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The beneficial effect of a speaker's gestures on the listener's memory for action phrases: The pivotal role of the listener's premotor cortex

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ABSTRACT

Memory for action phrases improves in the listeners when the speaker accompanies them with gestures compared to when the speaker stays still. Since behavioral studies revealed a pivotal role of the listeners' motor system, we aimed to disentangle the role of *primary motor* and *premotor* cortices. Participants had to recall phrases uttered by a speaker in two conditions: in the *gesture condition,* the speaker performed gestures congruent with the action; in the *no-gesture condition,* the speaker stayed still. In Experiment 1, half of the participants underwent inhibitory rTMS over the hand/arm region of the left *premotor cortex* (PMC) and the other half over the hand/arm region of the left *primary motor cortex* (M1). The enactment effect disappeared only following rTMS over PMC. In Experiment 2, we detected the usual enactment effect after rTMS over *vertex*, thereby excluding possible nonspecific rTMS effects. These findings suggest that the information encoded in the premotor cortex is a crucial part of the memory trace.

1. Introduction

Memory for action phrases improves when the phrases are accompanied by congruent gestures compared to when they are not (pure verbal tasks: VTs). This enactment effect has been replicated in several studies in which the participants either gestured (subject-performed tasks: SPTs) or observed a speaker gesturing (experimenter-performed tasks: EPTs), both in the case of single action phrases (see, e.g., Feyereisen, 2006) or more complex material as entire discourses or vignettes (Cutica, Ianì & Bucciarelli, 2014; Cook, Yip, & Goldin-Meadow, 2010). Since recall after SPTs is slightly better than after EPTs (Engelkamp & Zimmer, 1997; Hornstein & Mulligan, 2004), some scholars argued that the role of the motor processes is pivotal in SPTs (Engelkamp & Jahn, 2003). Neuroimaging findings are consistent with this assumption. Nyberg et al. (2001), using positron-emission tomography (PET), compared brain activity during learning and recall phases in SPTs (gestures were performed with the right arm). The authors observed an overlap of brain activity for the two phases in the left ventral motor cortex and in the left inferior parietal cortex. In a more fine-grained study, Masumoto et al. (2006) used the magnetoencephalography (MEG) to measure brain activity during a recognition task to disambiguate the role of motor and parietal regions in SPTs enactment effect. The experimental conditions were two: SPTs and VTs. The MEG data revealed an activation of the left primary motor cortex after SPTs condition in all participants immediately after the stimuli onset (between 150 and 250 ms), while after VTs condition the same activation appeared in only one participant. Matsumoto and colleagues concluded that the SPTs enactment effect is due to the reactivation of the motor information stored in the primary motor cortex (Heil et al., 1999; Nilsson et al., 2000).

Recently, Ianì and Bucciarelli (2017, 2018) argued that motor processes might play a role also in the EPTs enactment effect: the gestures observed in EPTs would favor in the listeners the construction of a model of the material to be learnt through the exploitation of their motor system. The argument is as follows. Gestures provide *procedural information* which favour the construction of an articulated *mental model* of the material to be learnt (see, e.g., Cutica et al., 2014). A mental model is an iconic, non-discrete, mental representation that reproduces the state of affairs described, and it favors a deep comprehension of the material to be learnt, as well as the subsequent recall (see, e.g., Johnson-Laird, 2006). A mental model contains both declarative (e.g., "what is a boat") and procedural knowledge (e.g., "how row a boat”). From this perspective, our memory employs more than one format of knowledge representation (e.g., visuo-spatial, motoric), and gestures observation activates and reinforces the motoric representation (Ianì, Cutica & Bucciarelli, 2016). Indeed, the information conveyed by the speaker’s co-speech gestures - represented in a non-discrete format - are easily included into the discourse mental model, as mental models use non-discrete representations (Bucciarelli, 2007; Cutica & Bucciarelli, 2008; Hildebrandt, Moratz, Rickheit & Sagerer, 1999). These motor representations are part of the listener’s mental models, the procedural aspects encoded in them. Hence, the observation of the experimenter’s pantomime would activate motor representations in the observers, in a covert way, through the activation of their motor system. The latter assumption relies on experimental evidence revealing a high degree of overlap between the neural circuits underlying the execution and the observation of the same action (see, e.g., Rizzolatti & Craighero, 2005), both in non-human (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996) and human primates (e.g., Rizzolatti, 2005). Besides area PF/PFG in the inferior parietal cortex, these neural circuits comprise area F5 in non-human primates and its human homologue BA 44, BA 6, namely the inferior frontal gyrus and the premotor cortex (in humans, mirror neurons were also found in the lower part of the precentral gyrus and in the rostral part of the inferior parietal lobule).

