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Research report

Is the human primary motor cortex activated by muscular or direction-dependent features of observed movements?

Kaat Alaerts, Stephan P. Swinnen and Nicole Wenderoth*

Motor Control Laboratory, Division of Movement Control and Neuroplasticity, Department of Biomedical Kinesiology, Group Biomedical Sciences, Katholieke Universiteit Leuven, Belgium

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ABSTRACT

Previous Transcranial Magnetic Stimulation (TMS) studies have shown that the observer's motor system is facilitated by the sole observation of motor actions. However, it has not been possible so far to decide whether the observer's motor system resonates primarily with the observed movement direction or the observed muscle activity, as both factors usually co-varied in these action observation studies. Here, we applied TMS to the wrist extensor and flexor during the observation of wrist motions such that the posture of the observer and the model in the video were either congruent or incongruent. Due to this manipulation, it was possible to disentangle whether the observer's primary motor cortex (M1) is facilitated in accordance to either the observed movement direction or the observed muscle activation. Findings revealed that M1 resonated predominantly according to muscle-specific rather than direction-specific parameters of observed movements. More specifically, muscle-specific facilitation was maximal during congruent postures and remained evident, even though to a lower extent, during incongruent postures in which muscle activation and movement direction parameters were discordant. Our findings support the hypothesis that M1 contributes to action observation, by representing the observed movement in intrinsic, muscle-related coordinates. This transformation from extrinsic to intrinsic coordinates might be an important prerequisite for action understanding and imitation. Additionally, our data offer a neurophysiological explanation for interference that emerges when an action is performed while an incongruent action is observed.

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1. Introduction

Mirror neurons have the unique property to discharge not only when an action is performed, but also when it is merely observed. Since the discovery of these neurons in the monkey premotor cortex (area F5) (Di Pellegrino et al., 1992; Gallese

et al., 1996), there is a growing body of evidence from imaging studies that a similar 'mirror' system also exists in humans (Rizzolatti et al., 1996; Iacoboni et al., 1999; Buccino et al., 2001). With single-pulse transcranial magnetic stimulation (TMS) it has been shown that the observer's motor system 'resonates' to the observed movements such that the muscles

* Corresponding author. Motor Control Laboratory, Division of Movement Control and Neuroplasticity, Department of Biomedical Kinesiology, Group Biomedical Sciences, Katholieke Universiteit Leuven, Belgium, Tervuursevest 101, B-3001 Heverlee, Belgium.

E-mail address: nici.wenderoth@faber.kuleuven.be (N. Wenderoth).

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that would be activated during execution become facilitated by the sole observation of the very same action (Fadiga et al., 1995; Strafella and Paus, 2000).

Since action execution and action observation share common neural processing sites (e.g., the inferior frontal gyrus (IFG) and parietal cortex), it has been proposed that movement performance can be influenced by simultaneously observing another movement (e.g., during interpersonal coordination) (Stanley et al., 2007; Blakemore and Frith, 2005; Craighero et al., 2002; Brass et al., 2000). For example, Kilner et al. (2003), found interpersonal interference to occur during the production of continuous arm movements due to the simultaneous observation of incongruent arm actions (Kilner et al., 2003). However, in this and other interference experiments, interference effects originated both on the basis of directional as well as muscular incongruency between the performed and observed movement (Gowen et al., 2007; Stanley et al., 2007). Previous research demonstrated that muscular aspects of observed movements are indeed translated into the observer's motor system (Fadiga et al., 1995; Strafella and Paus, 2000; Brighina et al., 2000; Maeda et al., 2001; Gangitano et al., 2001; Maeda et al., 2002; Koski et al., 2002; Aziz-Zadeh et al., 2002; Gangitano et al., 2004; Romani et al., 2005).

However, none of these previous studies could dissociate whether the motor system resonates according to the observed directional/spatial or to the muscular parameters since the direction of the observed movement was often confounded with its underlying muscle activity. In other words, it remains largely unclear whether mirror neuron networks are predominantly activated as a function of muscular versus directional parameters of observed movement.

