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Measuring Mimicry:

General Corticospinal Facilitation During Observation of Naturalistic Behaviour

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Abstract

Mimicry of others' postures and behaviours forms an implicit yet indispensable component of social interactions. However, whereas numerous behavioural studies have investigated the occurrence of mimicry and its social sensitivity, the underlying neurocognitive mechanisms remain elusive. In this study, single pulse transcranial magnetic stimulation was used to measure corticospinal facilitation during a naturalistic behaviour observation task adapted from the behavioural mimicry literature. Motor evoked potentials (MEPs) in participants' right hands were measured as they observed stimulus videos of a confederate describing photographs. MEPs were recorded while confederates were and were not carrying out hand and leg behaviours that also differed in spatial extent (i.e. *large behaviours*: face rubbing and leg crossing; *small behaviours*: finger tapping and foot bouncing). However, the cover task instructions did not refer to the confederate's behaviour but instead required participants to focus on the confederates' photograph descriptions in order to later perform a recognition test. A general arousal effect was found, with higher MEPs during stimulus video observation than during a fixation-cross baseline, regardless of whether or not the confederate was carrying out a behaviour at the time of the pulse. When controlling for this general arousal effect, results showed that MEPs during observation of the larger two behaviours were significantly higher than the smaller two behaviours, irrespective of effector. Thus, by using a controlled yet naturalistic paradigm, this study suggests that general sensorimotor arousal during social interactions could play a role in implicit behavioural mimicry.

Introduction

During social interactions, individuals mimic their interaction partners' postures and otherwise-meaningless behaviours. Behavioural studies indicate that this phenomenon occurs largely outside of awareness yet is closely intertwined with the social dynamics of the interaction (Chartrand & Bargh, 1999; Chartrand & Lakin, 2013). The social sensitivity of mimicry suggests that it plays an important role in social interactions and deviations in the occurrence of mimicry might be indicative of social cognitive disorders such as autism spectrum disorders (Wang & Hamilton, 2012; Duffy & Chartrand, 2015). Thus, investigating the neurocognitive mechanisms of behavioural mimicry can contribute to our knowledge of implicit social processes relevant for daily interactions. However, only a handful of studies have started to address naturalistic behavioural mimicry from a neuroscientific vantage point (e.g. van Ulzen *et al.*, 2013; Hogeveen, Chartrand, *et al.*, 2015; Hogeveen, Obhi, *et al.*, 2015).

The behavioural mimicry literature has advocated the "perception-behaviour link" as the basic mechanism underlying the behaviour (Chartrand & Bargh, 1999; Chartrand & van Baaren, 2009) and suggests that the phenomenon is underpinned by "mirroring" mechanisms (for a review see Rizzolatti & Sinigaglia, 2010). A myriad of human cognitive neuroscience studies have demonstrated that observation of another individual performing an action activates one's own motor system, a process referred to as sensorimotor simulation (Fadiga *et al.*, 1995; Chong *et al.*, 2008; Kilner *et al.*, 2009; Mukamel *et al.*, 2010; for reviews see Caspers *et al.*, 2010; Fox *et al.*, 2016). Similarly, behavioural studies inspired by the "common coding approach" have shown that action perception and action execution are mutually interdependent (Prinz, 1997). For instance, in response compatibility paradigms (RCPs), interference in motor performance of movements occurs when concurrently-observed movements are incongruent to those being carried out (Brass *et al.*, 2000, 2001; Kilner *et al.*, 2003).

However, these studies were not designed to capture the implicit, communicative nature of behavioural mimicry. For instance, in RCP tasks, although referred to as a laboratory version of behavioural mimicry (Heyes, 2011), participants are prepared to perform the simple, pre-defined target actions that they simultaneously observe. This experimental approach is fundamentally different from the unpredictable and open-ended nature of mimicry. It might be argued that some neuroimaging studies alleviate this problem by using passive observation of actions. This is often the case in single-pulse transcranial magnetic stimulation (spTMS) measuring corticospinal facilitation. In such paradigms, an individual's primary motor cortex (M1) is stimulated with a magnetic pulse and motor evoked potentials (MEPs) are recorded using electromyography (EMG) from the muscle controlled by that region of M1 (Fadiga *et al.*, 1995, 2005). This method has provided evidence for time-locked, effector-specific sensorimotor simulation; MEPs are higher during passive observation of someone else performing an action with the same effector as the effector being targeted on the participant's M1 than during the observation of a static hand or a baseline (Strafella & Paus, 2000; Gangitano *et al.*, 2001; Borroni *et al.*, 2005; Romani *et al.*, 2005; Alaerts *et al.*, 2009). Still, such studies use simple stimuli displaying single effectors and, importantly, lack an interactive context, limiting the translation of these findings to natural contexts.