Specifically, the premotor cortex (BA 6) is active during the observation of hand as well as other body movements, involving different effectors (i.e. mouth, arm and hand, and foot), and several studies show evidence of somatotopic organization during action observation (Buccino et al., 2001; Sakreida, Schubotz, Wolfensteller, & von Cramon, 2005; Wheaton, Thompson, Syngeniotis, Abbott, & Puce, 2004). The results of two *meta*-analyses enforce this evidence (Caspers, Zilles, Laird, & Eickhoff, 2010; Van Overwalle & Baetens, 2009). Michael et al. (2014) used off-line continuous theta-burst stimulation (cTBS) in order to investigate whether the pre-motor activation during action observation plays a critical role in action understanding. They applied inhibitory cTBS over the premotor hand or lip areas before a pantomime-recognition task (half of the stimuli were mouth actions and the other half hand actions). The results revealed a double dissociation: the participants were less accurate in recognizing the hand-pantomime after receiving cTBS over the hand area compared to the lip area, and vice versa, they were less accurate in recognizing mouth-pantomime after receiving cTBS over the lip area compared to the hand area. These results suggest that: (1) premotor regions contributing to action understanding and action production have a similar *somatotopic organization*, (2) during action observation, the premotor cortex plays a critical role in *action understanding*.

Ianì and Bucciarelli (2017, 2018) hypothesized that the processes described by Michael et al. (2014) take place and, most importantly, play a causal role in the beneficial effect of gestures on *speech comprehension* and on *memory* for action phrases in the EPTs paradigm. To test this hypothesis, the authors (Ianì & Bucciarelli, 2017) carried out a series of experiments and found that the participants’ recollection of action phrases was enhanced in the experimenter-performed tasks (EPTs) condition compared to the verbal tasks (VTs) condition, but a motor dual task during gestures observation, which involved the same effectors involved in the observed gestures (in this case, hands and arms), erased the enactment effect. On the other hand, a motor dual task involving different effectors from those involved in the observed gestures (legs and feet) did not erase the enactment effect. In a subsequent investigation, Ianì and Bucciarelli (2018) found that the listener’s motor system plays a crucial role also at the retrieval phase. In particular, the results of their experiments in which the participants stayed still while listening to the phrases, revealed that the speaker’s enactment of phrases improves memory in the listeners who stay still at recall, but it does not improve memory in the listeners who move their arms and hands at recall. On the other hand, the speaker’s enactment of phrases continues to improve memory in the listeners who move their feet and legs at recall, i.e. different effectors from those moved by the speaker. Overall, the results of these two studies confirm the predictions according to which the motor component plays an important role also in the enactment effect detectable in EPTs conditions. However, since the secondary motor task used in the experiments by Ianì and Bucciarelli (2017, 2018) involved both motor and premotor areas, it is not clear which of the two components is crucially involved in the beneficial effect observed in EPTs.

