State-Dependent TMS Reveals a Hierarchical Representation of Observed Acts in the Temporal, Parietal, and Premotor Cortices

Luigi Cattaneo1, Marco Sandrini1 and Jens Schwarzbach1,2

1Neuroimaging Laboratories, Center for Mind/Brain Sciences and 2Department of Cognitive Sciences and Education, University of Trento, 38100 Mattarello (Trento), Italy

Address correspondence to Luigi Cattaneo, Neuroimaging Laboratories, Center for Mind/Brain Sciences, University of Trento, Via delle Regole, 101, 38100 Mattarello (Trento), Italy. Email: luigi.cattaneo@unitn.it.

A transcranial magnetic stimulation (TMS) adaptation paradigm was used to investigate the neural representation of observed motor behavior in the inferior parietal lobule (IPL), ventral premotor cortex (PMv), and in the cortex around the superior temporal sulcus (STS). Participants were shown adapting movies of a hand or a foot acting on different objects and were asked to compare to the movie, a motor act shown in test pictures. The invariant features between adapting and test stimuli fitted a 2 × 2 design: same or different action made by the same or different effector. Neuro-navigated TMS pulses were delivered at the onset of each test picture. TMS over the left and right PMv and over the left IPL induced a selective shortening of reaction times (RTs) to stimuli showing a repeated (adapted) action, regardless of the effector performing it. In a second experiment, TMS applied over the left STS induced shortening of RTs for adapted actions but only if also the effector was repeated. The results indicate that observed motor behavior is encoded with the body part that performs it in the temporal lobe. A hierarchically higher level of representation is carried by neural populations in the parietofrontal regions, where acts are encoded in an abstract way.

Keywords: action observation, adaptation, hierarchy, magnetic stimulation, premotor

Introduction

It is a well-developed capacity in humans to extract effortlessly the meaning of an observed motor act from the visual scene that is presented to them. For example, others’ behavior is immediately categorized as “grasping” regardless either of the numerous possible kinematic variants of this movement or even of the body part (e.g., a right hand, a left hand, or a foot) that is used to perform the act. Neuroimaging studies have consistently shown that the observation of an individual acting upon an object activates in the observer an interconnected system of cortical nodes represented by extrastriate visual areas, the superior temporal sulcus (STS), and a parietofrontal system consisting of the intraparietal sulcus (IPS) and inferior parietal lobule (IPL) plus the ventral premotor cortex (PMv) and caudal part of inferior frontal gyrus (IFG). In some instances also, the superior parietal lobule (SPL) and the dorsal premotor cortex have been shown to be activated by observation of motor behavior (for a review, see Cattaneo and Rizzolatti 2009).

It has been proposed that the representation of observed actions is hierarchically organized (Grafton and Hamilton 2007). According to this view at some point of the action observation system, a transformation between the infinite physical variants of a movement into its meaning must occur, that is, a transformation into a hierarchically higher and more abstract representation of observed acts. Some studies have shown a capacity of abstraction of observed acts by neural populations in the inferior parietal and frontal cortices, demonstrating in some instances also a lower hierarchical level of processing by extrastriate visual areas (Hamilton and Grafton 2006, 2008; Grafton and Hamilton 2007; Urgesi et al. 2007; Candidi et al. 2008). On the other hand, other studies have reported representation of low-level features of observed actions within the frontoparietal system. Among others is, for example, the presence of spatially segregated representations of different effectors (Buccino et al. 2001) or the evidence of the processing of kinematics of the observed motor acts (Pobric and Hamilton 2006, Suchan et al. 2008). In summary, there is no agreement on what respective functional roles the different nodes of the action observation system play in recognizing motor behavior. Whereas some authors hypothesize that action understanding takes place in the ventral part of the dorsal stream (Rizzolatti and Matelli 2003), others claim that actions are fully recognized and categorized outside the motor system, in the ventral stream (Mahon and Caramazza 2008).