In an attempt to start bridging this gap, van Ulzen, Fiorio and Cesari (2013) used an spTMS approach to measure sensorimotor simulation in a mimicry-like paradigm. Participants observed an actor performing clerical tasks whilst either touching his face or not, and spTMS pulses occurred during face touching in the face-touch condition and at moments the actor was not moving his hands in the no-face-touch condition. Higher MEPs were recorded in the face-touch videos than in the no-face-touch videos and baseline, providing the first evidence for the feasibility of using MEP techniques in combination with noisier, more naturalistic stimuli (van Ulzen *et al.*, 2013). However, the stimulus videos entailed non-interactive observation, leading to two main limitations. First, contrary to what happens during social interactions, the task of remembering the order of clerical chores still required participants to focus on the actor's motor behaviour rather than on communication with an interaction partner. Second, the stimuli themselves did not yet capture the dynamics of a typical social interaction including eye contact and information exchange.

The aim of the current study was to investigate whether a well-controlled MEP paradigm that reflects natural interactions and is amiable to a communicative cover task can be applied to investigate the role of sensorimotor simulation in behavioural mimicry. Building on the methodology used in previous spTMS studies on sensorimotor simulation, we wished to test whether behavioural mimicry leads to effector-specific increases in sensorimotor excitability during naturalistic action observation. To this end, we adapted a photograph description cover task commonly used in behavioural mimicry experiments (Lakin, 2013). Participants were informed that the study concerned the neural underpinnings of memory and communication between two individuals. In the stimulus videos, the confederates (thought to be past participants) described photographs to the participant while concurrently performing predefined behaviours typical of the mimicry literature. The participant's task was to listen to the descriptions to be able to subsequently identify the photographs in a recognition task. spTMS was used to elicit MEPs in the participants' right index and little fingers while participants were viewing the confederates describe the photographs. Importantly, general arousal effects were assessed by applying spTMS at different timings during each video, both while the confederate performed a behaviour ("behaviour pulses") and while the confederate sat still and described the picture ("catch pulses", used as internally-valid baseline). Comparing these types of pulses to fixation cross pulses allows for discriminating between behaviour-specific facilitation and general task-related arousal. Indeed, while behaviour-specific facilitation would predict higher corticospinal excitability selective for observation of motor behaviours, an extension of facilitation to “catch pulses” would be indicative of general arousal due to observation of complex naturalistic visual scenes and task-related processing (see Labruna *et al*., 2011). Moreover, the sensorimotor and somatotopic specificity of our effect was investigated by exposing participants not just to the target behaviours performed with the same effector from which MEP were recorded (i.e. hand behaviours, face rubbing and finger tapping), but also to control behaviours performed with different effectors (i.e., leg crossing and foot bouncing). Here, behaviour-specific, somatotopic facilitation of corticospinal excitability would predict an heightening of MEP in hand muscles selective for observation of hand behaviours, while an extension of facilitation to observation of leg or foot behaviours would be indicative of general sensorimotor arousal due to the observation of unspecific biological motion. Finally, to allow for investigation of magnitude effects in the sensorimotor activation, behaviours of different spatial extents were used; for each effector, there was a behaviour in which the effector covered a larger distance across the body (referred to as large behaviours; face rubbing and leg crossing) and one in which the effector only moved slightly (referred to as small behaviours; finger tapping and foot bouncing).

Materials and Methods

Participants

Eighteen female participants between the ages of 20 and 33 were recruited for participation via a database of volunteers. Due to a technical problem, insufficient data was acquired for one participant. The final sample consisted of 17 female participants (M_{age} = 25.12 ± 4.08 years).

Only female participants were selected in order to avoid inadvertent gender-group effects that have been shown to influence mimicry (Lakin *et al.*, 2008). Participants were screened for any contraindications for TMS and gave their written informed consent prior to participation. All but one participant were right-handed as confirmed by the Standard Handedness Inventory (Briggs & Nebes, 1975; NB the conclusions of the statistical analyses reported in the results section were unchanged when run without the left-handed participant). Participants received monetary reimbursement and were debriefed as to the purpose of the experiment. The project was approved by the ethics committee of the Fondazione Santa Lucia and was carried out in accordance with the ethical standards of the 1964 Declaration of Helsinki.

Stimuli

Stimulus videos Each stimulus video depicted the full body of one of two female models sitting on a chair (Figure 1). The models were professional actresses paid for their participation in stimulus recording. Two models were used in favour of one in order to minimise the influence of possible idiosyncrasies of a single model (as a control, likeability was assessed, see Procedure). In each stimulus video, the model described a photograph following a script as though they were spontaneously describing it. They carried out target behaviours according to a pre-defined timing scheme. While not carrying out any upper or lower limb behaviours, the model sat with her legs crossed, her right hand resting on the arm of the chair and her left hand not visible (Fig.1.a,b). The models freely moved their gaze, looking at the photograph (adjacent to the camera), the camera, and upwards as if in thought. On average, stimulus videos lasted 50.2 ± 2.28 s.