From our assumptions and on the basis of the above mentioned studies on action observation, we predict a pivotal role of the premotor areas in EPTs. By contrast, there are studies implying that premotor areas do not play a critical role in SPTs, attributing more importance to M1. First, PET studies have revealed that verbal retrieval of phrases that participants accompanied with gestures at learning phase (SPTs) involves M1 to a greater extent than verbal retrieval of phrases that participants only imagined to accompany with gestures at learning (Nilsson et al., 2000). Second, although M1 can be active during action observation (see, e.g., Kilner, Marchant, & Frith, 2009), it seems to be mainly involved when the observer is later asked to imitate the action (see, e.g., Grèzes, Costes, & Decety, 1999). In order to disambiguate the above issue, we devised a rTMS study that allowed to disentangle the role of the premotor cortex (PMC) and the primary motor cortex (M1) in the EPTs enactment effect. Based on the literature on action observation, we tested the hypothesis that PMC, but not M1, is involved in the beneficial effect of gestures in EPTs. Specifically, we predicted a decreased enactment effect after inhibitory rTMS over the hand/arm region of the left PMC, but not after inhibitory rTMS over the hand/arm region of the left M1 (Experiment 1). Furthermore, to enforce our assumption and exclude possible nonspecific effects of rTMS on the EPTs enactment effect, we carried out a subsequent study, in which participants underwent inhibitory rTMS over the vertex (Experiment 2).

2. Experiment 1. Low-frequency rTMS over PMC or M1

2.1. Material and methods

The task of the participants in the experiment was to observe videos of an actress uttering a series of action phrases in two conditions: in the EPTs condition the actress accompanied the phrases with congruent gestures (hereafter we shall refer to the EPTs condition as the gesture condition), whereas in the VTs condition the actress uttered the phrases while keeping her hands and arms still (hereafter we shall refer to the VTs condition as the no-gesture condition). Then, in both conditions, participants were invited to recall as accurately as possible the phrases uttered by the actress. Further, before this task the participants were assigned to one of two possible stimulation conditions using 1 Hz rTMS at 90% of resting motor threshold, for 15 min (900 pulses) over the hand/arm region of the left PMC or over the hand/arm region of the left M1. Within the heterogeneous area of the premotor cortex we chose to inhibit the region just anterior to M1-hand hotspot, because studies with both nonhuman and human primates suggest that it features a somatotopic organization similar to M1 (Buccino et al., 2001 for a similar procedure see also Michael et al., 2014): the most dorsal areas encode features of leg and foot actions, whereas the most ventral areas encode hands’ and arms’ movements.

2.1.1. Design

Each participant in the experiment observed the videos of the actress uttering a series of action phrases in both the gesture and the no-gesture condition, and the order of presentation of the two conditions was counter-balanced across participants. The participants were randomly assigned to one of two groups, which received, before the task, 15 min (900 pulses) of inhibitory 1 Hz rTMS at 90% of resting motor threshold over the premotor cortex (PMC group), or the primary motor cortex (M1 group). The above stimulation protocol may indeed be used to induce inhibitory offline effects (Ricci, Salatino, Siebner, Mazzeo, &

Nobili, 2014; Salatino et al., 2014; Salatino, Momo, Nobili, Berti, & Ricci, 2014).

2.1.2. Participants

Participants were 32 right-handed adults, students at the University of Turin (8 males and 24 females, mean age = 22.6 years; SD = 2.5 years). None of them had history of neurological or psychiatric disorders, and they were free from any contraindication to TMS (Rossi, Hallett, Rossini, & Pascual-Leone, 2009). They took part in the experiment voluntarily in exchange of course credits. All participants provided written informed consent to participate in the study that was approved by the Ethical Committee of the University of Turin.

2.1.3. Stimuli

The stimuli, the same of the experiments by Ianì and Bucciarelli (2017, 2018), consist of a couple of videos for each of the 24 assertions illustrated in the Appendix A; in one video an actress accompanies the phrase with congruent gestures (gesture condition) and in the other she keeps her hands still (no-gesture condition). In the gesture condition, the actress was instructed to accompany each phrase with a congruent arms' and hands' movement and to gesture at the same time in which she started to pronounce the phrase. In the no-gesture condition, the actress was instructed to pronounce the phrase keeping her hands still on the knees. In both conditions, she was invited to use the same intonation while uttering the phrase. In Fig. 1, as examples, two frames from the videos created for the phrase *Sewing by hand.*

In addition, we used the same two experimental protocols as in Ianì and Bucciarelli (2017, 2018): in Protocol 1 half of the phrases occurred in the gesture condition (number of words in the list of phrases: 42) and the other half in the no-gesture condition (number of words in the list of phrases: 42). In Protocol 2, the phrases occurring in the gesture condition in Protocol 1 occurred in the no-gesture condition, and the phrases occurring in the no-gesture condition in Protocol 1 occurred in the gesture condition.