In order to further investigate the relative contribution of the distinct ventral and dorsal nodes of the action observation system, we applied a novel approach to TMS, the transcranial magnetic stimulation adaptation (TMSA) paradigm, (Silvanto et al. 2008) to action observation. TMSA is able to provide information on the cortical topography of brain functions and the causal relation of neural activity in the targeted areas to behavior. The TMSA paradigm is based on the well-established idea that the effects of TMS are state dependent. Specifically, TMS behaviorally facilitates the attributes encoded by adapted neural populations, compared with nonadapted, within the stimulated brain area (Silvanto et al. 2008). In the TMSA paradigm, the state of the cortex prior to the stimulus is manipulated in a controlled way by means of perceptual adaptation. The adapting stimulus induces habituation in a subset of cells that code particular stimulus features, making them a selective target for TMS. Stimulation time locked to the cognitive task delivered over the cortical area containing the adapted neurons should selectively improve the performance in processing the adapted stimulus. This TMS paradigm therefore allows targeting functionally distinct neuronal pools in spite of their spatial overlap with respect to each other or with other neural populations. The TMSA paradigm has been tested with stimulation of visual areas such as V1/V2 and V5/middle temporal whose properties are relatively well known (Silvanto and Muggleton 2008). Also, a recent study applied this paradigm to the language domain revealing abstract letter selectivity in the left posterior parietal cortex (Cattaneo, Rota, et al. 2009).
In the present experiments, we used the repeated visual exposure to the same motor act repeated in time as adapting stimulus, which participants had to match to test stimuli. We considered as an index of abstractness of action representation the presence of cross-adaptation between vision of the same motor behavior but performed by different effectors.

Materials and Methods

Participants
Fourteen healthy participants (7 females, mean age 25 years) with no history of neurological or psychiatric illness took part in Experiment 1 and 9 (5 females, mean age 28 years) took part in Experiment 2. All participants were right handed according to the Edinburgh Inventory. The experiments were undertaken with the understanding and written consent of each subject, with the approval of the appropriate local ethics committee, and in compliance with national legislation and the Code of Ethical Principles for Medical Research Involving Human Subjects of the World Medical Association (Declaration of Helsinki).

Setting and Protocol
Participants were sitting in an armchair with their head on a chin-rest in front of a 17-inch computer screen at viewing distance of 57 cm. All participants wore earplugs. The width of stimuli corresponded to 20° of visual angle. Trials consisted in the presentation of an adapting movie followed by the presentation of a series of 8 static test pictures (Fig. 1). Each trial began with a red fixation cross appearing in the middle of the screen for 15 s on a gray background. Participants were required to watch carefully the adapting movie that showed repeatedly a single motor act performed by a hand or a foot. They were then required to respond as fast and as accurately as possible to static test pictures whether the depicted motor act was same or different from the one seen in the adaptation movie. Responses were made with the index and middle finger of the right hand on a keyboard. Response mapping (same or different) to each finger was randomized between participants. They were explicitly told to ignore the effector and make a judgment on the type of act only. The visual presentation of the test picture was terminated by a manual response of the participant or, in case of no response, ended by default after 1500 ms. Each trial (adapting movie plus 8 test pictures) was repeated 16 times within each block, and therefore, a total of 8 × 16 = 128 single responses were collected in each block. A total of 6 blocks were carried out for each participant. The first one was always the baseline block, without TMS. In each of the remaining 5 blocks, one site of TMS was applied. The order of these 5 blocks was pseudorandomized between subjects. We used the E-Prime version 2.0 (Psychology Software Tools, Inc.) software for stimulus presentation and reaction time (RT) recordings. The experiment was preceded by a brief training session.

Adapting and Test Stimuli
Adapting movies contained a series of 40 consecutive clips of 1 s in duration, showing either a right hand or right foot that were either grasping or pushing an object. Half of the 40 clips showed a male actor and the other half a female actor. The manipulated objects were of 2 possible shapes (a cube and a ball, both 3 cm in diameter). All features were ordered pseudorandomly such that the only invariant features performed between 1-s clips belonging to the same adaptation movie were 1) the type of effector (a hand or a foot) and 2) the type of motor act performed upon the object. This resulted in 4 adapting movies (hand/grasp; hand/push; foot/grasp; foot/push), which were repeated 4 times in every block. The images in test pictures were single frames extracted from the adaptation movies. The frames corresponded to the moment of contact with the object. The test pictures represented, compared with the adapting movie, a different act performed by a different effector, the same act performed by a different effector, a different act performed by the same effector, or the same act performed by the same effector (Fig. 1). Pictures of each of these 4 types were presented twice following an adapting movie, for a total of 8 test pictures every trial.

