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# Transcranial magnetic stimulation reveals modulation of corticospinal excitability when observing actions with the intention to imitate

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## Abstract

Studies using transcranial magnetic stimulation have demonstrated that action observation can modulate the activity of the corticospinal system. This has been attributed to the activity of an 'action observation network', whereby premotor cortex activity influences corticospinal excitability. Neuroimaging studies have demonstrated that the context in which participants observe actions (i.e. whether they simply attend to an action, or observe it with the intention to imitate) modulates action observation network activity. The study presented here examined whether the context in which actions were observed revealed similar modulatory effects on corticospinal excitability. Eight human participants observed a baseline stimulus (a fixation cross), observed actions in order to attend to them, or observed the same actions with the intention to imitate them. Whereas motor evoked potentials elicited from the first dorsal interosseus muscle of the hand were facilitated by attending to actions, observing the same actions in an imitative capacity led to no facilitation effect. Furthermore, no motor facilitation effects occurred in a control muscle. Electromyographic data collected when participants physically imitated the observed actions revealed that the activity of the first dorsal interosseus muscle increased significantly during action execution compared with rest. These data suggest that an inhibitory mechanism acts on the corticospinal system to prevent the immediate overt imitation of observed actions. These data provide novel insight into the properties of the human action observation network, demonstrating for the first time that observing actions with the intention to imitate them can modulate the effects of action observation on corticospinal excitability.

## Introduction

Studies using transcranial magnetic stimulation (TMS) demonstrate that observing another person's actions can modulate the excitability of the corticospinal system (for a review see Fadiga *et al.*, 2005). For instance, Fadiga *et al.* (1995) revealed an increase in corticospinal excitability when participants observed experimenters perform actions (e.g. grasping objects) in comparison to non-action observation control conditions (e.g. observing objects with no accompanying actions). It has been proposed that this motor facilitation effect reflects increased premotor activity, which influences corticospinal excitability via cortico-cortical connections with the primary motor cortex, or descending connections with the spinal cord (see Fadiga *et al.*, 2005). This effect is widely attributed to activity of the human action observation network, a network of premotor and parietal areas similar to the 'mirror neuron' system found in primates (for a review see Rizzolatti *et al.*, 2001).

Evidence from neuroimaging suggests that the action observation network plays a role in imitation (for a recent meta-analysis see Caspers *et al.*, 2010). Iacoboni *et al.* (1999) asked participants to perform finger-raising movements in response to imitative, symbolic or geometric stimuli. Greater premotor and parietal blood-oxygen-level-dependent (BOLD) activity occurred when participants responded to imitative cues compared with the other conditions, suggesting that the action observation network represents a cortical mechanism used in human imitation. Similarly, Buccino *et al.* (2004) required musically naive participants to use the head of a guitar to perform either imitative or non-imitative actions. In both conditions, the observation of action was associated with activation in premotor and parietal areas. The change in the BOLD response, however, was greater when participants observed the same stimuli with the intention to imitate the action. These data demonstrate that the intention of the observer (e.g. if they observe an action to imitate it) can modulate the activity of the action observation network.

Observing actions in an imitative or non-imitative context modulates the BOLD signal (Buccino *et al.*, 2004). It is therefore difficult to

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interpret what this change actually represents (see Logothetis & Wandell, 2004). This is because the BOLD signal is a correlate of overall neural activity; therefore, an increase in the BOLD signal could be the result of increased activity of excitatory neurons, increased activity of inhibitory neurons, or a combination of both. Using TMS, it is possible to assess whether differences in the activity of the action observation network when observing to imitate represent a greater level of excitatory or inhibitory activity. Therefore, in the study presented here, we utilized the novel experimental approach of measuring corticospinal excitability while participants observed actions in an imitative or purely observational capacity.

## Materials and methods

### *Participants*

Eight right-handed participants (seven males, aged 22–34 years) with normal or corrected-to-normal vision were recruited for the study. The experiment was approved by the University of Birmingham School of Sport and Exercise Sciences ethics board and experimental procedures were conducted in accordance with the Declaration of Helsinki. Written informed consent was obtained from all participants prior to their participation.

