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Stimulation over primary motor cortex during action observation impairs effector recognition

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ABSTRACT

Recent work suggests that motor cortical processing during action observation plays a role in later recognition of the object involved in the action. Here, we investigated whether recognition of the *effector* making an action is also impaired when transcranial magnetic stimulation (TMS) – thought to interfere with normal cortical activity – is applied over the primary motor cortex (M1) during action observation. In two experiments, single-pulse TMS was delivered over the hand area of M1 while participants watched short clips of hand actions. Participants were then asked whether an image (experiment 1) or a video (experiment 2) of a hand presented later in the trial was the same or different to the hand in the preceding video. In Experiment 1, we found that participants' ability to recognise static images of hands was significantly impaired when TMS was delivered over M1 during action observation, compared to when no TMS was delivered, or when stimulation was applied over the vertex. Conversely, stimulation over M1 did *not* affect recognition of dot configurations, or recognition of hands that were previously presented as static images (rather than action movie clips) with no object. In Experiment 2, we found that effector recognition was impaired when stimulation was applied part way through (300 ms) and at the end (500 ms) of the action observation period, indicating that 200 ms of action-viewing following stimulation was not long enough to form a new representation that could be used for later recognition. The findings of both experiments suggest that interfering with cortical motor activity during action observation impairs subsequent recognition of the effector involved in the action, which complements previous findings of motor system involvement in object memory. This work provides some of the first evidence that motor processing during action observation is involved in forming representations of the effector that are useful beyond the action observation period.

1. Introduction

As we move through the world, we encounter numerous actions performed by other people in a range of contexts. How we perceive, interpret, and respond to these actions characterises social interaction. In the last two decades, the role of the motor system in how we recognise and understand observed action has received a lot of attention. Theories of the motor system's role in these functions followed the discovery of 'mirror neurons': cells in the premotor cortex of the macaque brain that respond both to the observation and the execution of actions (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). There appears to be a similar system in humans, with activity in the human motor system showing some modulation when a movement is passively observed (e.g., Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). Most theories and empirical studies have focused on how this **m**otor **m**odulation during **a**ction **o**bservation (referred to hereafter as 'MMAO') contributes to the perception of actions in real time, and there has been very little work on what happens *after* an action is observed. In this study, we investigated whether MMAO has a function beyond the real-time processing of actions. Specifically, we asked whether interfering with motor cortical processing during action observation affects the offline recognition of the effector executing the observed action.

A recent study by Decloe and Obhi (2013) suggested a causal role of motor processing during action observation in object recognition. Transcranial magnetic stimulation (TMS) was used to briefly disrupt motor processing during a recognition memory task. On a subset of trials, a single pulse of TMS was delivered over the thumb representation of the primary motor cortex (M1) while participants viewed a movie clip showing a hand typing (with the thumb) on a mobile phone. Subsequently, participants were required to judge whether a photograph of a mobile phone showed the same or a different phone to the one they had viewed

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previously in the trial. Accuracy was lower when TMS was delivered over M1 during action observation, compared to when TMS was delivered over the vertex, or when no stimulation occurred.

A role of motor processing in object memory is also implied by the results of studies by Downing-Doucet and Guérard (2014) and Guérard and Lagacé (2014), in which participants were required to recall lists of objects. Guérard and Lagacé (2014) found that objects were better retained when the manipulability of the object was different to the manipulability of other items in the list. Importantly, a motor suppression task (moving the fingers in sequence) performed by participants during the experiment abolished this effect of manipulability isolation. In a similar study, Downing-Doucet and Guérard (2014) found that lists were better recalled when there was variation within the list in the type of grasp afforded by the objects, compared to when all of the list items afforded the same grasp. Again, this effect was abolished when participants performed a motor suppression task. The fact that motor suppression abolished the effect of varying manipulability suggests that the motor system was involved in encoding, retaining, or recalling the manipulable objects. These studies (see also Mecklinger, Gruenewald, Weiskopf, & Doeller, 2004) suggest that the motor system plays a causal role in recognition memory for objects associated with action, but exactly what is represented or retained by the motor system is unclear. In Decloe and Obhi's (2013) study, for example, it is not clear whether viewing the hand typing on the cell phone evoked a representation of the phone alone (the formation or maintenance of which was disrupted by stimulation of M1), or alternatively whether the representation of the object was embedded within a representation of the action.