To address the interplay between muscle and directional parameters during movement observation, TMS was used to measure corticospinal excitability in M1 of the flexor and extensor carpi radialis muscles (FCR/ECR) during observation of video clips showing cyclical movements of a model's right hand in the vertical plane (Fig. 1). Movement direction in external space was always the same i.e., an upward movement of the hand from the table surface. However, the model's and observer's hand posture were either congruent or incongruent. Depending on the observed model's hand position (supinated or palm-up, pronated or palm-down), the muscle activated during upward movement in the video clip was either the wrist flexor or the wrist extensor. Depending on the observer's resting hand position (palm-up or palm-down), the muscle that would be activated by the observer during actual hand lifting was either the same as in the video or the antagonist. This resulted in a factorial design with four conditions, requiring either the same (both model and observer activate either the flexor or extensor) or different muscle activation patterns (model activates flexor and observer activates extensor, or vice versa) to generate an upward hand lifting movement from the table surface.

In particular, this factorial design enabled us to disentangle the influence of muscle- versus direction-specific encoding, by analysing those conditions in which the model's and observer's hand adopted different positions (i.e., incongruent postures). For example, when showing a model lifting the hand in palm-up position (requiring wrist flexor activation),

the observer resting in palm-down position would have to activate the wrist extensor to mimic the upward movement. The key question was whether this condition promotes 'muscle' or 'directional' encoding. This was operationalized as follows: 'Directional' encoding would imply that the muscle responsible for upward movement in the observer (in the aforementioned example, the observer's extensor), is primed by the observation of the model's upward movement (even though the model activates the flexor for upward movement). Conversely, 'muscle' encoding would imply that observation of flexor activation in the model would prime the flexor muscle in the observer, irrespective of the latter's posture.

2. Materials and methods

2.1. Subjects

Participants were 5 male and 7 female volunteers (mean $\pm$ SD age 25 ± 4 years) without any overt sensorimotor deficits. All participants were right-handed, as assessed with the Edinburgh Handedness Questionnaire (Oldfield, 1971) and were naive about the purpose of the experiment. Written informed consent was obtained before the experiment and all subjects were screened for potential risk of adverse effects during TMS. The experimental procedure was approved by the local Ethics Committee for Biomedical Research at the Katholieke Universiteit Leuven and conformed with The Code of Ethics of the World Medical Association (Declaration of Helsinki) (Rickham, 1964).

2.2. Electromyography (EMG) and TMS

Motor-evoked potentials (MEPs) were recorded simultaneously from the flexor (FCR) and extensor (ECR) carpi radialis muscles of the right forearm. Therefore, a surface electromyogram (EMG) was recorded with disposable Ag–AgCl surface electrodes (Blue Sensor SP), placed over the middle portion of the muscle belly and aligned with the longitudinal axis of the muscle. Responses were sampled at 5000 Hz, (CED Power 1401, Cambridge Electronic Design, UK) amplified, band-pass filtered (30–1500 Hz), and stored on a PC for off-line analysis. Pre-stimulus EMG recordings were used to assess the presence of unwanted background EMG activity in the 50 msec preceding the magnetic pulse.

Focal TMS was performed by means of a 70 mm figure of eight coil connected to a Magstim 200 stimulator (Magstim, Whitland, Dyfed UK). The coil was positioned over the left hemisphere, tangentially to the scalp with the handle pointing backward and laterally at 45° away from the mid-sagittal line, such that the induced current flow was in a posterior–anterior direction, i.e., approximately perpendicular to the line of the central sulcus. The optimal scalp position was defined as the position from which MEPs with maximal amplitude were recorded in the right FCR. The rest motor threshold (rMT) was defined as the lowest stimulus intensity evoking MEPs in the right FCR with an amplitude of at least $50 \mu\text{V}$ in 5 out of 10 consecutive stimuli (Rossini et al., 1994). For all experimental trials, the stimulation intensity was 130% of the subjects' rMT and ranged from 43% to 77% (mean 55%) of the maximum

Fig. 1 – Illustration of the four digital video clips presented to the subjects.

stimulator output. Though the parameter setting procedures were prioritised for FCR, MEPs were simultaneously obtained for the ECR. ECR stimulation parameters were assumed to be satisfactorily similar, due to the overlapping representations of forearm flexors and extensors (Scheiber, 1990) and the lower threshold of the forearm extensor muscles. Signal Software (2.02 Version, Cambridge Electronic Design, UK) was used for TMS triggering and EMG recordings.