Transcranial Magnetic Stimulation
Biphasic TMS pulses were applied with a figure-of-eight coil (MC-B70) and a MagPro ×100 stimulator (MagVenture A/S, Denmark). Before the experiment, the individual "visible" resting motor excitability threshold of stimulation was established as the lowest stimulation intensity applied over the primary motor cortex capable of evoking a visible contraction in the relaxed right first dorsal interosseus muscle on at least 4 out of 8 consecutive stimulations. The stimulation intensity used during the experiment was set at 110% of the individual threshold. The magnetic stimulator was triggered by Eprime through the parallel port. Single stimuli were delivered at the onset of each test picture. The coil was attached to a mechanical arm fixed to a tripod and placed tangentially to the skull. The coil position was monitored online with the BrainVoyager (Brain Innovation BV, The Netherlands) neuro-navigation system and adjusted to the target location based on reconstructions of individual brain anatomies. Prior to the experiment, a high-resolution T1-weighted magnetization-prepared rapid gradient echo sequence (176 axial slices, in-plane resolution 256 × 224, 1-mm isotropic voxels, generalized autocalibrating partially parallel acquisition with acceleration factor = 2, time repetition = 2700 ms, time echo = 4.180 ms, time to inversion = 1020 ms, flip angle = 7°) scan of the brain of each subject was obtained using a MedSpec 4-T head scanner (Bruker BioSpin, Ettlingen, Germany) with an 8-channel array head coil.

Experiment 1
Six blocks were carried out in every participant, each with a different TMS condition: 1) baseline—no TMS; 2) TMS over midline SPL; 3) TMS over left supramarginal gyrus (SMG); 4) TMS over left PIV; 5) TMS over right SMG; and 6) TMS over right PMv. The no-TMS block was always the baseline block. Stimulation sites were identified on individual brain reconstructions on the basis of macroanatomical landmarks. PMv was defined as the portion of the precentral gyrus posterior to the point where the inferior frontal sulcus meets the precentral sulcus.
The SMG was targeted over its dorsalmost portion, defined as the part of the SMG immediately ventral to the IPS and dorsal to the caudal end of the posterior branch of the Sylvian fissure. SPL was targeted on a point over the midline halfway between the postcentral sulcus and the caudal end of the IPS. The locations on a representative brain are shown in Figure 2.

Coil orientation was anteroposterior with the handle pointing backward for PMv, perpendicular to the midline with the handle pointing outward for the SMG, and anteroposterior with the handle pointing backward for the SPL position. To test for current spread to adjacent motor areas, participants were monitored off-line before the experiment for any muscular twitch in the hand, lips, jaw, or tongue time locked with the stimulus.

**Experiment 2**

Experiment 2 was designed to test the action observation node of the temporal lobe, that is, the cortex associated with the posterior part of the STS. It was constructed after the results of Experiment 1 had been analyzed, and therefore, a no-TMS condition was not carried out. Instead, the midline SPL stimulation was used as control. Three blocks were carried out in every participant, each with a different TMS condition: 1) TMS over the left STS, 2) TMS over midline SPL, and 3) TMS over left PMv; the order of the TMS conditions was randomized between subjects. The cortex around STS was targeted over its middle portion by dividing in 2 parts the STS from the temporal pole to the end of its posterior ascending branch in the parietal lobe and positioning the coil over the midpoint in a site roughly corresponding to where most activation foci are found for observation of transitive distal biological movements (Puce and Perrett 2005). An example of coil location is shown in Figure 2. Coil orientation was initially vertical with the handle pointing upward; however, due to the proximity of the ear, the coil orientation was changed in some participants for the purpose of minimizing discomfort and improving the contact of the TMS coil with the scalp. The midline SPL and the left PMv positions were localized as in Experiment 1.

**Data Processing and Analysis**

Analysis was conducted on RTs and error rates. Data from single trials with incorrect responses were discarded. Subsequently, RTs below 300 ms were excluded from analysis. As stated above, responses longer than 1500 ms were not logged by the system. In Experiment 1, the number of trials discarded because falling outside the 300- to 1500-ms time interval corresponded to 0.5% of all trials, ranging in all cells from 0% to 1.1%, and in Experiment 2, they corresponded to 0.6% of all trials, ranging in all cells from 0% to 1.2%.