In the present paper we report two experiments conducted to further explore what aspects of an object-directed action are represented in M1 and retained beyond the action observation period. Specifically, we examined the effect of stimulation applied over motor cortex on subsequent recognition of the *effector* itself. If memory for objects relies on motor representations of the action associated with the object (rather than the object alone), then effector recognition should also be disrupted by TMS. Conversely, if the effects of stimulation over M1 (Decloe & Obhi, 2013) and object affordances (e.g., Guérard & Lagacé, 2014) are mediated by representations of the object alone, then recognition of the hand associated with the object should not be affected by TMS. In the experiments reported here, participants were required to judge whether a static image of a hand (Experiment 1) or video clip of a hand action (Experiment 2) showed the same or a different hand to that seen in a video clip presented previously in the trial. In Experiment 1, on a subset of trials, TMS was delivered over the hand area of M1 during the action observation period. Participants' recognition accuracy on these stimulation trials was compared to accuracy on trials on which no TMS was applied, and trials on which stimulation was delivered over the vertex. Experiment 1 also included two non-action recognition tasks – recognition of a still hand or of a dot configuration – to examine whether any effects were specific to stimulation delivered during *action* observation. It was predicted that, if MMAO plays a role in effector recognition (as it seems to in object recognition; Decloe & Obhi, 2013), then participants' recognition of the hand should be *worse* on trials in which stimulation was delivered over M1 than when no stimulation or stimulation over the vertex was delivered. If these effects are specific to recognition of an *acting effector*, then no impairment of recognition of still hands or dots should be found.

In Experiment 2, we made three adaptations to the design of Experiment 1, to clarify certain aspects of the effects of motor stimulation on effector recognition. First, as stimulation was delivered at action *offset* in Experiment 1, we examined whether further visual exposure to the action *after* M1 interference allows recognition to recover. To address this question, the action clips used in Experiment 2 were 500 ms in duration, and TMS was delivered at 300 or 500 ms on different trials. That is, stimulation time was no longer conflated with action offset. Second, we introduced a new control condition that showed the ball (from the action clips) being compressed, but without the presence of the hand. This condition was designed to be as visually similar as possible to the action stimuli with the exception of hand presence. A final difference between Experiments 1 and 2 was that the test stimulus used in Experiment 1 was a static photograph of the hand, whereas in Experiment 2 we used moving action video clips as the stimulus that participants had to judge as the same or different.

Crucially, as our experimental designs included both control tasks (dot configurations, still hand, moving shape) *and* a control TMS site (the vertex), we eliminate the possibility that recognition impairment was a result of cortical stimulation *per se* (i.e., not specific to M1) or that the stimulation affected processing of visual stimuli generally (rather than being specific to effector recognition in an action context).

2. Experiment 1

2.1. Method

2.1.1. Participants

This sample consisted of 16 participants (11 female, 5 male) between the ages of 18 and 21. All were right-handed by self-report, and had normal or corrected-to-normal vision. Participants were students at Wilfrid Laurier University, who took part in the study for partial course credit. Prior to participation, participants provided written informed consent, and were screened for contraindications to TMS. Our screening questionnaire was based on the TMS adult safety screening questions proposed by Keel, Smith, and Wassermann (2001), with additional questions asking participants whether they experience claustrophobia, whether they had consumed alcohol in the previous 24 h, and whether they felt sleep deprived (as per the guidelines of Rossi, Hallett, Rossini, & Pascual-Leone, 2009). The study was approved by the local ethics committee, and conformed to the Declaration of Helsinki.