2.3. Stimuli and procedure

Experimental stimuli consisted of two digital video clips representing flexion/extension movements of the right wrist against a yellow background. The hand was viewed in palm-down position during the wrist extension video (EXT) and in palm-up position during the wrist flexion video (FLEX) (Fig. 1). The action required the wrist to move rhythmically from 0° (DOWN-position) to 30° (UP-position) away from the yellow surface at a frequency of .5 Hz and for a total duration of 10 sec. In addition, two control videos of the same duration were made: (1) extension of the right ankle (FOOT) (female model) and (2) a yellow background without any limb movement (BASELINE) (Fig. 1). Participants sat approximately at a distance of 40 cm from a Dell 1707 monitor (resolution, 1152 × 870 pixels; refresh frequency 60 Hz) that was mounted directly above the subject's hand, such that the observed movement could easily be incorporated into the body scheme of the observer (Fig. 2). As a previous study indicated that MEP responses are maximal when the observed action corresponds to the perspective of the observer (first person) (Maeda et al., 2002), we used this perspective to present the video clips (Fig. 1). The video files were displayed with a frame rate of 25 Hz (or frames per second). Video presentation timing was

controlled by Blaxton Video Capture software (South Yorkshire, UK) which could be triggered via the TMS stimulation and EMG recording software (Signal 2.02 Version, Cambridge Electronic Design, UK).

Fig. 2 – Illustration of the experimental setup. Participants sat approximately 40 cm away from the computer screen on which the four digital video clips are displayed. The participants were instructed to position their right hand in palm-up or palm-down position while observing the video clips. Vision of their own hands and forearms was never allowed.

While observing the four video clips, participants positioned their hand either palm-up or palm-down. However, vision of their own hand and forearm was never allowed. They were instructed to relax their forearm muscles while resting on a soft cushion directly underneath the video-screen. Muscle relaxation was monitored, and, whenever EMG activity became apparent during data collection, the trial was discarded and repeated.

Each of the four video clips (2 experimental, 2 control) was presented 20 times for each subject, with the presentation order randomized across subjects. During the observation of each video clip, two single TMS pulses were delivered at pseudo-random time points such that the inter-stimulus interval was always 5 sec (either at 3 and 8 sec after video start, or at 4 and 9 sec after video start). As such stimulation was applied in different movement phases, i.e., when the hand/foot in the video reached the peak (UP) position (at 4 and 8 sec after video start) and the other when the hand/foot reached the start (DOWN) position (at 3 and 9 sec after video start) (Fig. 1). For each subject and each of the 16 conditions (2 observer's postures $\times$ 4 video clips $\times$ 2 movement phases), 20 MEPs were recorded, resulting in a total of 320 MEPs. The experimental session lasted approximately 120 min with a pause every 30 min. Participants were instructed to pay full attention to the videos, such that they could answer at any time whether the model's hand/foot in the video was in UP- or DOWN-position, when randomly asked by the experimenter. After the experiment, participants scored their subjective level of attention by means of a questionnaire on a scale from 0 (no attention) to 5 (maximal attention).

2.4. Data analysis

From the EMG data, peak-to-peak amplitudes of the MEPs were determined. Additionally, the background EMG was quantified by calculating the root-mean-square error (RMSE) for the 50 msec interval prior to TMS stimulation to ensure that subjects were completely relaxed during the stimulation. No EMG artefacts were observed and all trials were included in the analysis.

