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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

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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, &