### *Apparatus and stimuli*

Stimuli were presented on an 18-inch cathode ray tube monitor via a desktop computer using DMDX software (Forster & Forster, 2003). Participants sat approximately 80 cm from the monitor with the centre of the screen at eye level. The head was maintained in a fixed position using a custom-designed frame and chin rest. Each participant sat with their hands positioned prone on a table directly in front of them, and during a subset of trials they performed actions at the table (e.g. grasping a cylindrical object on its surface).

Single-pulse TMS was delivered using a Magstim Rapid$^2$ stimulator (The Magstim Company, Whitland, UK) with a standard double 70 mm figure-of-eight coil. The motor hotspot was defined as the position over the left primary motor cortex from which the largest MEPs from the first dorsal interosseus (FDI) muscle were elicited. The coil was secured and clamped in position over the motor hotspot using a mechanical arm (Magic Arm, Lino Manfrotto & Co., Cassola, Italy), with the handle pointing backwards at a 45° angle. The resting motor threshold was defined as the lowest stimulation intensity to elicit MEPs with a peak-to-peak amplitude greater than 50 $\mu$V in 50% (6/12) of trials while participants observed a black fixation cross on a white background. During the main experiment, the stimulation intensity was set to 110% of the resting motor threshold (Gangitano *et al.*, 2004; Montagna *et al.*, 2005; Catmur *et al.*, 2007).

Electromyograms were recorded from the right FDI and abductor digiti minimi (ADM) muscles using a Delsys Bagnoli handheld system with DE-2.1 silver bar electrodes (Delsys Inc., Boston, USA). The signal was bandpass filtered from 20 to 450 Hz. The resulting electromyogram was digitized with a sampling rate of 2 kHz using a CED 1401 plus A-D convertor with SPIKE 2 (version 5) software (both by Cambridge Electronic Design, Cambridge, UK) and stored for offline analysis.

During the experiment, participants observed videos depicting movements of the right hand (i.e. grasping actions or abduction/adduction movements of the index finger, both illustrated in Fig. 1A); these videos were based on stimuli from previous studies that have successfully modulated corticospinal excitability using TMS (see Fadiga *et al.*, 1995; Gangitano *et al.*, 2001; Aziz-Zadeh *et al.*, 2002; Catmur *et al.*, 2007). The videos were s in duration, and presented movements in which the FDI muscle was clearly active [identifiably both visually and by increased electromyographic (EMG) activity] at a point 3.3 s into the clip, corresponding with the onset of the TMS pulse.

### *Procedure*

Once the motor hotspot and motor threshold were determined, a block of 12 baseline MEPs were collected while participants observed a black fixation cross presented against a white background. Following this, participants were presented with two further types of trials (referred to from here on as 'observe to imitate' or 'observe to attend' trials) in a pseudorandom order. Both trial types comprised three phases, as illustrated in Fig. 1B. Observe to imitate trials began with the presentation of the instruction to 'observe to imitate'. Following this, a video depicting one of the hand movements was presented to the participant. In the final phase of observe to imitate trials, an on-screen instruction ('perform action now') prompted the participants to imitate the action that they had just observed. Observe to attend trials began with a statement instructing participants to attend to a forthcoming video clip. One of the videos depicting a hand movement was then presented to the participant. In the final phase of observe to attend trials, participants were presented with a statement regarding the content of the video that they had just observed (e.g. ''In the last video, the hand grasped an object''), and were required to make a true or false response by pressing a corresponding button on a computer mouse held in their left hand. It should be noted that the same video stimuli were presented in both observe to imitate and observe to attend trials; only the observer's intention was manipulated as an independent variable.

Participants completed a total of 72 trials, including 12 baseline trials, 24 observe to imitate trials and 24 observe to attend trials (for each action observation condition, 12 trials presented grasping actions, whereas the remaining 12 presented finger movements). During action observation trials, a single pulse of TMS was delivered over the left motor cortex at a point 3.3 s into the video (a time at which the FDI muscle was clearly involved in the observed action) in 48 of these trials (24 trials per condition). TMS was not applied in the remaining 12 trials in order to reduce the participants' anticipation of stimulus delivery.

