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Research Report

Listening to action-related sentences modulates the activity of the motor system: A combined TMS and behavioral study

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Abstract

Transcranial magnetic stimulation (TMS) and a behavioral paradigm were used to assess whether listening to action-related sentences modulates the activity of the motor system. By means of single-pulse TMS, either the hand or the foot/leg motor area in the left hemisphere was stimulated in distinct experimental sessions, while participants were listening to sentences expressing hand and foot actions. Listening to abstract content sentences served as a control. Motor evoked potentials (MEPs) were recorded from hand and foot muscles. Results showed that MEPs recorded from hand muscles were specifically modulated by listening to hand-action-related sentences, as were MEPs recorded from foot muscles by listening to foot-action-related sentences. This modulation consisted of an amplitude decrease of the recorded MEPs. In the behavioral task, participants had to respond with the hand or the foot while listening to actions expressing hand and foot actions, as compared to abstract sentences. Coherently with the results obtained with TMS, when the response was given with the hand, reaction times were slower during listening to hand-action-related sentences, while when the response was given with the foot, reaction times were slower during listening to foot-action-related sentences. The present data show that processing verbally presented actions activates different sectors of the motor system, depending on the effector used in the listened-to action.

Theme: Motor systems
Topic: Language

Keywords: Motor evoked potential; Transcranial magnetic stimulation; Action-related sentence; Mirror neuron system

1. Introduction

We can understand actions done by others both when we observe these actions while being done and when we hear about them verbally. There is increasing evidence that there is a neural system formed by a particular set of premotor neurons, called “mirror neurons”, that plays a role in action understanding [6,23,41,45].

Mirror neurons were originally discovered in the monkey ventral premotor cortex (area F5). Their characterizing property is that they discharge both when the monkey performs specific goal-directed hand or mouth actions (i.e., grasping, tearing, holding, biting, sucking) and when it observes another individual performing the same or a similar action [17,21,43]. Mirror neurons were also described in the inferior parietal lobule [22], thus constituting a parieto-premotor circuit (mirror neuron system) for action understanding. Recently, it has been shown that many F5 mirror neurons, besides having visual properties, also have acoustic properties. These “audio-visual mirror neurons” discharge not only when the action is executed or observed, but also when its sound is heard [32].

A mirror neuron system similar to that described in the monkey has been also found in humans. Experimental evidence in this sense comes from neurophysiological, behavioral, and brain imaging studies. Using single-pulse transcranial magnetic stimulation (TMS), it was demon-

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strated that, during the observation of hand and arm movements, there is an increase of motor evoked potentials (MEPs) recorded from hand muscles involved in the actual execution of the observed movements [14,46]. A recent TMS study further showed that, during the observation of hand actions, there is a temporal modulation of the MEPs recorded from the hand muscles of the observer, which follows the temporal progress of the observed action [24]. Taken together, these results strongly suggest that the mirror neuron system matches the observed action with its motor representation in the observer, both in terms of the muscles involved and the temporal progress of the action.

The involvement of the mirror neuron system during action observation was also demonstrated using magneto-encephalography (MEG). With this technique, a suppression of the 15- to 25-Hz activity during both the execution and observation of goal-directed hand actions was found [29]. Similar results were obtained in a quantified electroencephalography study, showing a block of "mu" activity in the same conditions [9]. More recently, it was shown by means of chronically implanted subdural electrodes, a decrease of alpha band absolute power over the primary motor cortex and Broca's region during the execution and observation of finger movements [50].

Behavioral studies also demonstrated that action observation may modulate the activity of the motor system [4,11,51]. Brass et al. [4], using a reaction time (RTs) paradigm, compared the efficiency of symbolic cues with direct observation of finger movements done by another person in triggering finger movements. The results showed that participants were faster in lifting their fingers when the relevant cue for their response was the observation of the same finger movement, as compared to the symbolic cue. Similar results were obtained by Craighero et al. [11] in a study in which participants were required to prepare to grasp a differently oriented bar, after presentation of a picture showing the right hand. Participants were faster when the orientation of the observed hand corresponded to that achieved by the participants' hand at the end of the action.