The models carried out four types of behaviours in two effector categories, each with two types of behaviours; hand behaviours included face rubbing (Fig.1.c) and finger tapping (Fig.1.d), and leg behaviours included leg crossing (Fig.1.e) and foot bouncing (Fig.1.f). Per effector, one of the two behaviours was a large behaviour as the models' effector covered more distance (i.e. face rubbing and leg crossing), and the other was more subtle, only moving a small distance between start and finish positions (i.e. finger tapping and foot bouncing). With respect to the hand behaviours, face rubbing included a full hand behaviour while finger tapping entailed primarily the FDI. This distinction was included to allow for a further investigation of muscle-effector-specificity effects in the ADM and FDI, see Results section. Behaviours lasted on average 3.00 ± 0.84 s per stimulus video, the model carried out four behaviours of one effector category. In other words, in each video, four repetitions of either only hand or only leg behaviours were shown, resulting in "hand videos" and "leg videos".

Participants observed 18 stimulus videos per model (i.e. nine hand and nine leg videos), hence 36 stimulus videos in total. Model identification was aided by framing the stimulus video on the left and right sides with yellow for one model and blue for the other, counterbalanced across participants (see Fig.1). See Supplementary Materials for a selection of stimulus videos.

Stimulus photographs The photographs described in the stimulus videos belonged to one of three categories: landscape, abstract sculptures, and houses. Landscape and house photographs were acquired from Wikimedia Commons and sculpture photographs were selected from the stimulus set of Era, Candidi, and Aglioti (2015). A pilot survey was performed to match stimulus photographs on the extent to which they elicited arousal and attention and how beautiful they were, as well as each photograph's resemblance to a matched distracter stimulus photograph (see below).

EMG and TMS

EMG was measured with surface Ag-AgCl cup electrodes (1-cm-diameter) placed over the first dorsal interosseous (FDI) and abductor digiti minimi (ADM) of each participant's right hand using a belly-tendon montage, with the ground electrode on the ventral wrist. Two additional electrodes were placed on each participant's right leg, as if to measure EMG activity from the tibialis anterior muscle. The latter was done in order to not influence participants' covert attention to their own right hand over right leg. Accordingly, participants were briefly shown the online EMG signal of voluntary muscle contractions before stating the experimental session to ensure that they understood the procedure and necessity of remaining relaxed. EMG activity from the leg muscle was recorded but not further processed, as no MEP from the leg muscle can be expected by stimulation of the optimal scalp position for hand muscles.

Recordings were made using a CED Power 1401 (Cambridge Electronic Design Ltd., Cambridge, UK) connected to an Isolated Patient Amplifier System Model D360 (Digitimer Ltd., Hert- fordshire, UK), and interfaced with CED Spike 2 software. The second-order Butterworth filter was set between 20 Hz and 2.5 kHz (1 kHz sampling rate). A 50 Hz notch filter was also applied. Signals were displayed at a gain of 1000.

Focal TMS was performed with a figure-eight stimulation coil (outer diameter of each wing 70 mm, Magstim polyurethane-coated coil), connected to a Magstim 200 Mono Pulse (Magstim Whit- land, Dyfed, UK), over the left primary motor cortex. The optimal scalp position for eliciting MEPs in FDI was found by moving the coil in steps of 1 cm from the vertex while holding the coil tangential to the scalp with the handle pointing caudally and laterally at 45° from the midline. Individual resting motor threshold (rMT) was defined as the lowest stimulus intensity evoking five of ten MEPs with an amplitude of at least 50 μV. Participants' rMT ranged between 43% and 63% of maximum stimulator output (M = 53.41

± 7.43%). Stimulus intensity was kept at 20% above rMT during data collection (M = 64.65 ± 8.71%). EMG recording started 150 ms before TMS so as to be able to discard trials in which a muscular pre-activation (i.e. EMG signal exceeding 50 μV) was detected. The MEP peak-to-peak amplitude was measured as an index of corticospinal excitability (Fadiga *et al*., 2005) and stored for off-line analysis.

During the experiment, TMS pulses were triggered by a photodiode placed on the bottom left of the screen that sent a transistor-transistor logic signal discharging the TMS. The photodiode was triggered when the screen underneath it turned black on the target frame of the stimulus videos (not visible to participants).

Procedure

At the start of the experimental sessions, participants were comfortably seated in front of a 17-inch monitor (1151 × 964 pixels, refresh frequency of 60 Hz) at a distance of 60 cm with their right arm and right leg relaxed on supportive pillows. Participants were informed that the experiment would investigate the effects of TMS on memory and communication abilities. They were told that they had been selected to play the role of “receiver” and that they would be watching videos of two other participants previously selected to play the role of “senders”. These senders (in actuality the stimulus video models) would be describing pictures and the participant’s task would be to closely attend the videos in order to later identify the described pictures in a recognition test. In order to ensure that participants’ would remain attentive throughout the experiment, they were informed that their own and the senders’ reimbursements were dependent on their recognition performance. Participants were instructed to remain relaxed throughout the experiment and that the EMG measurement was used simply to ensure that they did not move as this could influence the effect of TMS during the task.

The experiment started and ended with a block of 18 fixation cross trials in which a fixation cross was presented at the center of the screen for 2 s. A TMS pulse was delivered between 1000 and 1600 ms from presentation of the fixation cross, with a random inter-trial interval ranging from 10 to 11 s.

