn't work that way*. Cambridge: MIT Press.
- Frison, L., & Pocock, S. J. (1992). Repeated measures in clinical trials: Analysis using mean summary statistics and its implications for design. *Statistics in Medicine*, *11*, 1685–1704.
- Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J. B., Frith, C. D., & Frackowiak, R. S. J. (1995). Statistical parametric maps: Confidence intervals on p-values. *Human Brain Mapping*, *2*, 189–210.
- Gallese, V. (2003). The manifold nature of interpersonal relations: The quest for a common mechanism. *Philosophical Transactions of the Royal Society of London. Series B*, *358*, 517–528.
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*, 593–609.
- Gallese, V., Fogassi, L., Fadiga, L., & Rizzolatti, G. (2002). Action representation and the inferior parietal lobule. In W. Prinz & B. Hommel (Eds.), *Common mechanisms in perception and action: Vol. 19: Attention and performance* (pp. 334–355). Oxford, UK: Oxford University Press.
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences*, *12*, 493–501.
- Gangitano, M., Mottaghy, F. M., & Pascual-Leone, A. (2001). Phase-specific modulation of cortical motor output during movement observation. *NeuroReport*, *12*, 1489–1492.
- Gerardin, E., Sirigu, A., Lehericy, S., Poline, J. B., Gaymard, B., Marsault, C., Agid, Y., & Le Bihan, D. (2000). Partially overlapping neural networks for real and imagined hand movements. *Cerebral Cortex*, *10*, 1093–1104.
- Grafton, S. T., Arbib, M. A., Fadiga, L., & Rizzolatti, G. (1996). Localization of grasp representations in humans by positron emission tomography: 2. Observation compared with imagination. *Experimental Brain Research*, *112*, 103–111.
- Grèzes, J., Costes, N., & Decety, J. (1998). Top-down effect of strategy on the perception of human biological motion: A PET investigation. *Cognitive Neuropsychology*, *15*, 553–582.
- Grèzes, J., & Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. *Human Brain Mapping*, *12*, 1–19.
- Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., & Rizzolatti, G. (1998). Activation of human primary motor cortex during action observation: A neuromagnetic study. *Proceedings of the National Academy of Sciences, U.S.A.*, *95*, 15061–15065.
- Hauk, O., Johnsrude, I., & Pulvermuller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, *41*, 301–307.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, *286*, 2526–2528.
- Jeannerod, M. (1997). *The cognitive neuroscience of action*. Oxford, UK: Blackwell.
- Jeannerod, M. (2001). Neural simulation of action: A unifying mechanism for motor cognition. *Neuroimage*, *14*, S103–S109.
- Kable, J. W., Lease-Spellmeyer, J., & Chatterjee, A. (2002).

- Neural substrates of action event knowledge. *Journal of Cognitive Neuroscience*, *14*, 795–805.
- Kohler, E., Keysers, C., Umiltà, M. A., Fogassi, L., Gallese, V., & Rizzolatti, G. (2002). Hearing sounds, understanding actions: Action representation in mirror neurons. *Science*, *297*, 846–848.
- Krams, M., Rushworth, M. F., Deiber, M. P., Frackowiak, R. S., & Passingham, R. E. (1998). The preparation, execution and suppression of copied movements in the human brain. *Experimental Brain Research*, *120*, 386–398.
- Lakoff, G., & Johnson, M. (1999). *Philosophy in the flesh*. New York: Basic Books.
- Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L., & Ungerleider, L. G. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science*, *270*, 102–105.
- Mesulam, M. M., & Mufson, E. J. (1982). Insula of the old world monkey: III. Efferent cortical output and comments on function. *Journal of Comparative Neurology*, *212*, 38–52.
- Moro, A., Tettamanti, M., Perani, D., Donati, C., Cappa, S. F., & Fazio, F. (2001). Syntax and the brain: Disentangling grammar by selective anomalies. *Neuroimage*, *13*, 110–118.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97–113.