These studies do not provide, of course, information on the localization of the mirror neuron system. Brain imaging experiments addressed this issue. These studies showed that during the observation of hand/arm actions, there was signal increase in the ventral premotor cortex and the adjacent posterior part of the inferior frontal gyrus (IFG), and in the inferior parietal lobule [13,26–28,44]. Thus, similarly to monkeys, in humans, the mirror neuron system also appears to be localized in the ventral premotor cortex and in the inferior parietal lobule. Furthermore, in a functional magnetic resonance (fMRI) study, it was shown that during the observation of hand, mouth, and foot actions, there is a selective activation of different sectors of the premotor cortex, the adjacent IFG, and of the inferior parietal lobule, depending on the effector involved in the observed action [5]. These results not only extend the domain of the mirror neuron system to effectors other than the hand, like the mouth and the foot, but also show that this system is somatotopically organized.

As mentioned above, the main functional role of the mirror neuron system appears to be that of understanding actions done by others. This appears to be true also when the observed action is done by non-conspecifics (monkey, dog), provided that the observed action belongs to the motor repertoire of the observer [7]. In humans, the mirror neuron system appears to be also involved in the imitation of hand and mouth actions present in the observer's motor repertoire [31,34,35,48]. Recent evidence showed that the mirror neuron system is also involved in imitation learning of novel complex actions [8].

Given the homology between the monkey's premotor area F5 and Broca's region [37,52], it has been suggested that the mirror neuron system represents the neural substrate from which human language evolved [1,10,40,42]. It is an open question, however, whether, in modern humans, this system plays a role in understanding the meaning of sentences.

The meaning of a sentence, regardless of its content, is classically considered to be understood by relying on symbolic, amodal mental representations [18,39]. An alternative hypothesis assumes that the understanding of language relies on "embodiment" [3,16,20,25,33,38]. Thus, for action-related sentences, the neural structures presiding over action execution should also play a role in understanding the semantic content of the actions verbally described.

A prediction of the embodiment theory of language understanding is that when individuals listen to action-related sentences, their mirror neuron system is modulated. The aim of the present study was to test this hypothesis. Two experiments were carried out: in Experiment 1, we recorded, in two distinct sessions, motor evoked potentials (MEPs) from hand and foot muscles, respectively, while participants were listening to hand-action-related sentences, foot-action-related sentences, and abstract content sentences; in Experiment 2, a similar task was used in a go/no-go paradigm. The results clearly show the involvement of the motor system in the processing of action-related sentences.

2. Methods

2.1. Experiment 1: TMS study

The aim of this study was to assess whether listening to action-related sentences modulates the activity of the primary motor cortex, as revealed by MEPs recorded from hand muscles when stimulating the hand motor area, and from foot/leg muscles when stimulating the foot motor area. In order to verify not only a possible modulation of MEPs, but also its specificity, related to the effector involved in the listened action, we presented sentences describing hand and foot actions. Abstract content sentences served as a control.

2.1.1. Participants

Eight normal, right-handed male volunteers entered the study. They all were native Italian speakers. Right-handedness was tested by means of the Edinburgh Inventory [36]. They all gave their informed consent to the experimental procedures, which were preventively approved by the local Ethic Committee.