Four experimental blocks were presented. Within each block, only one model's videos were presented: they consisted of four stimulus videos of one behaviour category (e.g. hands) and five of the other (e.g. legs) in randomised order within the block. Block order was pseudo-randomised per participant such that the model in the video alternated between blocks. Stimulus presentation and randomization were controlled by E-Prime v2.1 software (Psychology Software Tools Inc., Pittsburgh, PA).

Per stimulus video, three MEPs were induced, two during a behaviour (i.e. behaviour pulses) and one while the model in the video was describing the picture but not carrying out a target behaviour (i.e. catch pulses). This latter pulse was introduced to record corticospinal facilitation due to naturalistic observation independently from specific body movements. Since the models carried out four target behaviours per video and only two behaviours were pulsed, there were also two non-pulsed behaviours per video (i.e. catch behaviours). This ensured that participants would not form an association between the TMS pulses and the target behaviours as only half of the behaviours would be accompanied with a pulse. Behaviour pulses were pseudo-randomised to occur 1, 1.5, or 2 seconds into the start of a behaviour. Inter-pulse interval within the video was at least 10 s (M = 18.12 ± 7.40 s) based on research that showed no change in corticospinal excitability with repetitive TMS at 0.1 Hz for 1 h (Chen *et al.*, 1997). Similarly, behaviour onset always occurred at least 5 s after the end of the previous behaviour. Overall, 18 MEPs per pulse type were recorded per participant (i.e. 18 catch MEPs during hand videos, 18 catch MEPs during leg videos, 18 face rub MEPs, 18 finger tap MEPs, 18 leg cross MEPs, and 18 foot bounce MEPs).

At the end of each block, a recognition test was presented. Each of the described photographs from that block was shown paired with a distracter stimulus photograph for 5 s, after which participants were asked to indicate which of the two pictures had been described by the sender during the block. Stimulus photograph category was pseudo-randomised within and across stimulus video blocks; in doing so, each block contained three photographs of each of the three categories (i.e. landscape, sculptures, houses). After the recognition test of each block, participants were asked to rate how much the sender's descriptions helped them recognise the photographs, by using a visual analogue scale ranging from 'not at all' to 'very much so'. Finally, at the end of the experiment, participants were asked to rate the two senders on five measures of liking (i.e. similarity, niceness, beauty, trustworthiness, likability) on the same visual analogue scale.

Following the experiment, a funneled debriefing questionnaire was administered (Chartrand & Bargh, 1999). Participants were first asked whether they believed the cover story. Next, participants were asked whether they believed that the actresses were indeed past participants. Then, participants were asked whether they had noticed the models' behaviours, and if so, which behaviours they noticed. At the end, the participants were debriefed as to the true aim of the experiment.

Data Handling and Analysis

Individual mean MEP amplitudes were calculated as peak-to-peak distance in mV, and averaged for each experimental condition. MEP amplitudes that fell 2.5 SDs above or below each participant's mean for that experimental condition, trials contaminated by muscular pre-activation, and MEPs lower than 0.05 mV were excluded. On average, 1.99 ± 0.20 % of the total number of trials were excluded. To rule out the possibility of a general change in corticospinal facilitation during the course of the experiment, control analyses were performed comparing the pre- and post-fixation MEPs per muscle.

First, mean experimental MEP amplitudes were normalized on (i.e. divided by) the individual's mean MEP amplitude of the fixation blocks and compared to 1 using one-sample t-tests corrected for multiple comparisons. To double-check these results, we also performed a reversed normalisation dividing individual's mean MEP amplitude of the fixation blocks by each individual's mean experimental MEP amplitude, and we compared these values to 1 using one-sample t-tests. This comparison of "fixation-normalised" MEPs informs the extent to which there was a general enhancement of corticospinal facilitation during naturalistic observation as compared to the fixation cross baseline: in the first normalization, values that are significantly higher than 1 indicate heightening of corticospinal excitability; in the second analysis, values that after reversed normalisation are significantly lower than 1 indicate heightening of corticospinal excitability

Next, specific somatotopy of corticospinal facilitation during behaviour observation was investigated. In order to control for the possible general arousal effect stemming from the observation of the naturalistic videos, MEPs recorded in each video during the observation of a behaviour were normalised on the MEP recorded during the catch pulse of that specific video. Thus, we could investigate whether the corticospinal facilitation measured by MEP in hand muscle during the observation of a motor behaviour is effector-specific (i.e., selective for hand behaviours) or generalises to motor behaviours performed with a different effector than the one in which MEP are recorded (i.e., generalises to leg behaviours). This data preparation led to the inclusion of at least 9 and on average 14.82 ± 0.83 trials per behaviour type, per muscle, per participant. The mean "catch-normalised" MEPs were entered into a repeated measures within-participants ANOVA with the factors muscle (ADM vs. FDI), effector (hand vs. leg) and behaviour size (large vs. small). All tests of significance were based upon an α level of 0.05 and Bonferroni corrections were used where needed.