### *Data analysis*

For TMS trials, the EMG activity 200 ms prior to TMS onset was examined. Any trials that revealed background EMG activity (peak-to-peak electromyogram three SDs above the median average) were removed from the analysis. Peak-to-peak MEP amplitudes were calculated for each trial and then averaged for the imitation and attention conditions. Preliminary analyses of MEP data revealed non-normal (right skewed) distributions (Kolmogorov–Smirnov test, $P < 0.001$) that could not be improved using standard transformations (base 10, natural logarithm). Therefore, mean average MEP amplitudes for each condition were ranked within participant (to account for the inherent between-participant variability found in MEP data), and submitted to a 2 × 3 repeated-measures ANOVA with factors of muscle (FDI, ADM) and condition (baseline, observe to imitate, observe to attend).

To quantify muscular activity when participants executed imitative actions, the root mean square EMG amplitude was calculated from movement onset. For each participant, the average activity during

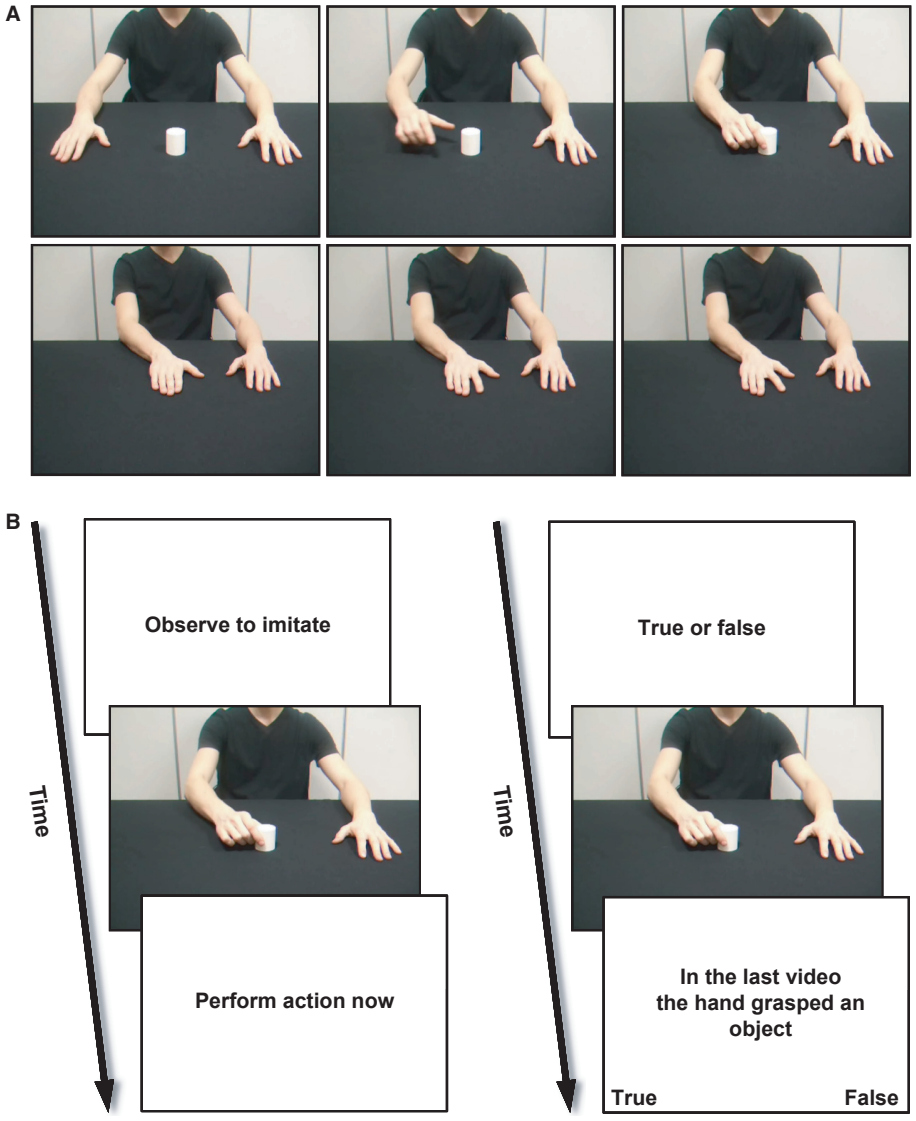


FIG. 1. Trials presented during the experiment. (A) Still frames illustrating the actions depicted in the two video stimuli used during the experiment. Upper images depict the hand reaching to and grasping an object. Lower images present repetitive abduction/adduction movements of the index finger. Far right frame of both images depicts the point at which TMS was applied. (B) Schematic representation of an 'observe to imitate' trial (left) and a corresponding 'observe to attend' trial (right) for the same action. The still-frame depicting the object being grasped presents the image shown on screen at the time at which TMS was delivered (3.3 s into the video).