RTs were grouped and averaged according to 3 different factors: 1) stimulation modality, 2) adaptation of action, and 3) adaptation of effector. Each measure was obtained by averaging of a pool of 32 single RTs (minus number of excluded error trials). In each of the 2 experiments, an analysis of variance (ANOVA) was performed with the 3 within-subjects variables: "stimulation modality" (6 levels in Experiment 1: no TMS, SPL, left SMG, left PMv, right SMG, and right PMv and 3 levels in Experiment 2: left STS, SPL, and left PMv); "action adaptation" (2 levels in both experiments: adapted or nonadapted); and "effector adaptation" (2 levels in both experiments: adapted or nonadapted). Post hoc comparisons were made with 2-tailed t-tests for paired data, and the P value was Bonferroni corrected for the number of comparisons. The same analyses were performed on raw error rates for both experiments.

**Results**

**Experiment 1**

None of the subjects experienced significant side effects from TMS aside from transient low-intensity neck pain in one case with an onset after the experiment and a moderate-severe frontal headache in another case that was reported during stimulation of the right PMv position.

A significant main effect of "TMS condition" was found ($F_{5,65} = 23.000, P < 0.00001$). RTs in all the conditions with TMS were faster than RTs in the no-TMS condition. These RT enhancements are probably due to nonspecific factors such as auditory intersensory facilitation of the click produced by the magnetic stimulator at the onset of the test pictures (Hershenson 1962; Marzi et al. 1998; Bien et al. 2009).

A significant main effect of action adaptation was also found ($F_{1,13} = 12.575, P = 0.004$) with RTs to adapted actions being overall faster than those to nonadapted actions. However, the most important finding was a significant interaction of the 2 factors TMS condition and action adaptation ($F_{5,65} = 3.7055, P = 0.005$). No other effect or interaction was found (all $P$ values $> 0.42$). In particular, no significant 3-way interaction was observed ($F_{5,65} = 0.99, P = 0.43$).

Significance level for post hoc comparisons was set to 0.0083. The post hoc comparisons investigating the TMS condition $\times$ action adaptation showed a significant difference between nonaction-adapted and action-adapted stimuli only in 3 TMS conditions: left SMG ($P = 0.006$), left PMv ($P = 0.0005$), and right PMv ($P = 0.008$). The mean values of the interaction are given in Table 1, whereas Figure 3 shows the mean differences between adapted and nonadapted action conditions. No significant effect of any factor was found in the ANOVA on error rates (all $P$ values $> 0.33$). The grand mean of the error rate across all blocks and participants was of 5.7%.

| Table 1 |
| RTs (ms) and error rates (%) from Experiment 1 |

<table>
<thead>
<tr>
<th>Condition</th>
<th>RTs (ms)</th>
<th>Error Rate (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Same action:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>No TMS</td>
<td>672 (78)/3.2</td>
<td>679 (80)/3.9</td>
</tr>
<tr>
<td>SPL</td>
<td>569 (54)/5.0</td>
<td>575 (78)/6.3</td>
</tr>
<tr>
<td>Left SMG</td>
<td>541 (55)/6.4</td>
<td>576 (68)/6.5</td>
</tr>
<tr>
<td>Left PMv</td>
<td>540 (60)/5.5</td>
<td>589 (69)/4.9</td>
</tr>
<tr>
<td>Right SMG</td>
<td>563 (80)/7.0</td>
<td>581 (77)/5.8</td>
</tr>
<tr>
<td>Right PMv</td>
<td>534 (69)/5.7</td>
<td>573 (77)/5.4</td>
</tr>
</tbody>
</table>

Note: Values represent mean RTs (standard deviation)/error rate. $P$ values refer to t-tests between RTs to same actions and RTs to different actions. Significance level is set to $P = 0.0083$. Significant $P$ values are highlighted in bold.