For both the FCR and the ECR, MEP amplitudes were averaged separately for each 'Observation condition' (FOOT, EXT, FLEX, BASELINE), 'Observer's posture' (PALM-UP, PALM-DOWN) and 'Movement phase' (UP, DOWN). Since MEP amplitudes usually exhibit large inter-individual variability, they were normalized relative to the BASELINE measure in order to make them comparable across subjects. To analyse modulations in background EMG across subjects, RMSE scores were also normalized relative to the BASELINE measure.

2.5. Statistics

MEP amplitudes. Peak-to-peak amplitude data of the MEPs were subjected to a four-way analysis of variance (ANOVA) with repeated measures, with the within factors 'Muscle' (FCR, ECR), 'Observer's posture' (PALM-UP, PALM-DOWN), 'Model's movement' (EXT, FLEX) and 'Movement phase' (UP, DOWN). With the analysis of the MEP amplitudes, we can specifically test the influence of muscle- versus direction-specific encoding in the following manner: **muscle-specific encoding** of the observed movements leads to the prediction

that observing wrist flexion will facilitate the observer's flexor and observing wrist extension the observer's extensor, irrespective of the observer's posture. Statistically, this would be reflected by an interaction effect of 'Muscle' and 'Model's movement'. Conversely, **direction-specific encoding** would imply that observing an upward movement of the model will facilitate the observer's muscle that is required for upward movement, i.e., with the observer's forearm in palm-down position, upward movement observation will facilitate the observer's extensor, whereas, with the observer's forearm in palm-up position, upward movement observation will facilitate the observer's FCR. This would be in agreement with an interaction effect of 'Muscle' and 'Observer's posture'.

It was expected that the condition-induced modulations in MEP responses are stronger when measured during the UP than during the DOWN movement phase.

RMSE-scores. A similar four-way repeated measures ANOVA was applied to the background EMG data (normalized RMSE-scores) to assess whether the MEP amplitude scores were confounded by modulations in background EMG. Additionally, an analysis of covariance was performed on the MEP amplitude data with the normalized RMSE-scores as a covariate, again, to check whether any significant interactions were influenced by background EMG.

All significant interactions were analysed further using Tukey HSD post-hoc tests.

3. Results

Subjects were alert while observing the videos, as indicated by a mean subjective score of $3.8 \pm .8$ on a scale ranging from 0 (no attention) to 5 (maximal attention).

Corticospinal excitability in M1 was modulated by movement observation and mainly reflected a muscle-specific mapping. This was indicated by the four-way-ANOVA which revealed a highly significant two-way interaction for the factors 'Muscle $\times$ Model's movement' [$F(1,11) = 24.68, p < .001$] but no significance for the 'Muscle $\times$ Observer's posture' interaction [$F(1,11) = .95, p > .3$]. No other main or interaction effects reached significance [All, $F \leq 2.8, p \geq .1$]. The factor 'Movement phase' had no significant influence on the MEP response recorded from different observation conditions [$F(1,11) = .27, p > .6$] such that MEP values recorded from the UP or DOWN movement phase were pooled for post-hoc analyses. In line with the design of our study, the results will be discussed separately for observation with congruent and incongruent postures.

3.1. Action observation with congruent postures: the observed movement direction corresponds to underlying muscle activity

Fig. 3A displays the averaged MEP responses evoked from the ECR (light grey bars) and FCR (dark grey bars) during the observation of extension or flexion movements with *congruent postures*, i.e., extension movements are observed with the observer's hand positioned in palm-down, flexion movements with the hand in palm-up position. In these conditions, both

Fig. 3 – Normalized Peak-to-peak Amplitude scores recorded during the observation of extension or flexion movements with congruent (A) or incongruent (B) postures. (A) Congruent postures. Extension movements are observed with the observer's hand positioned in palm-down, flexion movements with the hand in palm-up position. (B) Incongruent postures. Extension movements are observed with palm-up posture, flexion movements with palm-down-posture. MEP responses recorded from the ECR (light grey bars) and FCR muscle is presented as a change from the mean MEP response recorded during the baseline (control) observation condition (in %). [Significant differences between conditions are indicated; * $p < .001$; ** $p < .01$; * $p < .05$]. Vertical bars denote $\pm$ standard errors.**

muscular and directional mappings correspond between the observer and the model in the video.