Results

For each muscle, mean values of MEP amplitudes during the pre-fixation did not differ from the post-fixation (*p*s> 0.80, 2-tailed paired-sample t-tests per muscle), indicating that there was no change in corticospinal facilitation during the course of the experiment.

The analysis on the data normalised on fixation showed that MEPs were higher than 1 (indicating an enhancement of corticospinal excitability) in both muscles. More specifically, ADM MEPs showed significant corticospinal facilitation in all conditions (all $ps_{corr} < .027$). For the FDI, the finger tap MEPs showed a statistical trend towards significance ($p_{corr} = .06$), while all other MEPs also demonstrated significant general corticospinal facilitation as compared to fixation trials (all $ps_{corr} < .001$). With regard to the reversed normalisation, the analysis showed that reverse-normalised MEP values were lower than 1 (indicating an enhancement of corticospinal excitability) in all experimental conditions and in both muscles except than in FDI during the observation of finger tapping. More specifically, ADM MEPs showed significant corticospinal facilitation (all $ps_{corr} < .036$). For the FDI, the t-test on finger tap MEPs was not significant ($p_{corr} = .1$), while all other MEPs also demonstrated significant general corticospinal facilitation as compared to fixation trials (all $ps_{corr} < .001$). Results from the two analyses on fixation-normalized MEP were thus coherent.

The mean values of the catch-normalised MEP amplitudes are shown in Figure 2. In the RM ANOVA the only significant effect was the main effect of behaviour size (all other *p*s > 0.120). The larger behaviours (i.e. face rub and leg cross; M = 1.28) elicited significantly higher MEPs than the smaller behaviours (i.e. finger tap and foot bounce; M = 1.16; F(1,16)

= 7.71, p = .013, $\eta_p{}^2$ = 0.325). As there were no interactions, muscle-effector-specificity between the two types of behaviours and the two recorded muscles were not tested further.

Finally, the debriefing results were used to check for possible alternative explanations. Only two participants did not believe the cover story (i.e. that it concerned a memory experiment) but excluding them from the RM ANOVA did not affect the conclusions (main effect behaviour size: p = .035, all other *ps* >*.2*). Also, four participants did not believe that the models were past participants but excluding them from the RM ANOVA similarly did not change interpretation of the results (main effect behaviour size: p = .017, all other *ps* >*.2*). Participants' awareness of the behaviours reflected the main effect of behaviour size (see Table 1). Whereas nearly all participants noticed the face rub and leg cross behaviours, only 7 noticed the finger tap and just 1 noticed the leg bounce.

Additional Task Measures

Performance on the photograph recognition task was near ceiling, with an average accuracy of 96.57% ± 3.74. Participants did not rate one model's descriptions as better than the other's (p > .250), nor did they prefer one model over the other on any of the liking measures at the end of the experiment (*p*s > .144).

Discussion

Whereas in other areas of social interaction research neuroscientific methods are used online during naturalistic behavioural paradigms (Kourtis *et al.*, 2010; Meyer *et al.*, 2011; Sacheli, Aglioti, *et al.*, 2015; Candidi, Curioni, *et al.*, 2015), this has rarely been realised in mimicry research (for exceptions see Hogeveen, Obhi, *et al.*, 2015; van Ulzen *et al.*, 2013). Instead, our understanding of the neural mechanisms of behavioural mimicry is limited to indirect translations from neuroimaging during observation of simple behaviours and RCPs. To start addressing this disparity between artificial paradigms and natural mimicry behaviour, this study used spTMS to measure corticospinal facilitation while participants observed naturalistic stimuli as part of a cover task.

Comparisons of MEPs recorded while participants observed confederates only describing photographs and while the confederates were also performing behaviours allows us to disentangle the extent to which general and effector-specific sensorimotor simulation is elicited during naturalistic action observation. If naturalistic behaviour observation triggers non-time-locked general sensorimotor arousal, MEPs recorded during video observation (hence also including pulses occurring while the confederate was only describing the photographs without performing a target behaviour) should be higher than during a fixation-cross baseline. Also, if natural sensorimotor simulation during a realistic communicative task is generally triggered by observed behaviours, higher MEPs for larger behaviours than smaller behaviours should be expected. Finally, if sensorimotor simulation is effector-specific as during passive action observation paradigms (Strafella & Paus, 2000; Urgesi, Candidi, *et al.*, 2006; Urgesi, Moro, *et al.*, 2006; Alaerts *et al.*, 2009), MEPs during observation of hand behaviours should be significantly higher than leg behaviours.