2.1.4. Procedures

Half of the participants in each group (PMC and M1) were randomly assigned to Protocol 1 and half to Protocol 2. Further, within each protocol we balanced the order of presentation of the gesture and the no-gesture condition. The order of presentation of the phrases within each condition in the protocols was randomized for each participant.

The experiment took place at the sole presence of the experimenter and an assistant. The experimenter invited the participant to sit down on a chair next to the TMS equipment and in front of a desk. The TMS session consisted of a site localization procedure followed by rTMS. For the localization procedure, the index finger area in left primary motor cortex and its motor threshold (rMT) were first identified. Participants' rMT was defined as the lowest stimulus intensity able to elicit a visible twitch in the FDI (First Dorsal Interosseous) muscle of the right hand in at least 5 of 10 consecutive stimulations of the motor hotspot. This procedure allowed us to identify the hand/arm region of the left M1 for the M1 group. For the PMC group, the hand/arm premotor site was defined as 3 cm anterior to the previously identified M1 hotspot for FDI activation (see also Michael et al., 2014).

After the rTMS session, the participant, sitting on a chair in front of the desk where a computer was placed (approximately at 8 in. from the subject), started the behavioral task. The instructions in both the gesture and the no-gesture conditions were as follows:

> Thanks for your participation and for your time. Your task in the experiment is to carefully watch and listen to a series of videos in which an actress utters a series of phrases representing actions. At the end of the last video, when the word "Now" will appear on the screen, repeat as accurately as you can the phrases you heard. The order of the recollections does not matter, and you can repeat twice the same phrase. The word "Now" will remain on the screen for 90 seconds, that is the time you have at disposal for your free recall. After 90 seconds the word "End" will appear on the screen.

2.1.5. Coding of participants' recollections

In the enactment literature, the coding of participants' recollections includes those consistent in meaning with the original phrases, in which the participants recalled the gist of the phrases with some missing details (e.g., Feyereisen, 2006). Following Ianì and Bucciarelli (2017, 2018), we distinguished correct recollections in two categories:

- *Literal recollection*: a phrase recalled exactly in its literality.
- *Paraphrase*: a phrase recalled using different words or different prepositions, but with the same meaning of the original phrase. Examples are the paraphrases of the following elements: plural/singular (e.g., *wringing out the dress* instead of *wringing out the clothes*), article (e.g., *driving a car* instead of *driving the car*), verb (e.g., *casting a stone* instead of *throwing a stone)*.

All the other types of recollection were considered errors:

- *Erroneous recollection*: a recollection inconsistent in meaning with any of the original phrases (e.g., the phrase *wearing the sunglasses*, absent from the list of phrases, or the phrase *throwing a basketball* which is a blending of two original phrases, *throwing a stone* and *dribbling with a basketball*).


(a) (b)

Fig. 1. The actress utters the phrase *Sewing by hand* in the gesture (a) and in the no-gesture (b) conditions.

Table 1

Means (and standard deviations in italics) of types of recollection in the gesture and the no-gesture condition as a function of the experimental group (Experiment 1).