action execution for each muscle was normalized relative to its activity at rest. Preliminary analyses of EMG data also revealed a non-normal distribution (Kolmogorov–Smirnov test, $P < 0.001$) that could not be improved using standard transformations. Separate Wilcoxon signed rank tests were therefore used to compare EMG activity from the FDI and ADM muscles during action execution and rest. In order to assess differences in the activation of each muscle during action imitation, a further Wilcoxon signed rank test was used to compare activity between the FDI and ADM muscles during action execution. All statistical tests were completed using SPSS 16.0 for Windows (IBM, New York, NY, USA).

## Results

The context in which actions were observed (i.e. whether the participant observed an action in an observe to imitate trial or observe to attend trial) led to a significant modulation of MEP amplitudes recorded from the FDI muscle, but not the ADM muscle (see Fig. 2A; mean ranked MEP data are presented in Table 1). A repeated-measures ANOVA revealed a significant main effect of muscle ($F_{1,7} = 7.6$, $P = 0.028$) and an interaction between muscle and condition ($F_{2,14} = 6.3$, $P = 0.05$). The main effect of condition was not statistically significant ($F_{2,14} = 1.3$, $P = 0.31$). The significant interaction between muscle and condition was analysed using pairwise comparisons. For the FDI muscle, MEPs collected during the attention condition were larger than MEPs collected during the baseline condition ($P = 0.025$) and the imitation condition ($P = 0.05$). MEPs collected during the imitation condition did not differ from MEPs collected during the baseline condition ($P = 0.28$).

The EMG recordings revealed that significant increases in muscular activity occurred as participants executed imitative movements (see Fig. 2B). Wilcoxon signed rank tests revealed that EMG activity was significantly higher during action execution than during rest in the FDI muscle ($Z_7 = 2.52$, $P = 0.01$) and the ADM muscle ($Z_7 = 2.52$,

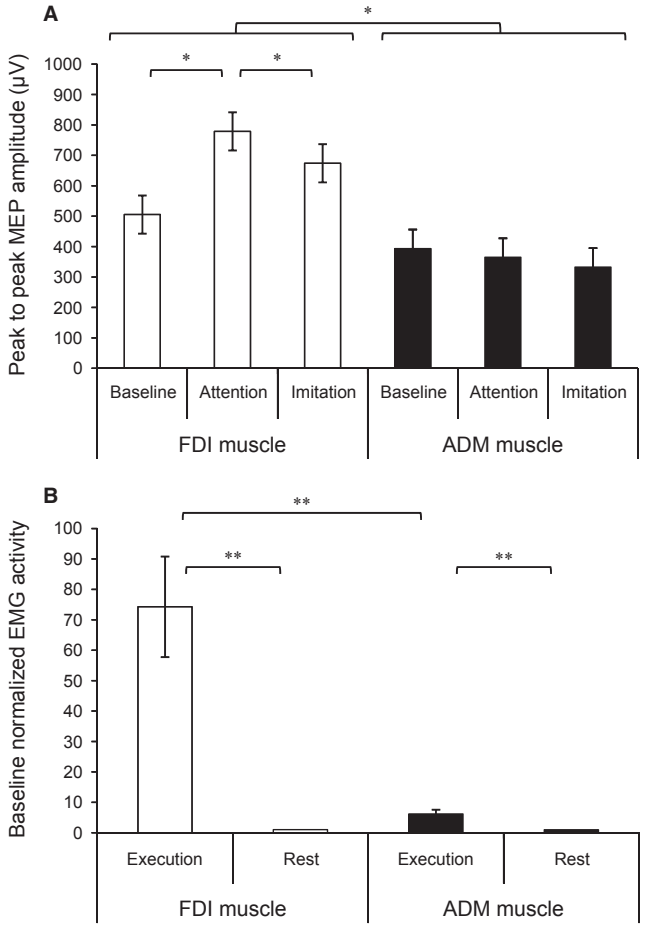


FIG. 2. MEP and EMG activity. (A) Data presenting the mean ranked MEP scores for each condition illustrating the significant main effect of muscle (MEPs collected from the FDI had greater amplitudes than those collected from the ADM), and the significant interaction effect (MEPs collected during the observe to imitate condition had significantly greater amplitudes than MEPs collected during the baseline condition). Error bars present 95% within-participant confidence intervals (see Loftus & Masson, 1994; Masson & Loftus, 2003). (B) Mean group EMG data collected during action execution and at rest for each muscle. Whereas the activity of both the FDI and ADM muscles increased during action execution in comparison to rest, the FDI muscle was significantly more active during action execution than the ADM muscle. Error bars present SEM. $*P < 0.05$, $**P < 0.01$.