MEPs were higher during video observation than during a fixation-cross baseline, regardless of whether or not the confederate was performing a behaviour or which behaviour it was. This indicates that, *per se*, observation of naturalistic visual scenes depicting a person talking enhances corticospinal excitability: this might be possibly associated with a general arousal effect due to the complexity of the "social" situation or to the requirement of paying attention to the video in order to later perform the recognition task. This result is in line with previous evidence indicating that task-related processing might enhance corticospinal excitability independently from action observation (Labruna *et al.*, 2011). However, when correcting data for this general arousal effect by normalising MEP recorded during "behaviour pulses" on those recorded during "catch pulses", corticospinal facilitation was higher for the larger behaviours, face rubbing and leg crossing, than the smaller behaviours, finger tapping and foot bouncing, regardless of effector. This was the case for both recorded muscles and for both hand and leg behaviours. The above pattern of results indicates that the enhancement of corticospinal excitability during behaviour observation was independent from somatotopy and rather modulated by the spatial extent of the observed motor behaviour.

This finding of general sensorimotor arousal occurring during naturalistic observation of another individual is in line with past MEP studies. Van Ulzen, Fiori, and Cesari (2013) did not find significant differences in MEPs from the face-touch condition and those measured during observation of a static image of the seated confederate, suggesting that the motor cortex is already generally active when observing an individual (in a static image or in a video). Correspondingly, Hogeveen and Obhi (2012) found that following a social interaction, participants' MEPs while observing human actions were significantly higher than for robotic actions, while this was not the case for participants who had not first engaged in a social interaction. Together, these MEP findings indicate that sensorimotor simulation during naturalistic observation of others is generally heightened and that this general enhancement extends beyond the duration of a single observed action.

Furthermore, in the present study, there was also behaviour-related corticospinal facilitation as evident from the statistically large effect of behaviour size ($\eta_p^2 = 0.325$) in the main analysis of the catch-corrected data. In other words, beyond the general arousal effect of observing another individual, observing that individual performing a behaviour caused additional sensorimotor arousal. This suggests that during a natural interaction in which mimicry typically occurs, observing a behaviour will increase general sensorimotor arousal, perhaps to the extent that a behaviour would actually be executed. In line with this more general sensorimotor simulation mechanism, behavioural mimicry experiment methodologies are not always specific regarding the precise behaviour execution nor the timing thereof (van Ulzen *et al.*, 2013). Repetitive behaviours, such as face touching, are used widely in behavioural mimicry studies and are often demonstrated regularly throughout the interaction by the confederate (Lakin, 2013). The description of how these face touch behaviours are coded is often limited, such that it could be interpreted by the reader to be considered mimicry if an individual *rubs* his chin several *seconds* after seeing an interaction partner *scratch* her forehead. Thus, the subjective experience of mimicry and related social consequences (Chartrand & Lakin, 2013) might not require a one-to-one matching of effectors, muscles and timing. Interestingly, the results from this study indeed reflect this more general type of sensorimotor simulation.

While this study provides evidence for general sensorimotor arousal occurring during naturalistic observation of others, no clear effects of observed-effector specificity were found in the analysed MEPs, which were recorded in participants' right hands. This might seem in contrast with previous studies (see Fadiga *et al.*, 2005 for a review) showing a time-locked and highly specific somatotopic effect of action observation on corticospinal excitability. In interpreting this finding, it is important to consider that the corticospinal facilitation measured here was elicited in a different context with respect to that of past studies. Typical MEP studies ensure participants' full visual attention by presenting simplistic single-effector actions, and can hence carefully manipulate action-pulse timing (Fadiga *et al.*, 2005). Such paradigms have shown that corticospinal facilitation during action observation is effector-specific (Strafella & Paus, 2000; Romani *et al.*, 2005; Urgesi, Candidi, *et al.*, 2006; Urgesi, Moro, *et al.*, 2006; Alaerts *et al.*, 2009), anticipates the time-course of action kinematics (Urgesi *et al.*, 2010) and is influenced by whether the observed action is successful (Aglioti *et al.*, 2008; Candidi *et al.*, 2014). Importantly, these findings highlight characteristics of sensorimotor simulation that can be crucial in other social contexts, such as when coordinating with a partner during joint action (Knoblich & Jordan, 2003; Bekkering *et al.*, 2009; Vesper *et al.*, 2010, 2013, Sacheli, Candidi, *et al.*, 2015). On the contrary, in our "social" context we find evidence in favour of an unspecific, general facilitation that is independent from the specific motor behaviour observed by the participant. Crucially, the confederates' motor behaviour was irrelevant for the participants' task, which instead focused on the verbal descriptions: this differentiates our task from "classical" MEP studies on action observation (Fadiga *et al.*, 2005) and makes it more similar to real-life communicative situations in which mimicry usually occurs. Taken together, the relevance of the observed behaviours and the need for fast predictions to ensure appropriate interactive responses likely dictate the level of sensorimotor simulation. This also indirectly suggests that the highly specific somatotopic effects shown by previous spTMS studies on action observation might capture a slightly different sensorimotor effect than that entailed in social situations in which behavioural mimicry usually emerges.