Group		Type of recollection			
		Literal	Paraphrases	Correct (Literal + Paraphrases)	Errors
Motor (N = 16)	Gesture	6.3 *(2.1)*	2.5 *(1.5)*	8.8 *(1.5)*	0.1 *(0.3)*
	No-gesture	5.5 *(1.4)*	1.9 *(1.3)*	7.4 *(1.8)*	0.2 *(0.4)*
Premotor (N = 16)	Gesture	5.2 *(1.8)*	2.8 *(1.8)*	8.0 *(2.0)*	0.3 *(0.5)*
	No-gesture	6.6 *(1.9)*	1.3 *(1.1)*	7.9 *(2.0)*	0.3 *(0.6)*

2.2. *Results*

The frequencies of correct recollections by the two groups of participants were not normally distributed. The Kolmogorov-Smirnov test determined that the frequencies of correct recollections in gesture condition did significantly differ from the normal distribution in the M1 group (KS-test: df(16), $d = 0.25$, $p < .007$) as well as the frequencies of correct recollections in no-gesture condition in the PMC group (KS-test: df(16), $d = 0.23$, $p < .03$). Thus, statistical analyses were performed using nonparametric statistical tests.

Table 1 shows the mean of types of recollections in the M1 and PMC groups. The results for the overall correct recollections (literal and paraphrases) revealed that the predicted crucial interaction occurred: the difference between the number of correct recollections in the gesture condition and in the no-gesture condition differed in the two groups of participants (Mann Whitney test: $z = 1.80$, one-tailed $p < .04$; *Cliff's* $\delta = 0.37$). An analysis by group revealed that, as predicted, the enactment effect occurred in the M1 group: correct recollections were greater in the gesture condition compared to the no-gesture condition (Wilcoxon test: $z = 2.40$, one-tailed $p < .009$; *Cliff's* $\delta = 0.43$). Also, in line with the predictions, the enactment effect did not occur in the PMC group (Wilcoxon test: $z = 0.16$, $p = .88$; *Cliff's* $\delta = 0.05$).

The results for literal recollections, considered separately from recollections in the form of paraphrases, also revealed the crucial interaction: the difference between the number of literal recollections in the gesture condition and in the no-gesture condition differed in the two groups of participants (Mann Whitney test: $z = 2.76$, one-tailed $p = .003$; *Cliff's* $\delta = 0.56$). An analysis by group revealed that, as predicted, the enactment effect occurred in the M1 group, but not in the PMC group. Specifically, literal recollections were greater in the gesture condition compared to the no-gesture condition in the M1 group (Wilcoxon test: $z = 1.67$, one-tailed $p < .05$; *Cliff's* $\delta = 0.31$), whereas in the PMC group literal recollections were greater in the no-gesture condition compared to the gesture condition (Wilcoxon test: $z = 2.28$, $p = .02$; *Cliff's* $\delta = 0.39$).

The analysis for the paraphrases detected no interaction: the difference between the number of paraphrases in the gesture condition and in the no-gesture condition did not differ in the two groups of participants (Mann Whitney test: $z = 1.45$ one-tailed $p = .075$; *Cliff's* $\delta = 0.29$). Also, the analysis for errors detected no interaction: the difference between the number of errors in the gesture condition and in the no-gesture condition did not differ in the two groups of participants (Mann Whitney test: $z = 0.55$, $p = .58$; *Cliff's* $\delta = 0.09$).

To sum up, the results revealed that overall the enactment effect disappears in the PMC group, but not in the M1 group: only participants of the M1 group performed better in the gesture condition compared to the no-gesture condition in terms of literal recollection, and in terms of correct recollections (literal plus paraphrases) in general. The greater production of literal recollections in the no-gesture condition compared to the gesture condition in the PMC group also evidences the disappearance of the enactment: when the premotor cortex is inhibited, the literal recollections are even greater in the no-gesture condition than in gesture condition.

In order to enforce our assumption we tested the effect of inhibitory rTMS on the enactment effect when a different control area was stimulated in Experiment 2. To this end, we chose to target a site often used as a control condition in TMS studies (Ricci et al., 2012), i.e. the vertex. Importantly, this site is anatomically contiguous to the sites targeted in Experiment 1, although is not expected to be involved in the enactment effect.

3. Experiment 2. Low-frequency rTMS over the vertex

3.1. *Material and methods*

The experiment was a replication of Experiment 1, with the exception that the rTMS was applied to a control site, the vertex. The Ethical Committee of the University of Turin approved the experiment and all participants provided written informed consent.