2.1.2. Materials and procedure

The experiment took place in a soundproofed room and consisted of two experimental sessions. All participants underwent the two experimental sessions, which took place in different days. During the experimental sessions, participants were seated on a comfortable armchair, with their elbow flexed at 90° and their hands prone in a relaxed position. The head of the participants lay on a headrest in order to maintain a comfortable and stable position. In each experimental session, either the hand motor area or the foot/leg motor area in the left hemisphere was stimulated by means of single-pulse TMS (ESAOTE, Biomedica, Italy). Magnetic stimuli were delivered through an eight-shaped coil placed on the skull with the handle positioned in a medio-lateral orientation. MEPs were recorded from the right *opponens pollicis* and first dorsal *interosseus* muscles, when the hand motor area was stimulated, and from the *tibialis anterior* and *gastrocnemius* muscles when the foot motor area was stimulated. Before each experimental session, either the hand or the foot motor area was searched for by applying magnetic stimuli on fixed positions of a grid, with a resolution of 1 cm, drawn on a bathing cap worn by participants. The coordinate origin was located at the Cz reference point determined according to the international 10–20 EEG system. The cortical hand motor area and the cortical foot motor area were searched for by moving the center of the coil by 1-cm steps, according to the grid. Stimulus intensity was adjusted in order to determine the motor threshold for the recorded muscles (the right *opponens pollicis* and first dorsal *interosseus*, when the hand motor area was stimulated; the *tibialis anterior* and *gastrocnemius*, when the foot/leg motor area was stimulated). During each experimental session, stimulus intensity of 120% of the measured motor threshold was used.

In each experimental session, participants were asked to attentively listen to different acoustic stimuli consisting of hand-action-related sentences and foot-action-related sentences. They were also asked to attentively listen to abstract content sentences, as control. During both experimental sessions, they listened to the same sentences. What changed were the motor area being stimulated (hand *motor area* or foot/leg motor area) and the corresponding recorded muscles. The order of experimental sessions (hand motor area or foot/leg motor area *stimulation*) was counterbalanced across participants. Acoustic stimuli were delivered through a loudspeaker connected to a computer at fixed intensity (80 dB). All sentences were in Italian. All action-related sentences expressed a concrete action on an appropriate object (e.g., “cuciva la gonna”, English translation: “he sewed the skirt”). All abstract content sentences expressed an abstract action on an appropriate object (e.g., “amava la patria”, English translation: “he loved his land”). All verbs were formed by three syllables and were conjugated in the third person of the past tense. To build up this tense in the third person, a suffix is added (-va) to the verbal stem. Fifteen hand-action-related and 15 foot-action-related sentences were presented. As control stimuli, 15 sentences with verbs expressing an abstract content were delivered. The frequency of use of the presented verbs was maintained similar in the three types of sentences, based on the available frequency of use norms for the Italian language [12].

Sentences were presented in blocks, each containing one type of sentences (foot, hand, or abstract-content-related sentences). The order of the blocks was counterbalanced across participants. All sentences acoustically presented in the TMS study are reported in Table 1. During acoustic stimuli presentation, single-pulse TMS delivery was automatically triggered by a computer in coincidence with the end of the second syllable of the verb (e.g., “cuci’-va la gonna”), between the verbal stem and the suffix. We chose this stimulus delivery time to be sure that participants were aware of the content of the verb. Stimulus delivery occurred on average 500–700 ms after the beginning of the sentence, according to the length of the verb. For each sentence, only one TMS stimulus was delivered. Since each block consisted of 15 sentences, as a whole, 45 TMS stimuli were delivered in each experimental session. The interval between two consecutive sentences was 2 s. MEPs recorded during listening to all the three types of sentences were band-pass filtered (20–1000 Hz), digitized (sampling frequency 2000 Hz), and stored on a computer. After rectification, the area underlying MEPs was calculated for each trial and was used for successive statistical analysis. The pre-TMS electromyographic activity, recorded from 100 ms before TMS, was also acquired in all trials. The analysis of pre-TMS rectified data showed no difference among conditions.

2.1.3. Data analysis

MEP areas of all subjects were normalized (z scores) separately for the two sessions (hand motor area or foot/leg motor area stimulation). These data entered into two separate analyses of variance (ANOVAs), concerning hand and foot MEPs, respectively, with “sentence” (hand-, foot-, and abstract-related sentences) and “muscles” (*opponens pollicis* and first dorsal *interosseus* for hand, *tibialis anterior* and *gastrocnemius* for foot/leg) as within-participants factors. Besides these ANOVAs, pairwise comparisons with the Newman–Keuls method were conducted whenever appropriate. The significance level was always set at 0.05.