2.1.2. Design

The experiment used a 2×3 repeated-measures design, with the factors TMS site (M1, vertex) and stimulus type (action, still hand, dot configurations). The experimental session for each participant involved two blocks: one in which TMS was delivered over M1 and one in which it was delivered over the vertex. The order of these blocks was counterbalanced between participants. Each block contained a total of 240 trials, and TMS was delivered on 50% of these trials. For both TMS and non-TMS trials, all three types of stimuli were shown in equal numbers, such that participants saw a total of 80 action trials, 80 still hand trials, and 80 dot trials. Each individual trial showed two stimuli from the same category, with participants' task being to judge whether the second was the same or different to the first. Within every condition, half of trials were 'same' and half were 'different'. The order of trials within each block was randomised for each participant.

2.1.3. Apparatus and stimuli

The experiment was programmed using Superlab v.4.5 (Cedrus Corporation, San Pedro, CA, USA), and was run on a Dell desktop computer. Biphasic pulses of stimulation were delivered over either the hand region of M1 or the vertex (depending on the block) using a figure-of-eight coil attached to a Magstim Rapid^2 system. Electromyography (EMG) data was recorded using an MP150 data acquisition system (Biopac Systems). One ground

electrode was placed on the ulnar styloid of participants' right wrist, and two 8 mm surface electrodes were placed in a belly–tendon arrangement over participants' abductor pollicis brevis (APB) muscle (a thumb abductor). The EMG signal was acquired with a 5 kHz sampling rate, amplified (to 5 mV), and band-pass filtered at 10–500 Hz.

Action stimuli showed a female Caucasian right hand squeezing a rubber ball between the index finger and thumb. Movements performed by five different actors (i.e., five unique movie clips) contributed to the stimulus set, and all movie clips were 300 ms in duration. The non-action stimuli comprised photographs of dots and still hands. The dot photographs consisted of 6–10 white dots presented on a black background. The still hand images were stills taken from the action videos, with the ball edited out. That is, each image in the 'still hand' condition showed a hand in a grasp position but with no object visible (see Fig. 1). A single TMS pulse was delivered 300 ms post stimulus onset (i.e., at stimulus offset). At the end of each trial, participants were presented with a static image from the same category (action, still hand, or dots) and were required to indicate, via a key press, whether the stimulus was the same or different to the stimulus they had seen previously in the trial. On action trials, the stimulus used for the recognition test was a still image of the final frame of one of the action videos, with the ball itself edited out (i.e., the same type of image as those comprising the 'still hand' condition). On 50% of trials, the still showed the hand from the video that was seen previously in the trial (i.e., a 'same' trial), and on the other 50% the still was taken from one of the other four videos (a 'different' trial). For both the still hand and the dot conditions, the recognition stimuli were taken from the hand and dot stimulus sets previously described. As with the action condition, half of the trials for each of these conditions were 'same' and half were 'different' trials. For all conditions, the first (video or still) stimulus appeared centrally on the screen, but the second stimulus was presented 3.5 cm higher. This was to eliminate position-related cues that could be used by participants in the recognition task. Example stimuli and trial structure can be seen in Fig. 1. The stimuli were adjusted to achieve around 75% accuracy across the conditions. Fifteen participants (who did not take part in the main experiment) completed the experiment without TMS to ensure that performance on each condition was similar.

2.1.4. Procedure

Participants were seated in front of a 20″ LCD monitor, with their right arm placed on the desk in front of them. Their right hand was occluded by a box to eliminate the possibility that the participants would watch their hand for TMS-induced movement. The first part of the procedure involved localising the scalp position overlying the APB muscle. As a landmark, the vertex was located using the inion–nasion line and the preauricular points at the posterior end of each zygomatic arch. Next, the standard scalp position for APB representation was located at 5 cm lateral and 1 cm anterior to the vertex (Conforto, Z'Graggen, Kohl, Rösler, & Kaelin-Lang, 2004). Stimulation began at 70% of stimulator output and the coil was moved systematically around this point until the site eliciting the greatest MEP in the right APB muscle was identified. The optimal location was marked on a lycra swim cap worn by participants. Individual resting motor threshold was then defined as the lowest stimulator intensity necessary to generate MEPs ($\geqslant$50 μV peak-to-peak amplitude) in the relaxed APB muscle in 5 out of 10 consecutive TMS pulses (e.g., Cavallo, Bucchioni, Castiello, & Becchio, 2013; Rossini et al., 1994). During the experiment, stimulation intensity was set to 115% of the resting motor threshold. Stimulation intensity during recording ranged from 53% to 75% (M = 64.9%).