3.1.1. *Design*

Each participant observed the videos in the gesture and the no-gesture conditions and the order of presentation of the two conditions was counter-balanced across participants. The participants received, before the observation, 15 min (900 pulses) of inhibitory 1 Hz rTMS at 90% of resting motor threshold over the vertex.

3.1.2. *Participants*

The participants in the experiment were 16 students of the University of Turin (5 males and 11 females, mean age 22.6 years; SD = 2.4). Inclusion criteria were the same as in Experiment 1. They took part in the experiment voluntarily in exchange of course credits. All participants provided written informed consent to participate in the study that was approved by the Ethical Committee of the University of Turin.

3.1.3. *Stimuli and procedures*

The stimuli and the procedures were identical to those in Experiment 1, with the exception that inhibitory rTMS was applied over the vertex. This site was identified according to the international 10–20 EEG system. The participants' recollections were coded as in Experiment 1.

3.2. *Results*

The frequencies of correct recollections by the group of participants in the experiment were normally distributed. The Kolmogorov-Smirnov test determined that the frequencies of correct recollections in both gesture and no-gesture conditions did not significantly differ from the

Table 2
Means (and standard deviations in italics) of types of recollection in the gesture and the no-gesture condition (Experiment 2).

		Type of recollection			
		Literal	Paraphrases	Correct (Literal + Paraphrases)	Errors
Vertex	Gesture	5.6	2.6	8.2	0.2
(N = 16)		*(1.8)*	*(1.1)*	*(1.5)*	*(0.5)*
	No-gesture	5.1	2.1	7.3	0.2
		(1.9)	*(1.4)*	*(2.0)*	*(0.4)*

normal distribution (KS-test: df(16), $d = 0.16$, $p = .20$; $d = 0.21$, $p = .06$). Statistical analyses were thus performed using parametric statistical tests.

Table 2 shows the mean of types of recollections in the Experiment 2. Correct recollections were greater in the gesture condition compared to the no-gesture condition (t test: $t = 2.39$, one-tailed $p = .015$, Cohen's $D = 0.62$), whereas both literal recollections and paraphrases did not differ in the two conditions ($t = 1.13$, one-tailed $p = .14$, Cohen's $D = 0.28$; $t = 1.37$, one-tailed $p = .095$, Cohen's $D = 0.35$, respectively). In addition, errors did not differ in the two conditions ($t = 0$, $p = .1$, Cohen's $D = 0$).

To sum up, the results revealed that low-frequency rTMS over the vertex does not cancel the enactment effect.

4. Discussion

The aim of our investigation was to test the prediction that the premotor cortex plays a pivotal role in enhancing a listener's memory for action-related phrases when the speaker accompanies them with congruent gestures. In two experiments, participants listened to and then recalled action phrases accompanied or not by the speaker's congruent gestures. Experiment 1 revealed a selective involvement of the PMC in the EPTs enactment effect: the effect occurred in the participants who underwent inhibitory rTMS over the M1 before listening to action-related phrases, but not in the participants who underwent inhibitory rTMS over the PMC. Experiment 2 revealed that the enactment effect occurred when the participants underwent inhibitory rTMS over the vertex, thus enforcing our assumption that PMC is selectively involved in the effect. The relevance of these results is twofold. First, they enforce the assumption that in EPTs, as in SPTs, memory improvement relies on motor information retrieval. Second, consistent with previous findings on action *observation* (Michael et al., 2014), our results reveal that in EPTs is the activation of PMC - rather than M1 – that plays a causal role on motor information retrieval. M1 would instead be relevant to SPTs (Heil et al., 1999; Masumoto et al., 2006; Nilsson et al., 2000; Nyberg et al., 2001). To sum up, the results of the present investigation enrich the literature on the enactment effect by demonstrating the involvement of PMC in EPTs. They also provide new evidence to the literature on action observation by demonstrating that the activation of PMC, besides supporting action understanding, is also causally involved in memory for action.