2.2. Experiment 2: behavioral study

Because in the TMS study participants were not explicitly required to semantically process the listened sentences, we

Table 1

Hand-action-related sentences	Foot-action-related sentences	Abstract content sentences
1. Cuciva la gonna (English = he sewed the skirt)	1. Marciava sul posto (×2) (English = he marched on the place)	1. Amava la moglie (English = he loved his wife)
2. Girava la chiave (English = he turned the key)	2. Calciava la palla (×2) (English = he kicked the ball)	2. Amava la patria (English = he loved his country)
3. Lavava i vetri (English = he washed the glasses)	3. Calciava la porta (×2) (English = he kicked the door)	3. Gradiva la mela (English = he liked the apple)
4. Prendeva la tazza (English = he took the cup)	4. Calciava la sedia (English = he kicked the chair)	4. Odiava il mare (×2) (English = he hated the sea)
5. Scriveva il tema (English = he wrote the essay)	5. Pestava l'erba (×3) (English = he trod on the grass)	5. Godeva la vista (×2) (English = he enjoyed the sight)
6. Sfilava il filo (English = he paraded the thread)	6. Pestava le foglie (English = he trod on the leaves)	6. Pativa il caldo (English = he suffered from the heat)
7. Sfogliava il libro (English = he turned over *the pages* of the book)	7. Saltava la corda (English = he jumped the rope)	7. Soffriva il freddo (English = he suffered from the cold)
8. Spalmava la crema (English = he spread the cream)	8. Saltava il fosso (English = he jumped the ditch)	8. Serbava l'odio (English = he kept the hate)
9. Spezzava il pane (English = he broke the bread)	9. Saltava il muro (English = he jumped the wall)	9. Scordava il nome (English = he forgot the name)
10. Stringeva la mano (English = he shook the hand)	10. Pestava la coda (English = he trod on the tail)	10. Scordava la data (English = he forgot the date)
11. Suonava il piano (English = he played the piano)		11. Temeva il buio (English = he feared the dark)
12. Svitava il tappo (English = he unscrewed the stopper)		12. Temeva la pena (English = he feared the penalty)
13. Tagliava la carne (English = he cut the meat)		13. Vinceva la gara (English = he won the competition)
14. Tagliava la stoffa (English = he cut the cloth)		
15. Timbrava la busta (English = he stamped the envelope)		

Hand- and foot-action-related sentences and abstract-content-related sentences used in the TMS study. Some foot-action-related sentences and abstract-content-related sentences were presented more than once during the experimental sessions. For these sentences, the number of times they were repeated is given in parentheses, before their English translation.

ran a second experiment, using a Go/No-Go behavioral paradigm (reaction time, RT), during which participants were explicitly required to semantically code the listened to sentences in order to discriminate between action-related sentences and abstract content sentences.

2.2.1. Participants

Twenty volunteers (ten males and ten females, 19–28 years of age) participated in the experiment. They were all right-handed according to the Edinburgh Inventory [36], had normal or corrected-to-normal vision, and were not aware of the purpose of the experiment. None of them had taken part into the first experiment.

2.2.2. Materials and procedure

The experiment was carried out in a sound-attenuated room, dimly illuminated by a halogen lamp directed towards the ceiling. During the experimental session, the participant sat comfortably in front of a computer screen at a distance of about 50 cm from it. Participants were randomly divided into two groups. The first one (10 participants, 5 males and 5 females) used the right hand as effector for the response, whereas the second one (5 males and 5 females) used the right foot as effector for the response.

As in Experiment 1, participants listened to different types of sentences: hand-action-related sentences, foot-action-related sentences, and abstract-content-related sentences. Twenty sentences of each type were presented. Some sentences were the same used in Experiment 1, some others were new, but with the same syntactic structure. Each sentence was presented twice during the experiment. In addition, thirty catch trials (see below) were presented. Thus, on the whole, the experiment consisted of 150 trials, run in a single session. Participants were asked to make a judgment on sentence content. They were instructed to carefully listen to all sentences and give a motor response (either with the hand, for the first group, or with the foot for the second group) when the listened sentence expressed a concrete action (hand- and foot-action-related sentences), and refrain from responding when the sentence expressed an abstract content. Sentences, as in Experiment 1, were delivered by means of two loudspeakers, both located at the same distance from participants' ears (about 50 cm) and driven by a PC. Differently from Experiment 1, sentences (hand-action-related sentences, foot-action-related sentences, and abstract content ones) were randomly presented.