TABLE 1. Mean ranked MEP amplitudes for each condition

| | FDI muscle | | | ADM muscle | | |
|---|---|---|---|---|---|---|
| | Baseline | Attention | Imitation | Baseline | Attention | Imitation |
| Mean MEP amplitude | 3.4 | 5.5 | 4.1 | 3.0 | 2.5 | 2.5 |
| SEM | 0.6 | 0.3 | 0.5 | 0.6 | 0.4 | 0.6 |

$P = 0.01$). A further Wilcoxon signed rank test revealed that the increase in activity during action execution was greater in the FDI muscle than in the ADM muscle ($Z_7 = 2.52$, $P = 0.01$).

## Discussion

In the experiment presented here, MEPs collected during the observation of a fixation cross were compared with MEPs collected when participants observed actions in order to either answer a question, or to imitate the movement that they observed. MEPs collected from a prime mover involved in the observed actions were significantly larger in the observe to attend condition when compared with the baseline and observe to imitate conditions. Interestingly, MEPs collected during the observe to imitate condition were not facilitated in comparison to the baseline condition, even though these trials presented exactly the same actions used in the observe to attend condition. These data demonstrate that the intentional context in which actions are observed can modulate the effect that action observation has on the corticospinal system, and are consistent with previous studies demonstrating that the intention of the observer can modulate action observation effects (Buccino *et al.*, 2004; Newman-Norlund *et al.*, 2007; Becchio *et al.*, 2008; van Schie *et al.*, 2008). The EMG activity of both the FDI and ADM muscles increased during action execution compared with their respective baselines. Further analysis also revealed that, during action execution, the excitability of the FDI muscle was significantly greater than the activity of the ADM muscle. These data illustrate the extent to which each muscle was used during the execution of actions; whereas the FDI muscle acted as a prime mover and played a large role in movement execution, it is likely that the ADM muscle acted as a stabilizer and played only a minor role in movement execution. We suggest that this interpretation of the EMG data may explain why MEPs recorded from the FDI muscle were modulated during action observation, whereas those recorded from the ADM muscle were not. Such an interpretation is consistent with previous studies that have demonstrated muscle-specific modulations of corticospinal excitability during action observation (Fadiga *et al.*, 1995; Gangitano *et al.*, 2001; Montagna *et al.*, 2005).

A key point for discussion is the finding that corticospinal excitability was only facilitated in the observe to attend condition, and not the observe to imitate condition. This is of particular interest as participants observed exactly the same actions in each condition; only their intention was manipulated as an experimental variable. The facilitation effect revealed in the observe to attend condition suggests that these results cannot be attributed to a lack of mirror system activation in the observe to imitate condition; this is supported by strong evidence from a recent meta-analysis (Caspers *et al.*, 2010) that demonstrated that premotor and parietal areas traditionally associated with the human mirror system are activated by both the observation of action and imitation. There is also evidence that mirror system activity is in fact greater when participants observe actions in an imitative compared with a purely attentive capacity (Buccino *et al.*, 2004). Instead, we suggest that some process acts to prevent the facilitation effect that normally occurs with action observation when participants observe actions with the intention to imitate them.