On each trial, a fixation cross was presented in the centre of the screen for 500 ms, followed by a blank screen. Following a variable interval of 200, 400, or 600 ms, this blank screen was replaced with a video of a right hand squeezing a rubber ball between the index finger and thumb, an image of a static hand, or an array of static dots (depending on the condition) presented for 300 ms. Following this, a visual mask was presented for 500 ms, before the second stimulus (an image of a hand squeezing the edited-out ball or a dot configuration) was presented. The participants were then required to indicate whether the hand (or the number of dots) was the same or different to that presented previously in the trial. Participants were asked to respond as quickly and as accurately as possible, and used their left middle finger to press the 'a' key to indicate the stimulus was different, or their left index finger to press the 's' key to indicate the stimulus was the same. Left hand responses were used to minimise the chance that stimulation affected manual responding itself, as stimulation over left M1 was expected to mainly affect the right hand (however, it is possible that stimulation could have affected movement of the ipsilateral effector; e.g., Donchin, Gribova, Steinberg, Bergman, & Vaadia, 1998). On 50% of trials, a single pulse of TMS was delivered (to either M1 or the vertex depending on the block) at 300 ms from stimulus onset. A blank screen was presented for 1000 ms at the end of each trial to ensure a minimum of at least three seconds remained between potential consecutive TMS pulses.

2.1.5. Data analysis

To control for any performance differences between blocks that were unrelated to our experimental manipulation (e.g., fatigue or practice effects), we calculated difference scores for participants' performance on stimulation trials (for each condition) compared to their performance on the non-stimulation trials within the same block. In this way, the analysed values represented the change in performance during stimulation compared to when no stimulation occurred. The difference scores were entered into a 2 × 3 repeated-measures ANOVA, with TMS site (M1, vertex) and stimulus type (action, still hand, dots) as factors.

For the reaction time (RT) data, any responses that were outside 3 standard deviations from the participant's original mean RT for a particular condition were excluded from the analyses. This procedure resulted in the removal of 1.38% of trials overall. Similar to the accuracy data, difference scores were calculated to represent the change in participants' RTs on TMS trials in each of the condition relative to their RTs for the same condition when TMS was *not* applied. The difference scores were then entered into a 2 × 3 repeated-measures ANOVA, with TMS site and stimulus type as factors.

All inferential statistical analyses were performed using SPSS. In cases where the assumptions of sphericity were violated (indicated by significant Mauchly's W values), Greenhouse–Geisser correction was applied. Bonferroni correction was applied for comparisons following up effects that were *not* predicted. In these cases, we reduced the alpha criterion for significance based on the number of comparisons performed within that particular follow-up analysis; the number of comparisons corrected for is specified in each case for clarity.

2.2. Results[1]

2.2.1. Accuracy

The ANOVA performed on the difference scores revealed a significant interaction between TMS site and stimulus type ($F(2,30) = 5.84$, $p = .007$, $\eta^2 = .280$; Fig. 2). Post-hoc paired-sample

[1] Please note that regrettably we no longer have the trial-by-trial data for Experiment 1, so are unable to provide or perform any additional analyses of these data in their rawest form. Summary data (averages for each condition per subject) are provided as Supplementary material.