The general results of our investigation enforce the assumption that the PMC is the specific area of the motor system involved in the EPTs effect, but since studies in the enactment literature showed the role of the listener's motor system both at encoding (Ianì & Bucciarelli, 2017) and at retrieval (Ianì & Bucciarelli, 2018), future rTMS studies are necessary to specifically explore the different contributions of the premotor cortex to encoding and retrieval processes.

Our results are consistent with those of behavioral studies on gesture observation suggesting that the motor system plays a pivotal role in gesture understanding. For example, the participants in the experiments described by Ping, Goldin-Meadow and Beilock (2014) observed a series of videos in which an actor uttered a series of phrases (e.g., "The woman hammered the nail into the wood"), each one accompanied by a gesture. Immediately after, they saw a figure of an object that could be in a position *congruent* or *incongruent* with the gesture observed (for instance, a nail in vertical or horizontal position) and their task was to respond "yes" if the name of the object in the figure was mentioned in the phrase and "no" if it was not. In the congruent condition, compared to the incongruent condition, the participants were faster in responding correctly. This "congruent effect" disappeared when the participants were asked to move their arms while watching the videos, but not when they moved their legs. Ping and colleagues concluded that gesture understanding involves motor system activation in the listener. Our results extend these findings, highlighting the involvement of the listeners' motor system in the beneficial effect of observed gestures on *memory* for action phrases.

5. Conclusions

Overall, the results of this study enforce the assumption that the visual gestural information presented in the EPTs condition activates "covert motor representations in the absence of any explicit and related task demands" (Wilson, 2002, p. 631). At the same time, this activation is crucial for memory enhancement, thereby suggesting that the information encoded in the premotor cortex is part of the episodic memory trace. This evidence enforces the assumption that memory is "evolved in service of perception and action in a three dimensional environment" and we can view it as "the encoding of patterns of possible physical interaction with a three-dimensional world" (Glenberg, 1997, p. 1).

Our investigation is only a first step in the deep comprehension of the brain areas playing a pivotal role in the enactment effect, but demonstrates, for the first time, that PMC activation during gestures observation is involved in enhanced recall of action phrases, not only in gestures understanding. Future more fine-grained studies may explore the effect of inhibitory rTMS on leg and hand premotor cortices to ascertain whether the enactment effect occurs in case of inhibitory rTMS over the leg premotor area, but not in case of inhibitory rTMS over the hand premotor area, as it was done here.

Finally, future studies may explore the implications of the present findings for rehabilitation. In particular, the behavioral studies on the enactment effect seem suggest that the phenomenon might inspire useful strategies to enhance performance in patients with memory deficits (Karlsson et al., 1989) as well as to facilitate foreign language or other subjects acquisition in educational contexts (Cook, Yip, & Goldin-Meadow, 2012; Cutica et al., 2014; Macedonia & von Kriegstein, 2012). More in general, because of the tight link existing between memory and motor systems (see, e.g., Dijkstra & Zwaan, 2014), facilitatory protocols, reinforcing the sensorimotor representation of a memory trace, might be designed to contrast its natural or pathological decay.

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Conflict of interest

None.

Statement of significance

Speech is often accompanied by hand gestures intertwined with the spoken content. Studies on so-called “enactment effect” purported that observing gestures enhance memory for speech through the exploitation of the listener’s motor system. In the present study, we aimed to disentangle the role of primary motor and premotor cortices.

Appendix A

The phrases used in the experiments (translated from Italian, from Ianì and Bucciarelli (2017)):

Rowing a boat
Conducting an orchestra
Playing the violin
Dribbling with a basketball
Playing the piano
Cleaning a window
Driving the car
Painting a painting
Ironing a shirt
Beating eggs
Wringing out the clothes
Throwing a stone
Getting shampoo
Polishing silver
Hammering a nail into the wall
Brushing the teeth
Creaming the body
Laying some blocks one above another
Sewing by hand
Typing
Hugging someone
Shooting with the gun
Rolling up the ball of yearn
Sharpening a knife.

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