MEPs evoked from the ECR were higher than those evoked from the FCR during the observation of upward **extension** movements [post-hoc $p < .001$]. MEPs evoked from the FCR were higher than those evoked from the ECR during the observation of upward **flexion** movements [post-hoc $p < .05$].

Overall, observation of an upward extension or flexion movement resulted in a selective facilitation of the ECR or FCR respectively. Since the movement direction corresponded to underlying muscle activity, the highly resonant motor response is likely to reflect the simultaneous encoding of both muscular and direction-dependent aspects of the observed movement.

3.2. Action observation with incongruent postures: predominance of muscular versus directional encoding of the observed movement

Since the observed movement direction no longer corresponded to the underlying muscle activity during incongruent postures, predominance of either muscle-dependent versus direction-dependent encoding can be revealed from these conditions. Fig. 3B displays the averaged MEP responses evoked from the ECR (light grey bars) and FCR (dark grey bars) during the observation of extension or flexion movements with incongruent postures, i.e., extension movements are observed with the observer's hand positioned in palm-up, flexion movements with the hand in palm-down position.

MEPs evoked from the ECR were higher than those evoked from the FCR during the observation of upward **extension** movements, irrespective of the fact that actual activation of the ECR would result in a downward movement [post-hoc $p < .01$]. MEPs evoked from the FCR were slightly higher than

those evoked from the ECR during the observation of the flexion movement, but this difference was small and did not reach significance [post-hoc $p = .97$].

Fig. 3 suggests that for the congruent conditions (Fig. 3A), ECR facilitation was substantially higher for observing extension than for observing flexion motion, whereas in the incongruent conditions (Fig. 3B), ECR facilitation was moderate in both cases. This potential modulating effect of posture in the ECR was tested by performing three-way ANOVAs on the ECR and FCR data separately with the factors 'Observer's posture', 'Model's movement', and 'Movement phase'. This revealed a strong effect of 'Model's movement' in both muscles [both, $F(1,11) > 5.4$, $p < .05$], whereas no significant main effect of 'Observer's posture' [$F(1,11) \leq 2.9$, $p \geq .11$] or any interaction effects were found [$p \geq 2.22$], which strongly supports our main analysis.

3.3. Observation of foot movements

One might argue that the observed changes of MEP amplitude are unspecific effects induced by any moving stimuli. As control condition, wrist MEPs were measured during the observation of foot movements. No systematic changes in MEP amplitude were found when foot instead of hand

Table 1 – Normalized peak-to-peak MEP amplitude scores recorded during the observation of foot movements (expressed as changes from baseline MEP size (in %) $\pm$ standard errors of mean).

	ECR	FCR
Observer's Posture 'Palm-down'	-3.61 ± 4.99	$-.89 \pm 4.061$
Observer's Posture 'Palm-up'	7.35 ± 6.05	-5.76 ± 2.44

Table 2 – Normalized RMSE scores (expressed as changes from baseline RMSE score (in %) $\pm$ standard errors of mean).

Model's movement		Foot	Extension	Flexion
FCR	Observer's Posture 'Palm-down'	-2.31 ± 5.03	-1.79 ± 6.01	8.28 ± 8.50
	Observer's Posture 'Palm-up'	-4.02 ± 1.51	-2.09 ± 2.26	$.83 \pm 2.36$
ECR	Observer's Posture 'Palm-down'	12.15 ± 4.67	5.43 ± 2.82	5.67 ± 4.38
	Observer's Posture 'Palm-up'	-6.45 ± 5.01	3.21 ± 5.22	1.46 ± 4.13

movements was observed (Table 1). This indicates that our main findings reported above are specific for mapping observed *hand* movements onto the observer's motor system.