Moreover, it can also be the case that both the specific and more general functions of sensorimotor simulation might be interlinked and concurrently occur in interactive situations. For example, this is evident when participants need to precisely synchronise with a partner but still show a socially-induced modulation of involuntary simulation of their movements (Sacheli, Christensen, *et al.*, 2015). Indeed, the terms perception-behaviour link or sensorimotor simulation have been used to refer to the mechanisms of a range of behaviours and processes and likely indicate activity of a shared neural substrate. Importantly, however, only through context-specific investigations does it become clear which sub-mechanisms are involved and to which extent. Future work could investigate this possible distinction between specific and general sensorimotor simulation by comparing observed-effector specificity for a range of motor movements across a spectrum of non-social to social contexts.

The notion of context-specific investigations has proved insightful in other areas of sensorimotor simulation research. For example, neuroimaging studies have long since identified differences in simply observing an action versus observing an action to subsequently imitate it (Grezes *et al.*, 1998; Suchan *et al.*, 2008; Schuch *et al.*, 2010). The notion of context-specificity therefore emphasises that using substitute tasks like RCPs to infer possible mechanisms of another behaviour, like mimicry, should be exercised with caution. Indeed, this distinction was recently demonstrated in a transcranial direct current stimulation study. The roles of two regions thought to influence sensorimotor simulation, the inferior frontal cortex and the temporal-parietal junction, were dissociated, demonstrating that each had a distinct effect on producing behavioural mimicry and performance on a RCP (Hogeveen, Obhi, *et al.*, 2015).

Overall these observations and our results highlight the caveats of using non-naturalistic set-ups as a proxy for natural social behaviours. This might also hold when social modulations of behavioural mimicry are taken into account. Many of the social factors found to influence behavioural mimicry also affect performance in RCPs (Leighton *et al.*, 2010; Wang *et al.*, 2011; Hogeveen & Obhi, 2013). Correspondingly, corticospinal facilitation can be also influenced by social factors, such as social groups (Désy & Théoret, 2007; Molnar-Szakacs *et al.*, 2007) and social power (Hogeveen *et al.*, 2014). However, just like the features of corticospinal facilitation might change depending on the context, RCPs and spTMS results are perhaps not sensitive to all of the same social factors as mimicry (see for instance Farmer *et al.*, 2016). Thus, future behavioural mimicry research should take further steps to closely match experimental context with the ecological context of interest.

Although the general sensorimotor arousal effects found in this study can go a long way in explaining the breadth of temporally spaced effects found in the behavioural mimicry literature, some level of anatomical specificity would nevertheless be required for mimicry to be experienced as such. Subjectively, it would not be perceived as mimicry if one individual crossed their legs after they observed their interaction partner rub their face. However, such evidence for somatotopic mapping between observed behaviours and corticospinal facilitation was not clear in this study. One limitation of the cover task and naturalistic stimuli is that participants were free to look anywhere, likely leading them to primarily fixate on the face. Indeed, only 41% of the participants reported noticing the finger tap at all during the experiment and just a single participant noticed the leg bounce. Moreover, for those participants who did notice, the likely fewer trials in which the behaviour was observed was averaged with the likely more numerous trials that the behaviour was not being observed at the time of the TMS pulse. This matter could be investigated in future simultaneous TMS and eye-tracking studies utilizing such naturalistic stimuli. It would then be expected that particularly when the behaviours were fixated on, the enhancement of sensorimotor arousal would be highest. Also, expanding our experimental design by recording MEPs from both hand and leg muscles (i.e., by targeting M1 on both the hand and leg area in different sessions) could further help to understand the specificity of somatotopic effects during naturalistic behaviour observation. Nonetheless, the pattern of results found in this study provide a starting ground for further investigations into the role of sensorimotor simulation in producing behavioural mimicry.

In conclusion, this study employed a naturalistic spTMS paradigm to measure the nature of online sensorimotor simulation that could play a role in producing behavioural mimicry. General arousal effects were found, as observing the stimulus videos elicited increased corticospinal facilitation as compared to a fixation-cross baseline. Additionally, the size of observed behaviours affected MEP amplitudes. Taken together, this study provides support for general sensorimotor simulation being involved in producing behavioural mimicry and opens the door for novel perspectives on sensorimotor simulation in naturalistic interactions.

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Conflict of Interest Statement

The authors declare that there are no conflict of interest.

Author Contributions

JEvS, LMS, HB, SMA designed the experiment. JEvS and LMS collected and analysed data. IT supported data analysis. JEvS and LS drafted the manuscript. HB, IT and SMA edited the manuscript. SMA supervised the project. All authors approved the final version.

Data Accessibility Statement

The authors have made selected stimulus videos and the data file available.

Abbreviations

ADM: abductor digiti minimi
EMG: electromyography
FDI: first dorsal interosseous
M1: primary motor cortex
MEP: motor evoked potential
RCPs: Response compatability paradigms
rMT: resting motor threshold
spTMS: single pulse transcranial magnetic stimulation

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Tables

Table 1

Counts and percentages of participants who reported noticing each behaviour during the debriefing.