Figure 2. Depiction on a representative brain surface of the macroanatomical landmarks used for coil positioning in the 2 experiments. The sulci are represented as thick white lines. IFS, inferior frontal sulcus; PoCS, precentral sulcus; CS, central sulcus; PoCS, postcentral sulcus; PBSF, posterior branch of the Sylvian fissure. The putative stimulation spots are indicated as white circles.
Experiment 2
Three subjects reported moderate pain associated with stimulation of the left STS position, which was solved by varying the orientation of the coil. Overall, the STS stimulation site was surprisingly painless for such a lateral scalp position.

A significant interaction of the 2 factors TMS condition and action adaptation ($F_{2,16} = 4.2215, P = 0.034$) was found. However, the most relevant finding was a significant 3-way interaction of the factors TMS condition, action adaptation, and effector adaptation ($F_{2,16} = 3.9755, P = 0.039$). No other significant effect was found (all $P$ values $> 0.24$). Significance level for post hoc $t$-tests was set to 0.0083. The post hoc analysis of this interaction showed the following pattern: with left PMv TMS, the RTs to adapted actions were faster than to nonadapted actions regardless of the effector being the same or different ($P = 0.0080$ and $P = 0.0099$, respectively). With SPL stimulation, no difference was observed between adapted and nonadapted actions. For TMS over the left STS, responses to adapted actions were significantly faster than to nonadapted actions only if also the effector was repeated ($P = 0.0051$). The mean values of the interaction are shown in Table 2. Figure 4 shows the mean differences between adapted action and nonadapted action conditions. No significant effect of any factor was found in the ANOVA on error rates (all $P$ values $> 0.24$). The grand mean of the error rate across all blocks and participants was of 5.2%.

![Figure 3](https://cerebrox.oxfordacademic.com/cercor/article-abstract/20/9/2252/293991)

**Figure 3.** Experiment 1: mean values of the individual differences between adapted action trials and nonadapted action trials for all TMS conditions. The values represent the behavioral effects of adaptation. Positive values indicate a relative cost of adaptation in terms of reaction time, and negative values indicate a relative advantage of adaptation. Error bars indicate 95% confidence intervals. Conditions with significant $P$ values of post hoc comparisons are labeled with an asterisk.

<table>
<thead>
<tr>
<th>TMS condition</th>
<th>Same action</th>
<th>Different action</th>
<th>Same action</th>
<th>Different action</th>
</tr>
</thead>
<tbody>
<tr>
<td>StS</td>
<td>573 (100)/5.1</td>
<td>612 (101)/5.9</td>
<td>0.0051</td>
<td>615 (81)/6.1</td>
</tr>
<tr>
<td>Spl</td>
<td>588 (89)/4.6</td>
<td>580 (65)/5.7</td>
<td>0.081</td>
<td>568 (60)/5.4</td>
</tr>
<tr>
<td>Left PMv</td>
<td>531 (64)/4.1</td>
<td>574 (61)/5.3</td>
<td>0.0009</td>
<td>540 (67)/5.7</td>
</tr>
</tbody>
</table>

Note: Values represent mean RTs (standard deviation)/error rate. $P$ values refer to $t$-tests between RTs to same actions and RTs to different actions. Significance level is set to $P = 0.0083$. Significant $P$ values are highlighted in bold.

![Figure 4](https://cerebrox.oxfordacademic.com/cercor/article-abstract/20/9/2252/293991)

**Figure 4.** Experiment 2: mean values of the individual differences between adapted action trials and nonadapted action trials for all TMS conditions. The values represent the behavioral effects of adaptation. Positive values indicate a relative cost of adaptation in terms of reaction time, and negative values indicate a relative advantage of adaptation. Error bars indicate 95% confidence intervals. Conditions with significant $P$ values of post hoc comparisons are labeled with an asterisk. D-Eff, different effector; S-Eff, same effector.

Discussion
The results of the present experiments demonstrate that TMS applied over a cortical area produces different effects, depending on the quality of visual experience to which the subjects have been previously exposed. In particular, we observed that TMS induced an improved performance in tasks involving the analysis of features to which participants have been previously adapted. Such pattern of findings suggests that TMS has specifically enhanced performance of the neural subpopulations that respond to the invariant features between the adapting stimulus and the test stimulus.