3.4. Background EMG activity

EMG RMSE scores were generally low during movement observation (Table 2). The four-way ANOVA revealed no significant main or interaction effects [all, $F < 4.1$]. Additionally, the analysis of covariance with RMSE scores as a covariate revealed no change in any of the effects found in the traditional four-way ANOVA model used above. This indicates that the MEP amplitude scores were not confounded by modulations in background EMG.

4. Discussion

A large body of evidence supports the view that perception of others' actions is accompanied by facilitation of the observer's motor system and it is broadly assumed that this facilitation is a result of the input from premotor mirror neurons. Importantly, various TMS studies report this facilitation to be highly specific to the underlying muscle activity of the observed action (Aziz-Zadeh et al., 2002; Brighina et al., 2000; Fadiga et al., 1995; Gangitano et al., 2001; Gangitano et al., 2004; Koski et al., 2002; Maeda et al., 2002; Maeda et al., 2001; Romani et al., 2005; Strafella and Paus, 2000). However, since the encoding of the underlying muscle activity nearly always coincided with the encoding of movement direction, it was until now impossible to explore the relative importance of the two.

In the present study, we aimed to disentangle muscle-versus direction-specific encoding by means of posture manipulations that were either congruent or incongruent between the observer and the perceived model. More specifically, we addressed whether the pattern of activation in M1 was preferably determined by the observed movement direction or by its underlying muscle activation pattern. In the observed actions, the movement direction was always 'upward', whereas the muscles required to generate this action were systematically varied.

4.1. Predominance of muscle-specific encoding

Our results showed that the observation of upward extension movements resulted in an increased response in the ECR, even when hand postures were incongruent such that activating the observer's ECR would result in a downward wrist movement, which is at odds with the general movement direction conveyed by the video (i.e., an upward movement of the wrist). A similar pattern of results was obtained for the

FCR, showing maximal facilitation during observation of wrist flexion movements.

Overall, our findings suggest that muscle-specific facilitation predominated over direction-dependent facilitation of M1 during action observation. Although indirectly, this result is in good agreement with a previous TMS study by Urgesi and colleagues (2006a) who studied the observation of finger movements (either the index or the little finger). In their design they measured whether MEP excitability of the observer varied either in accordance to the finger used or in accordance to the spatial requirements of the movement i.e., in terms of the spatial correspondence between the space of the model's movement and the posture of the observer (Urgesi et al., 2006a). Analogous to our results, they showed that cortico-spinal excitability is modulated in an effector specific way.

The present data provide a possible neurophysiological basis of interference in movement performance due to simultaneous observation of incongruent actions. For example, in a study by Kilner et al. (2003), subjects were instructed to make arm movements while observing the same (congruent) or qualitatively different arm movements and the results showed that observing incongruent movements generated significant interference with actual movement (Kilner et al., 2003). However, since the observed movements were incongruent both in terms of movement direction as well as the muscles used in the observed action, it remained unclear whether the interference effect originated from directional or muscular movement parameters. Our results suggest that 'motor contagion' (i.e., incongruent co-activation of shared action performance-observation networks) may have originated predominately from muscle-related encoding of the observed movement in M1, as opposed to direction-related encoding effects. One important methodological aspect is that actions were observed from the first person perspective in our study, whereas they were observed from a third person perspective in the study by Kilner et al. (2003). However, a recent experiment indicated that the predominance of muscle-related encoding over direction-related encoding appeared to be independent of the observer's perspective, even though facilitation was generally stronger for the first person perspective (Alaerts et al., 2009).

Our findings also contribute to a broader debate over the role of M1 in the context of movement observation. Recent evidence confirms that M1 neurons exhibit mirror properties during movement observation of a highly over-trained task in monkeys (Tkach et al., 2007). However, this M1 activation might simply be a result of strong projections from monkey area F5 located in the IFG (Dum and Strick, 2005), which was argued to represent the core center of the mirror neuron system (Craighero et al., 2007). Thus, M1 might simply be "co-activated," thereby representing the same information as IFG.