- Paulesu, E., Perani, D., Blasi, V., Silani, G., Borghese, N. A., De_Giovanni, U., Sensolo, S., & Fazio, F. (2003). A functional-anatomical model for lipreading. *Journal of Neurophysiology*, *90*, 2005–2013.
- Petrides, M., & Pandya, D. N. (1994). Comparative architectonic analysis of the human and the macaque frontal cortex. In F. Boller & J. Grafman (Eds.), *Handbook of neuropsychology* (Vol. 9, pp. 17–58). Amsterdam: Elsevier.
- Pulvermueller, F. (2002). *The neuroscience of language*. Cambridge: Cambridge University Press.
- Pulvermuller, F., Lutzenberger, W., & Preissl, H. (1999). Nouns and verbs in the intact brain: Evidence from event-related potentials and high-frequency cortical responses. *Cerebral Cortex*, *9*, 497–506.
- Pylyshyn, Z. W. (1984). *Computation and cognition: Toward a foundation for cognitive science*. Cambridge: MIT Press.
- Rizzolatti, G., & Arbib, M. A. (1998). Language within our grasp. *Trends in Neurosciences*, *21*, 188–194.
- Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Brain Research, Cognitive Brain Research*, *3*, 131–141.
- Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Paulesu, E., Perani, D., & Fazio, F. (1996b). Localization of grasp representations in humans by PET: 1. Observation versus execution. *Experimental Brain Research*, *111*, 246–252.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews: Neuroscience*, *2*, 661–670.
- Shapiro, K. A., Pascual-Leone, A., Mottaghy, F. M., Gangitano, M., & Caramazza, A. (2001). Grammatical distinctions in the left frontal cortex. *Journal of Cognitive Neuroscience*, *13*, 713–720.
- Stephan, K. M., Fink, G. R., Passingham, R. E., Silbersweig, D., Ceballos-Baumann, A. O., Frith, C. D., & Frackowiak, R. S. (1995). Functional anatomy of the mental representation of upper extremity movements in healthy subjects. *Journal of Neurophysiology*, *73*, 373–386.
- Tettamanti, M., Alkadhi, H., Moro, A., Perani, D., Kollias, S., & Weniger, D. (2002). Neural correlates for the acquisition of natural language syntax. *Neuroimage*, *17*, 700–709.
- Théoret, H., & Pascual-Leone, A. (2002). Language acquisition: Do as you hear. *Current Biology*, *12*, R736–R737.
- Tonkonogy, J., & Goodglass, H. (1981). Language function, foot of the third frontal gyrus, and Rolandic operculum. *Archives of Neurology*, *38*, 486–490.
- Tootell, R. B., Reppas, J. B., Dale, A. M., Look, R. B., Sereno, M. I., Malach, R., Brady, T. J., & Rosen, B. R. (1995). Visual motion aftereffect in human cortical area MT revealed by functional magnetic resonance imaging. *Nature*, *375*, 139–141.
- Tranel, D., Adolphs, R., Damasio, H., & Damasio, A. R. (2001). A neural basis for the retrieval of words for actions. *Cognitive Neuropsychology*, *18*, 655–670.
- Tyszka, J. M., Grafton, S. T., Chew, W., Woods, R. P., & Colletti, P. M. (1994). Parceling of mesial frontal motor areas during ideation and movement using functional magnetic resonance imaging at 1.5 tesla. *Annals of Neurology*, *35*, 746–749.
- Ungerleider, L. G., & Haxby, J. V. (1994). What and where in the human brain. *Current Opinion in Neurobiology*, *4*, 157–165.
- Van Essen, D. C., Dickson, J., Harwell, J., Hanlon, D., Anderson, C. H., & Drury, H. A. (2001). An integrated software system for surface-based analyses of cerebral cortex. *Journal of American Medical Informatics Association*, *8*, 443–459.
- Watson, J. D., Myers, R., Frackowiak, R. S., Hajnal, J. V., Woods, R. P., Mazziotta, J. C., Shipp, S., & Zeki, S. (1993). Area V5 of the human brain: Evidence from a combined study using positron emission tomography and magnetic resonance imaging. *Cerebral Cortex*, *3*, 79–94.