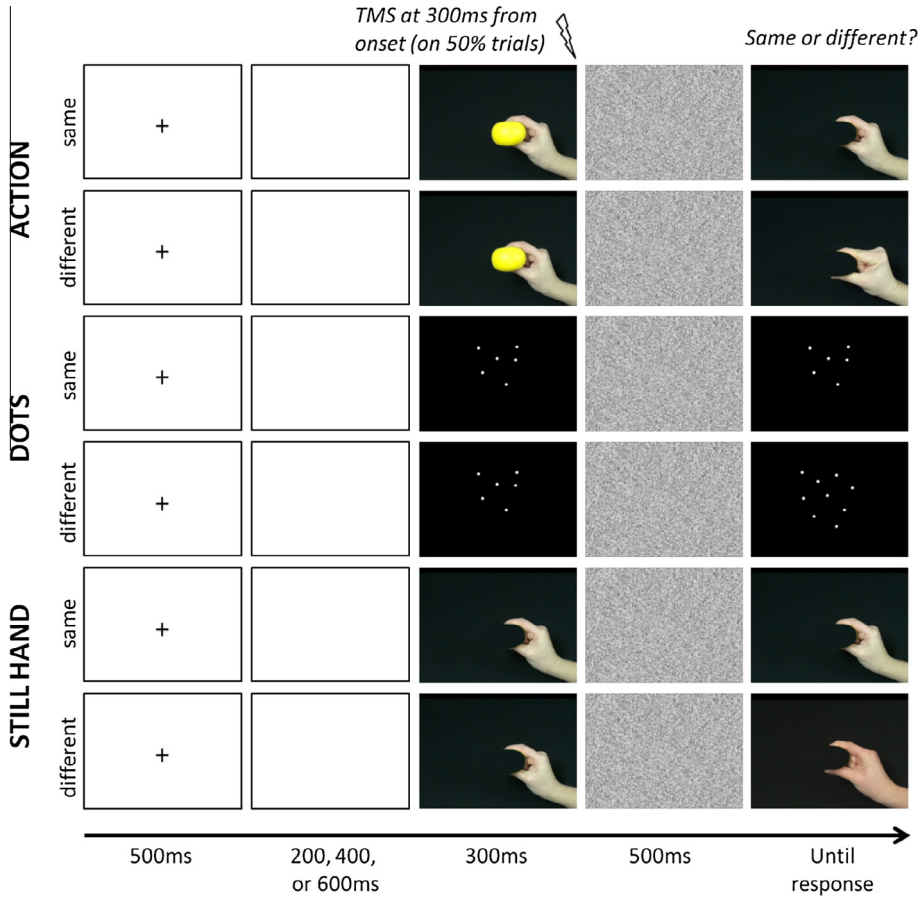

Fig. 1. Trial structure and example stimuli from Experiment 1. Note that the first stimulus was a movie for the 'Action' condition, but a still image for the 'Dot' and 'Still hand' conditions. The final 'same or different?' stimulus was always a static image.

t-tests were conducted to examine the effect of TMS site on each stimulus type (i.e., three *t*-tests comparing M1 to vertex for each stimulus type). As we predicted an effect of M1 stimulation on recognition of the action stimulus specifically, we did not apply a correction for multiple comparisons for this analysis. The *t*-tests showed a significant difference between M1 and vertex stimulation on effector recognition on action trials ($t(15) = 2.69$, $p = .017$), but no difference between M1 and vertex for either still hand ($t(15) = -.177$, $p = .862$) or dot trials ($t(15) = -.776$, $p = .450$). One-sample *t*-tests comparing the difference scores to zero showed that the only condition in which the effect of stimulation was significant (i.e., stimulation trials significantly different to non-TMS trials) was the action condition when TMS was applied over M1 ($t(15) = 3.69$, $p = .002$). No other stimulation conditions showed significant changes relative to no stimulation ($ps > .600$).

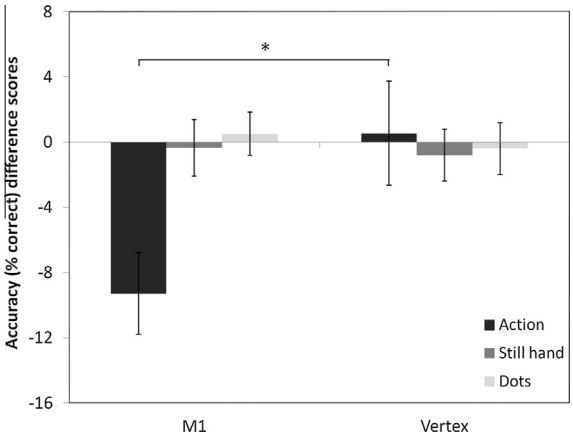

Fig. 2. Difference in accuracy (% correct) between stimulation and no-stimulation trials for each stimulus condition for each site (Experiment 1). Error bars represent standard error of the mean, and asterisks denote significant differences between conditions at the $p < .05$ level. Accuracy on action trials was significantly impaired when TMS was delivered over M1 compared to when no stimulation occurred (one-sample *t*-test comparing difference score against zero: $p = .002$).