The concept that repeated visual exposure to motor behavior can produce perceptual aftereffects in the observer is not surprising. This has been shown in one study in both humans and in single cells of monkeys using grasping or placing acts (Barraclough et al. 2009). Another study showed the feasibility of inducing an effect compatible with priming to the meaning of the act with visual presentation of motor acts (Costantini et al. 2008). Imaging studies have also shown that several brain structures have adaptation effects in the form of repetition suppression for observed motor behavior (Chong et al. 2008; Kilner et al. 2009; Lingnau et al. 2009). In the present experiment, a clear correlate of adaptation was not evident behaviorally as an increase in reaction times to repeated (adapted) stimuli in the no-TMS session. However, the clear state dependency of the effects induced by TMS shows that we did induce a “state change” in the subjects’ perceptual system by means of visual exposure to acts even in the absence of clear behavioral effects without TMS. It has been already proposed that state-dependent effects of TMS can be obtained without a behavioral effect of adaptation in the no-TMS condition. TMS state-dependent effects have been obtained in spite of a weak behavioral effect not present in all the subjects or not present at all (Cattaneo et al. 2008; Cattaneo, Rota, et al. 2009; Cohen Kadosh and Walsh 2009). Also, in the case of adaptation to color, the effects of TMS have been shown to be present several
In Experiment 1, we clearly establish a causal role of the parietofrontal nodes in the task that we tested, that is, categorizing the semantics of 2 well-distinct types of distal goal-directed motor behavior. In particular, we identified as active nodes the left PMv, left SMG, and right PMv. Neuronal populations in these 3 areas are able to code the type of act (push vs. grasp), irrespective of physical features such as the effector that performs them. Indeed, the only invariant feature between adapting stimuli and test stimuli was the type of act. The fact that TMS facilitated responses to the adapted action regardless of the effector indicates that neuronal populations in this region perform abstract coding of the motor act.

A role of the left PMv-IFG complex in the encoding of observed actions has been hypothesized in previous works using either a “virtual lesion” TMS approach (Pobric and Hamilton 2006; Avenanti et al. 2007; Canditi et al. 2008) or describing real lesions in patients (Saygin, Wilson, Dronkers, and Bates 2004; Moro et al. 2008; Pazzaglia et al. 2008). Also the left SMG has been found to be active in action coding in imaging experiments (Hamilton and Grafton 2006). It is not surprising that we did not find an effect of right SMG stimulation. In the literature, right-lateralized effects of action observation have been found in tasks that contained features of prediction in time of the outcome of the action or of the final intention of the agent (Iacoboni et al. 2005; Hamilton and Grafton 2008; Liepelt et al. 2008). These tasks are clearly different from the one of the present experiment, which consists in recognizing “what” an observed agent is doing in that exact moment as opposed to “why” the agent is doing it (Boria et al. 2009). Aside from imaging experiments, however, prior to the present study, a causal role of the inferior parietal cortex in action coding has been suggested only by human lesional studies (Hellman et al. 1982; Rothi et al. 1985). In these descriptions, apraxic patients with parietal lesions failed to distinguish well-performed from poorly performed gestures. They also failed to recognize the meaning of pantomimes in both verbal and nonverbal tasks. These descriptions in patients confirm the role of the inferior parietal cortex in generalizing the type of action as suggested by our data.

It has been suggested that the parietofrontal coding of motor acts happens through a process of internal simulation of the same observed acts (Gallese et al. 1996; Grafton 2009). In this context, the results from Experiment 1 support the hypothesis that motor representations within PMv and IPL are coded in terms of goals rather than movements of body parts made to achieve them. This capacity of the motor system to code action meanings has been shown in animals and humans for both execution of movements (Alexander and Crutcher 1990a, 1990b; Kakei et al. 2001; Fogassi et al. 2005; Umilta et al. 2008) and their observation (Umilta et al. 2001; Gangitano et al. 2004; Cattaneo, Caruana, et al. 2009). To this respect, our findings are clearly supported by previous experiments investigating motor resonance to observed actions by applying TMS over the motor cortex, which have shown that the simulation process occurring with action observation can be tuned to action goals rather than to the physical features of the behavior (Gangitano et al. 2004; Cattaneo, Caruana, et al. 2009).