Trials began with the appearance of a white circle in the center of the computer screen. Soon after, a sentence was acoustically presented. The circle changed its color from white to green in coincidence with the end of the second syllable of the verb (e.g., cu-ci'va la gonna). This occurred on average 500–700 ms after the beginning of the sentence, according to the length of the verb. The color change was the "go" signal for the response, when the sentence contained a verb expressing a hand-related action or a foot-related action. In a small percentage of trials (20%), the circle changed its color in coincidence with the second syllable of the object noun or at the end of the sentence (catch trials). This manipulation was introduced to avoid response habituation. Catch trials were excluded from data analysis.

The key used by the participants who had to respond with the hand was a round-shaped knob (6 mm diameter), glued on a plastic box positioned on the right side of the same table on which the computer screen was located. During the experiment, participants' right hand was positioned over the knob and, when required, the response was given by pressing it with the right index finger.

The key used by the participants who had to respond with the foot was a quadrangle-shaped pedal (6 cm side), partially inserted in a wood footboard. During the experiment, participants' foot rested on the wood footboard. Participants pressed the pedal with their foot, when required.

Trials in which RTs were faster than 130 ms (anticipations) or slower than 1000 ms (missing responses) were considered errors and discarded. The allowed number of errors (anticipations, missing responses, or wrong semantics coding) was 10% of all trials, but no participant exceeded it.

2.2.3. Data analysis

For each participant, median values were calculated for correct RTs in relation to each type of sentences. These values were submitted to analysis of variance (ANOVA) with "sentence" (hand or foot action) as within-subject variable, and "effector" (hand or foot) as between-subject variable.

3. Results

3.1. TMS study

The ANOVA carried out on MEPs recorded from first dorsal *interosseus* and *opponens pollicis* after single-pulse TMS of the hand motor region showed that only the main effect of "sentence" was significant, $F(2,14) = 5.85$, $P < 0.02$, demonstrating that MEP amplitude decreased specifically during listening to hand-action-related sentences with respect to the other two types of sentences. The Mauchley's test showed that the sphericity assumption was not violated ($P > 0.05$). No significant difference was found comparing MEPs related to foot-action-related sentences and abstract-content-related sentences. The data are shown in Fig. 1.

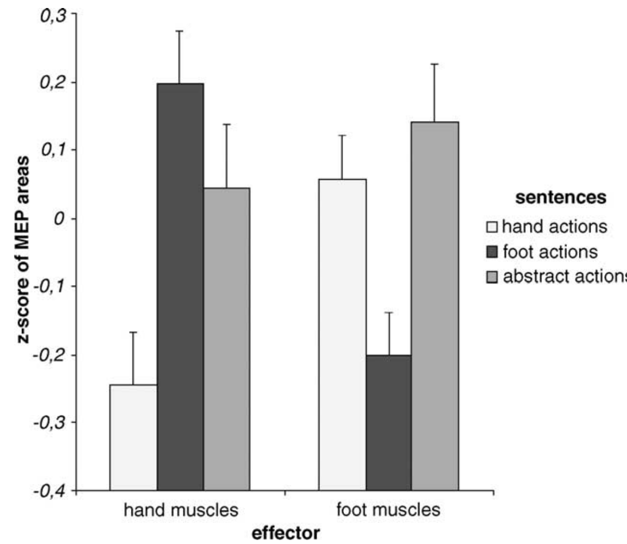

Fig. 1. Mean value (plus SE) of MEP total areas, after intra-subject normalization, recorded from both hand (opponens pollicis and first dorsal interosseus) and foot (tibialis anterior and gastrocnemius) muscles during listening to each type of sentences (hand- and foot-action-related sentences and abstract content sentences).