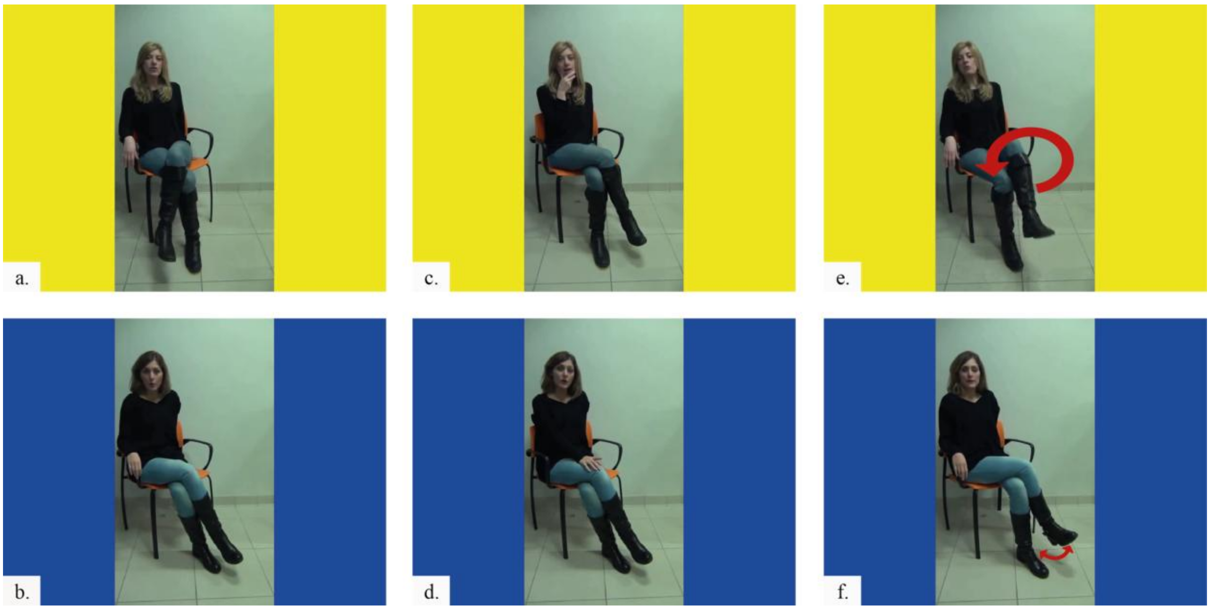
	Face Rub	Finger Tap	Leg Cross	Foot Bounce
Noticed (n)	13	7	16	1
Percentage of Sample (%)	76	41	94	6

Note. Sample size = 17.

Figure Captions

Figure 1: Still frames from the stimulus videos. Model 1 (a) and 2 (b) while not performing target behaviours; face rub (c); finger tap (d); leg cross (e); and foot bounce (f). *Note.* Arrows superimposed on still frames to illustrate movement direction. The white rectangle on the bottom left of each still frame indicates placement of photodiode. The models always sat with their right hand resting on the arm of the chair and their legs crossed to ensure that body posture was consistent across catch-pulses and across hand and leg videos. *(Color figure available online).*

Figure 2: Mean catch-normalised MEPs for each of the four observed behaviours; data recorded from the FDI and ADM muscles have been averaged, as results did not show any significant effect of muscle. Catch-normalised MEPs were calculated by dividing each behavioural MEP by the catch MEP of that video. The grey dots indicate single-subject data while the bigger black dots indicate group mean values. The bars indicate the significant main effect of behaviour size.


a.
c.
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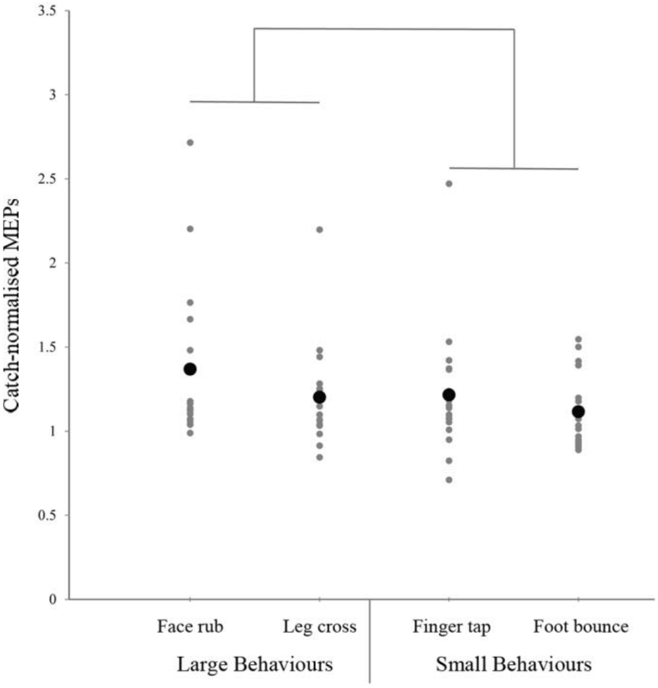
3.5
3
2.5
2
1.5
1
0.5
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Catch-normalised MEPs
Face rub
Leg cross
Finger tap
Foot bounce
Large Behaviours
Small Behaviours