Given the partial left lateralization of the effect that we found, it could be argued that what we see is the effect of habituation to verbal material, provided that subjects employed a strategy based on subvocal rehearsal for this task rather than a real adaptation to the visual features of the stimulus. However, no subject reported any such strategy. Some semantic aspects of verbal processing have been found in the SMG, but in reading tasks (Stoeckel et al. 2009). Previous TMS studies on action or object naming would localize such processes in distant areas such as dorsolateral prefrontal cortex (Cappa et al. 2002) or posteriorly in Wernicke’s area (Mottaghy et al. 2006).

The results of Experiment 2 on the other hand indicate that coding of observed motor acts is performed by neural populations within the STS-associated cortex with distinct properties than in the ventral parietofrontal network. Neurons in STS can code distal goal-directed motor acts, but they cannot categorize motor acts disjoint from the effector that performs them. In other words, neurons in STS have the capacity to recognize motor behavior, but they cannot generalize its semantic valence across all its possible physical variants. We have observed evidence for such a capacity of abstraction only in the parietofrontal system among the locations that we tested. Our results on STS stimulation are also of interest considering that the active task required discriminating the observed actions while ignoring the effector. However, we find an interactive effect of stimulation and effector, that is, we are acting with TMS on an implicit or passively adapted feature. This type of implicit effect has never been reported with TMSA paradigms (Silvanto et al. 2008) and shows that TMS can act on passively induced aftereffects in a complex manner.

The data on body part specificity in STS are controversial; though most papers show tuning of different neural structures to different body parts (Puce and Perrett 2003; Pelphrey et al. 2005), other work seems to contradict this (Thompson et al. 2007). At this point, one methodological remark needs to be made. For the sake of simplicity, we have been attributing our functional results to entire areas that we have targeted. However, the main advantage of the TMSA technique is that we can define functionally distinct neural populations embedded within other topographically overlapping population with different properties. Therefore, all our findings, including that of effector-dependent representation of motor behavior in STS, are not mutually exclusive with other findings, especially when investigating complex polymodal areas.

Experiment 2 was designed to test the action observation node of the temporal lobe, the cortex associated with the posterior part of the STS. The choice of stimulation sites, aside from STS, was limited to one site where TMS had proven to be ineffective in Experiment 1 (SPL, serving as control) and one site where TMS had proven effective (left PMv) in order to show replicability of the data. STS was stimulated on one side only (the left side) for 2 reasons. First, though previous TMS work applying off-line repetitive TMS over right posterior STS disrupted the processing of point-light displays of biological motion (Grossman et al. 2005), there is no clear evidence for a lateralization of STS activity in biological motion processing (Saygin 2007), so we chose the side where we found TMS effects in both parietal and frontal stimulation sites. Second, we wanted to minimize the number of stimulation sites due to discomfort of TMS applied to a spot near to the ear and to the “temporalis” muscle fascia. Such discomfort, however, was not subsequently reported by participants.

Our work combines 2 advantages: we have employed the innovative method of state-dependent TMS and second we have
investigated simultaneously all the putative cortical stations of the action observation system. Taken together, these 2 experiments demonstrate that the task of recognizing a motor act is a 2-step process occurring at first in the STS-associated cortex in a low-level modality that actually describes the physical features of the observed scene. The second step occurs in the ventral parietofrontal network where the perceptive features of the observed scene are transformed into the abstract coding of the motor act. Our data show that the parietofrontal action observation system is "downstream" to the point where the transformation between the infinite variants of a motor act are transformed into the abstract coding of the motor valence of the act independent of physical instantiation. On the contrary, the STS node of the action observation system seems to "upstream" of such transformation.

The idea of a 2-step processing is indirectly suggested but not clearly demonstrated by previous imaging studies. However, there is general agreement that a preliminary coding of observed acts linked to the physical features of the observed behavior is carried out in STS, with a subsequent addition of motor meaning in the parietofrontal system. Evidence for this is found in one paper where STS did not show the capacity for visual learning when observing other’s acts (Cross et al. 2009). Others have shown that the premotor system probably "fills" point-light biological motion displays with motor significance (Saygin, Wilson, Hagler, et al. 2004). Aside from human data, the model of the 2-step processing of action cognition has been also proposed on the basis of extensive physiological and anatomical data in monkeys (Rizzolatti and Matelli 2003).

Notes
Conflict of Interest: None declared.

References