The ANOVA carried out on MEPs recorded from *tibialis anterior* and *gastrocnemius* after single-pulse TMS of the foot motor area showed that the main effect of "sentence", $F(2,14) = 4.96$, $P < 0.03$, and the sentence–muscle interaction, $F(2,14) = 4.28$, $P < 0.04$, were both significant. As in the case of hand muscles, MEP amplitude decreased specifically when participants listened to sentences expressing actions performed by foot, and no significant difference was found between MEPs recorded when participants were listening to the two other types of sentences. The interaction was due to the fact that only the *tibialis anterior* muscle showed a significant modulation during listening to foot-action-related sentences. No effect was present for the *gastrocnemius* muscle. It is worth noting that the *tibialis anterior* is the muscle recruited when the actions expressed by the listened foot-action-related sentences are actually performed. The Mauchley's test showed that the sphericity assumption was never violated ($P > 0.05$).

Examples of MEPs recorded from the opponens pollicis and the tibialis anterior of one representative participant, during listening to the three types of sentences, are shown in Fig. 2.

3.2. Behavioral study

Only the interaction between "sentence" and "effector" was significant, $F(1,18) = 9.60$, $P < 0.007$. The data are shown in Fig. 3. In the group of participants responding with the hand, RTs were slower when the listened action expressed a hand action as compared to those expressing a foot action (320 vs. 302 ms). In contrast, in the group of

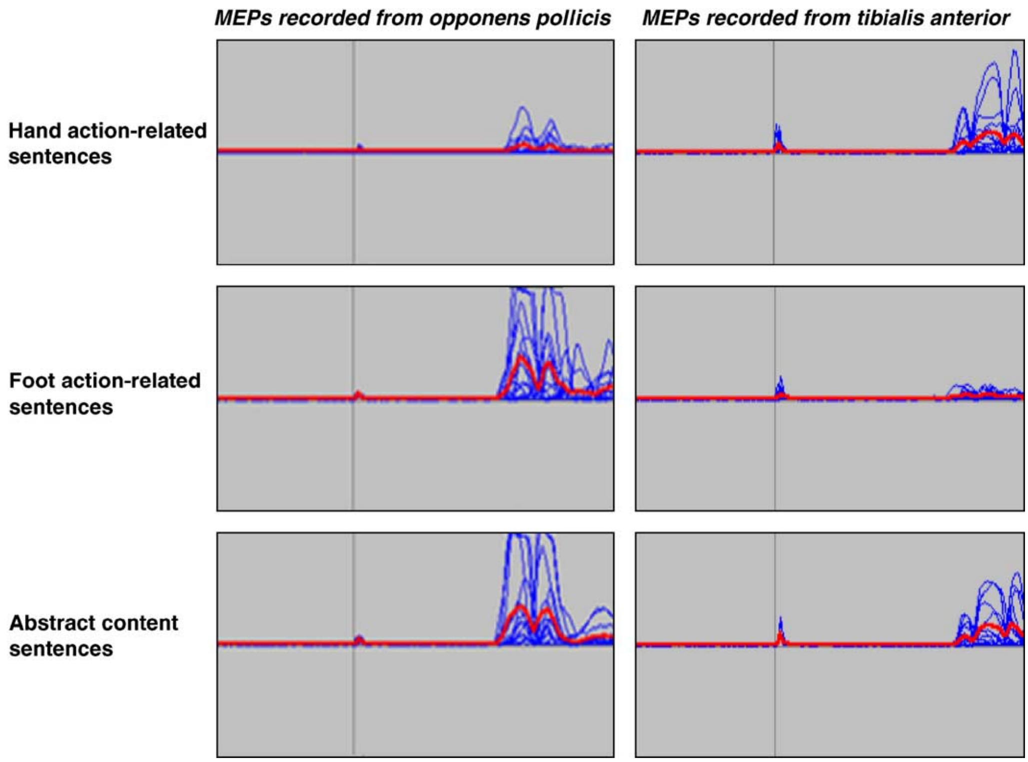

Fig. 2. Typical modulation of MEPs recorded from a hand muscle (opponens pollicis) and a foot muscle (tibialis anterior), respectively, during listening to each type of sentences (hand- and foot-action-related sentences and abstract content sentences) in one of the participants.

participants responding with the foot, RTs were slower when the listened action expressed a foot-related action as compared to those expressing a hand-related action (392 vs. 376 ms). As a whole, responses given with the hand were faster than those given with the foot (311 vs. 384 ms), although this difference did not reach the level of significance ($P = 0.15$).