2.2.2. Reaction times

Analysis of the RT difference scores showed no effect of TMS site ($F(1,15) = .640$, $p = .436$) or stimulus type ($F(2,30) = .149$, $p = .862$), and no significant interaction between the two ($F(1.44,21.6) = 1.77$, $p = .199$). Additionally, one-sample *t*-tests comparing difference scores to zero (testing the significance of differences between stimulation and non-stimulation trials) did not show significance for any of the conditions, although there was a trend for response times to be slower on dot trials where TMS was applied over M1 compared to non-stimulation trials ($t(15) = -2.13$, $p = .051$).

2.3. Discussion

Experiment 1 examined the effects of applying TMS over the primary motor cortex during action observation – putatively interfering with motor processing – on participants' subsequent recognition of the effector involved in an action. Our results showed that recognition of the action stimuli was significantly impaired when

TMS was delivered over M1 compared to when no stimulation was applied. In contrast, TMS over M1 did not impair recognition of still hand stimuli or dot configurations, and TMS over the vertex did not affect recognition of any stimulus type. This finding builds on the work of Decloe and Obhi (2013), who found that individuals' recognition of the *object* involved in an action was impaired when TMS was delivered over M1 during action observation. Together, these findings indicate that stimulation over the motor cortex impedes some part of the encoding, maintenance, or retention process involved in the subsequent recognition of components of observed actions.

In this experiment, TMS was delivered at 300 ms into action observation, which also marked the *end* of the action observation period. As TMS was delivered at this time point only, we do not know whether stimulation at alternative times during the observation period would have similar effects. More specifically, we do not know whether further visual exposure to the action *after* stimulation would allow the system to 'recover' or a new representation to be formed. Indeed, it is possible that this effect was specific to motor disruption occurring at action offset and not at 300 ms *per se*. In Experiment 2, we further explored the stage of processing that is affected by motor interference by presenting action clips of 500 ms in duration, and applying TMS both at 300 ms and at action offset (500 ms) on different trials. As in Experiment 1, the effects of these stimulation conditions were determined by comparing participants' performance to trials on which stimulation was delivered over the vertex or not at all.

Our use of control stimulus types (still hand, dots) in Experiment 1 ensured that the impairment of effector recognition did not arise as part of a global impairment of visual processing or recognition. However, as both of the control conditions in this experiment were static, we do not know whether the effects were specific to interfering with processing during observation of biological motion and subsequent recognition of the effector specifically. It is possible that the motor processes that were affected by stimulation are involved in the processing of any movement – biological or not – and that interfering with these processes would impair recognition of any moving stimulus. To investigate this possibility, in our second experiment we introduced a moving non-action stimulus by taking still images from the action video clips, editing out the hand, and concatenating these images into a new video clip showing the ball compressing without the hand. The result was a movement condition that was visually identical to the action stimuli apart from the presence of the effector itself.

3. Experiment 2

3.1. Method

3.1.1. Participants

Twelve students (9 female, 3 male) from McMaster University participated in the experiment in return for partial course credit or monetary reimbursement. Participants were aged 18–21 years (M = 19.6, SD = .996), and all were right-handed by self-report. The study was approved by the McMaster University Research Ethics Board, and conformed to the guidelines of the Declaration of Helsinki. Participants gave written informed consent, and underwent the same screening procedure as described for Experiment 1.