To explain this effect, it is important to consider that TMS studies of action observation promote the inhibition of self-made movements, as participants are instructed and reminded to remain still during the collection of MEPs, and trials in which increased background EMG activity is detected are typically removed from the analysis. It has been suggested that these experimental conditions lead participants to engage an inhibitory process in order to counteract the excitatory influence of action observation (Villiger *et al.*, 2011). They highlight that such an inhibitory process has been implicated as a key neural response during action observation (Brass & Heyes, 2005; Keysers & Gazzola, 2010), and is supported by studies of motor control and action observation (Howard & Tipper, 1997; Castiello *et al.*, 2002; Sohn & Hallett, 2004; Welsh & Elliott, 2004; Bien *et al.*, 2009). This inhibitory process is thought to underlie selective imitation during action observation by preventing unwanted motor responses from reaching the threshold at which they are overtly executed (Brass &

Heyes, 2005; van Leeuwen *et al.*, 2009). Evidence of a similar inhibitory process has been demonstrated in previous TMS studies examining the sensorimotor response to observing painful stimuli (Avenanti *et al.*, 2005). Such an inhibitory mechanism is also consistent with single-cell recordings from macaques and humans (Kraskov *et al.*, 2009; Mukamel *et al.*, 2010) demonstrating the existence of neurons that are inhibited during action observation and excited during action execution. These data demonstrate that inhibitory processes act on the corticospinal system to prevent the execution of movements during action observation.

In a previous TMS study, Villiger *et al.* (2011) provided evidence that a marker of this inhibitory process can modulate MEP activity. We also suggest that the effect revealed in the present study is due to differences in the activity of this inhibitory process. The inhibitory process was present during action observation in order to prevent participants from performing overt movements. When actions were observed during attention trials, only a relatively low level of inhibition was required to prevent the participant from moving. In contrast, when actions were observed during imitation trials, the participant's intention to imitate the observed action meant that a relatively high level of inhibition was required to prevent them from moving. This inhibitory influence led to a reduction of the level of corticospinal excitability revealed during action observation.

The origin of the inhibitory effect revealed here is unclear. Evidence from previous studies suggests that a variety of subcortical and cortical mechanisms may contribute to this effect. Frontal lesions in humans and primates lead to a disruption of performance in go/no-go tasks (Piribram *et al.*, 1952; Drewe, 1975), and single-cell recordings in primates have implicated prefrontal cells in the active suppression of motor responses (Wantabe, 1986). It has been suggested that the prefrontal cortex may act to inhibit movements in coordination with the basal ganglia, as it has been reported that stimulation of areas surrounding the globus pallidus can immediately halt the performance of movements in the macaque (Horak & Anderon, 1984). Sensorimotor areas may also contribute to the inhibitory effect. The authors of a recent functional magnetic resonance imaging study have shown that BOLD activity in the primary motor cortex is, in some cases, decreased during action observation, and went on to suggest that the supplementary motor area may contribute to the inhibition of movement during action observation (see Gazzola & Keysers, 2009). There is also evidence that mirror neurons in the premotor cortex that influence corticospinal excitability could contribute to suppressive effects during action observation. As discussed above, Kraskov *et al.* (2009) found 'suppression' mirror neurons in the macaque premotor cortex that had an inhibitory influence on the corticospinal system during action observation. Furthermore, it is often overlooked that early studies detailing the properties of mirror neurons also demonstrated that their firing rates could decrease during action observation (see p. 135, Fig. 4 of Rizzolatti *et al.*, 1996). As the mirror neuron system in primates appears to have a role in the inhibition of movement during action observation, it is likely that the action observation network in humans may play a similar role. On a related note, data from primate studies have also demonstrated suppression of metabolic activity in the spinal cord during action observation; the authors suggested that premotor cortical areas may underlie this effect as previous evidence demonstrates that they inhibit the spinal cord (Stamos *et al.*, 2010). Wherever the inhibition arises, the data presented in this study are consistent with the notion that suppressive mechanisms act on the corticospinal system to prevent the execution of movements during action observation.

In summary, whereas corticospinal excitability was found to increase when participants simply observed actions, no corresponding increase in corticospinal excitability was found when participants observed the same actions with the intention to imitate them. Although previous evidence has linked the human action observation network with imitation, the data here demonstrate for the first time that observing actions with the intention to imitate them can modulate the corticospinal excitability of the observer. These data are consistent with the notion that suppressive mechanisms act to inhibit the excitability of the human motor system during action observation, in order to prevent the immediate overt imitation of observed actions. These data provide novel insight into the properties of the human action observation network, demonstrating for the first time that observing actions with the intention to imitate them can modulate the effect that action observation has on corticospinal excitability.

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## Abbreviations

ADM, abductor digiti minimi; BOLD, blood-oxygen-level-dependent; EMG, electromyographic; FDI, first dorsal interosseus; TMS, transcranial magnetic stimulation.

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