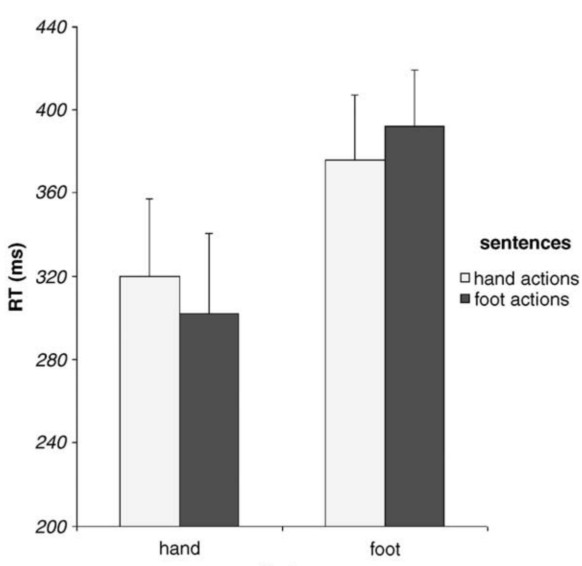

Fig. 3. Mean reaction times (plus SE) expressed in milliseconds when either the hand or the foot was used as effector to give the response, during listening to hand- and foot-action-related sentences.

4. Discussion

The main finding of the present study was a clear modulation of the activity of the motor system during listening to sentences expressing foot/leg and hand/arm actions. This modulation was specific for the effector involved in the listened-to action. Listening to hand-action-related sentences induced a decrease of MEP amplitude recorded from hand muscles. Similarly, listening to foot-action-related sentences induced a decrease of MEP amplitude recorded from foot muscles. Listening to abstract content sentences led to results which did not differ from those obtained during listening to action-related sentences involving an effector different from the one motorically represented in the stimulated area.

Coherently with these findings, the behavioral data showed that RTs were slower when participants responded with the same effector that was involved in the listened action. Taken together, these data strongly support the notion that the processing of language material modulates, at least for sentences expressing a motor content, the activity of the motor system and that this modulation specifically concerns those sectors of the motor system where the effector involved in the processed sentence is motorically represented.

These results are in keeping with recent findings from brain imaging studies. In an event-related fMRI study, during silent reading of words referring to face, arm, or leg actions, activation of different sectors of the premotor–

motor areas that depended on the referential meaning of the read action words was found [30]. Additionally, in a further fMRI study, it was shown that listening to sentences expressing actions performed with the mouth, the hand, and the foot produces activation of different sectors of the premotor cortex, depending on the effector used in the listened action-related sentence [49]. Interestingly, these distinct sectors coincide, albeit only approximately, with those active during the observation of hand, mouth, and foot actions [5]. These data support the notion that the mirror neuron system is involved not only in understanding actions visually presented, but also in coding acoustically presented action-related sentences.

It is important to note that, unlike during action observation, the modulation of the motor system found in the present TMS study consisted of a decrease of MEP amplitude rather than of an increase. Consistently, the behavioral study showed an increase of RTs for the effector congruent with listened to action. Two main accounts can be proposed to explain these findings.

The first is that this difference might be related to the modality used to deliver the stimuli. In a TMS study aiming at assessing the excitability changes of the primary motor cortex induced by auditory stimuli, it was shown that a loud auditory stimulus transiently suppresses the excitability of the human hand motor area [19]. Furthermore, Sundara et al. [47] recorded MEPs from tongue muscles involved in speech production during either the visual or auditory presentation of speech gestures. These authors showed an enhancement of MEP amplitude in muscles involved in speech production during the observation of speech gestures, but not during listening to their sounds.