Alternatively, it was argued that M1 could play a more functional role in movement observation by representing the observed movement in an intrinsic coordinate frame (Kilner and Frith, 2007). Single-cell recordings have shown that most F5 neurons encode movement in an extrinsic coordinate frame, i.e., related to the target position in space (Kakei et al., 2001). By contrast, M1 contains neurons encoding movement in an intrinsic reference frame, i.e., with respect to joints and muscles, which are nearly as frequent as neurons encoding extrinsic space (Kakei et al., 1999; Kakei et al., 2003). As such, M1 was hypothesized to play an important role within the mirror system, as it might “translate” the observed movement into intrinsic coordinates, which in turn, might be necessary for action understanding and imitation. Our study supports the latter hypothesis, as M1 excitability was mainly modulated by the muscular requirements of the observed movement. Note that this finding is not trivial, as M1 contains both space-related and muscle-related neurons to a nearly equal extent (Amirikian and Georgopoulos, 2003; Georgopoulos et al., 1982; Kakei et al., 2001; Kakei et al., 2003).

One might wonder however, whether the predominance of muscle-related encoding over direction-related encoding will persist when the observed movement is directed towards a goal in peripheral space, e.g., towards an object. It is possible that observing how an actor manipulates or moves towards an object will modulate the observer’s response, such that directional coordinates of the observed action (i.e., direction towards the object) become of primary importance (rather than muscular coordinates). Thus, future research might reveal whether muscular- versus directional encoding in M1 changes when the observed movements serve an explicit action goal (e.g., manipulation of an object).

4.2. Anticipatory mental continuation of the observed action

During the observation of each video clip, TMS pulses were delivered when the hand was in the start (DOWN) and peak (UP) position. Because TMS measures corticospinal excitability with a high temporal resolution, we hypothesized that the observation of the hand in DOWN position would not yield a modulation in MEP facilitation as no overt flexion or extension is made during this movement phase.

Surprisingly, we found that excitability during the DOWN movement phase showed the same MEP modulation as observed during the UP movement phase. Different interpretations may be attributed to this observation.

First, it should be noted that the observed actions were directed in the vertical plane such that the moving muscle always acted as the anti-gravitational muscle. Therefore, the comparable activations in the different movement phases might be attributed to the fact that the anti-gravitational muscle was either eccentrically or concentrically contracted, for respectively the DOWN and UP movement phase.

On the other hand, it is possible that this finding results from the rhythmical nature of the task such that participants perform some kind of anticipatory mental continuation of the observed movement phase. Similarly, Urgesi et al. (2006a) showed that even in the absence of explicit motion, observation of static photographs of pincer grips produced a clear

increase in corticospinal excitability of the congruent muscle (Urgesi et al., 2006b). Similar results were found in a functional imaging study (Johnson-Frey et al., 2003). Together, these results might put forward another property of the mirror neuron system, namely that it is highly associative in the sense that little information is sufficient to activate related motor structures. Such associations are likely to arise from daily life experience but also from the specific context induced by the experimental setup, which requires many repetitions of observing the same actions. This associative property of the mirror neuron system may be related to the functional significance of implied motion perception. In a dynamic world, a full motion sequence is rarely visible, forcing us to anticipate the continuation of moving stimuli to bridge discontinuities in visual inputs and interact optimally with the environment.

5. Conclusions

During observation of hand movement, the mirror neuron system activates the motor cortex in a muscle-specific rather than direction-dependent manner, i.e., movement observation leads to highly muscle-specific resonating activity in M1, even when this is at odds with implied movement direction. This supports the hypothesis that M1 plays a functional role within the mirror neuron system by representing the observed movement in intrinsic, muscle-specific coordinates. Accordingly, we propose that interference effects due to the simultaneous observation–performance of incongruent actions, originate predominantly from motor contagion in terms of muscle-related rather than direction-related movement aspects.

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Abbreviations

ECR: extensor carpi radialis
 EMG: electromyography
 FCR: flexor carpi radialis
 M1: primary motor cortex
 MEP: motor-evoked potential
 RMSE: root-mean-square error
 rMT: rest motor threshold
 TMS: transcranial magnetic stimulation