In contrast with these results, a recent study carried out using the same technique demonstrated a greater cortico-spinal excitability of hand muscles while participants listened to sounds associated to hand actions as compared to control sounds [2]. Similarly, using speech stimuli, Fadiga et al. [15] showed that listening to phonemes induces an increase of MEP amplitude recorded from the tongue muscles involved in their execution. This result was interpreted as an acoustically related resonance mechanism at the phonological level. These results have been fully confirmed by a further TMS study of Watkins et al. [53], who showed that listening to and viewing speech gestures enhanced the amplitude of MEPs recorded from lip muscles. An activation of motor areas devoted to speech production during passive listening to phonemes has been recently demonstrated also in an fMRI study [54]. Thus, the different modality used does not seem to provide per se a satisfactory explanation for the results of the present study.

A second account of the present results could be offered taking into consideration the putative mechanisms involved in processing action-related sentences, as postulated by the theories that assume that language understanding relies on "embodiment". As mentioned in the Introduction, according to these theories, the understanding of action-related sentences implies an internal simulation of the actions expressed in the sentences, mediated by the activation of the same motor representation that are involved in their execution. The results of the present study clearly show that there is a specific modulation of the motor representation of the effector involved in the listened-to action-related sentences. In the behavioral study, this involvement implied a lengthening of RTs when participants had to respond with the same effector used in the heard action. The most likely explanation of this finding is that the motor representation elicited by listening to the sentence interfered with the motor program activated in order to respond with the required effector.

Interference may also account for the results of our TMS study. At first glance, one would expect here the same kind of modulation that has been described for visually presented actions, that is, an increase of MEP amplitude. There are, however, substantial differences between observing an action and listening to an action-related sentence. When observed, an action is dynamically followed in its progress, frame by frame, as confirmed by TMS studies [24]. In contrast, when the same action is verbally presented, as in the present study, the action is not followed in its progress. Furthermore, unlike in the observed actions, in which the observer is always facing a specific agent and a specific context, actions, when verbally presented in an agent-neutral and decontextualized fashion as in our experiments, are understood globally, that is, without relying onto a specific actor doing the action, a specific context in which the action is done, and a precise temporal sequence. In other words, when an action (e.g., grasping) is observed, the way in which it is executed is ostensively clear. We do not only see a grasping hand, but we also see *how* the hand grasps the object. This enables the observer to activate a specific motor schema, directly matching that of the observed action.

In contrast, all the details specifying how the action is carried out are lacking when the action is listened to, as in the case of our experiments. Furthermore, in the present study, TMS stimuli were delivered at the end of the second syllable of the verb, hence before participants listened to the predicate of the action. This likely prevented the listener to simulate a specific motor schema, but most likely activated sub-threshold a variety of motor schemata experientially related to the listened action. Since reciprocal inhibition between different motor schemata is the basic principle of motor organization, the "large-scale" simulation could have interfered with specific motor programs and specific muscle activations as tested by TMS.

An alternative interpretation is that the decrease of MEP amplitude, as well as the increase of RTs for the effector used in the listened-to action-related sentences, reflects the excitation of an abstract "higher order" action representation of the heard action (see above). The activation of this "higher order" action representation, in the absence of specifications of how the action should be done, could, in turn, exert an inhibitory effect on all "specific" more concrete motor representations at the basis of action implementation. It is interesting to note that this hypothesis might also explain the MEP amplitude increase obtained during action observation. In this condition, one could postulate a direct activation of these "specific", more concrete motor representations, closely involved in action execution.

In conclusion, our data suggest that processing language material, at least for sentences expressing concrete actions, involves the motor system. Motor representations involved in coding observed actions are also involved in coding action-related sentences, when verbally presented. Of course, the precise functional relevance of this involvement for language understanding cannot be clarified by the present results.

Acknowledgments

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