3.1.2. Design

The study followed a $2 \times 2 \times 2$ within-subject design, with the factors TMS site (M1, vertex), stimulation time (300, 500 ms) and stimulus type (action, shape). Participants completed two blocks of 320 trials (i.e., 640 trials in total). TMS was applied to M1 in one experimental block, and to the vertex in the other; the order of these blocks was counterbalanced across participants. Within each block, TMS was delivered on 50% of the trials, with an equal number of 300 ms and 500 ms stimulation trials. Half of the trials were action trials and half were shape trials. Thus, for each TMS site and each stimulus type, there were 40 trials on which TMS was delivered at 300 ms, 40 on which it was delivered at 500 ms, and 80 on which no stimulation occurred. The order of trials was randomised within each block and for each participant.

3.1.3. Apparatus and stimuli

The technical setup for this experiment was the same as that used in Experiment 1, apart from the use of 23×22 mm self-adhesive snap electrodes in the current experiment to record muscle activity.

The same action stimuli as described for Experiment 1 – showing a prone female Caucasian right hand squeezing a rubber ball – comprised the 'action' stimulus set. However, the videos were presented at a slower speed and were seen for 500 ms. The 'shape' stimuli were created using four still frames taken from one of the action videos, in which the hand was edited out. These frames were then put together to create a new movie clip which portrayed the compression of the ball with no hand visible. This stimulus was designed to be as visually similar as possible to the action condition in every respect apart from the presence of the effector. All stimuli (action and shape) were presented in greyscale so that skin tone could not be used as a cue in the subsequent recognition task. The shade (of grey) of the original shape stimulus was manipulated to create five different shape stimuli, each of which was presented on one fifth of trials for this condition (to be consistent with the action stimulus set). On stimulation trials, TMS was delivered at either 300 ms or 500 ms (i.e., action offset) relative to movie onset.

Whereas in Experiment 1 the stimulus shown at test (i.e., the second stimulus) was always a static image, in the current experiment both the first and second stimuli within a trial were movie clips. The movie clip at test was an action or shape movie clip presented at twice the speed of the clip presented at the beginning of the trial, which was repeated six times (i.e., six squeezes of the ball) or until the participant made their response. As in Experiment 1, the second movie was presented 3.5 cm higher than the original movie clip. Presenting the second stimulus higher up and at an increased speed eliminated spatial and temporal cues that could be used by participants in the recognition task. The looping of the video on its second presentation was implemented so that participants did not base their judgement on the static end position of the hand.

3.1.4. Procedure

Two EMG electrodes were positioned in a belly–tendon arrangement to record activity from the APB of the right (dominant) hand. The ground electrode was placed over the lateral epicondyle of the elbow. Coil position and stimulation intensity were determined using the approach described for Experiment 1. The stimulation intensity for participants in this experiment ranged from 62% to 90% of the maximum stimulator output (M = 77.6, SD = 9.04).

As in Experiment 1, each trial began with a fixation cross presented for 500 ms. This was followed by a blank screen presented for 200, 400, or 600 ms (randomly selected), followed by the 500 ms movie clip showing a hand action or the moving shape. Following the action or shape movie clip, a visual mask was presented for 500 ms, followed by either the same or a different movie from the same category (i.e., on each trial participants would either see two action clips or two shape clips). Participants were instructed to press the 's' key if they thought that the second movie was the same as the first, or 'd' if they thought it was different. Key press responses were made using the index and middle finger of the left

hand. Participants were instructed that on action trials they should judge whether the second clip showed the same or a different hand action, but on the shape trials they should judge whether the *colour* was the same or different in the first and second stimulus. They were instructed to respond as quickly and accurately as possible. All participants completed practice trials, which the experimenter monitored and ended once it was evident that the participant understood the task. Example stimuli and the trial structure can be seen in Fig. 3.

3.1.5. Data analysis

The data were analysed using the same approach as was used for Experiment 1. Difference scores were calculated (reflecting the effect of stimulation on performance), and these values were submitted to an ANOVA assessing effects of TMS site and stimulus type. As this experiment included the additional factor of 'time', we ran a $2 \times 2 \times 2$ repeated-measures ANOVA, with TMS site (M1, vertex), stimulation time (300, 500 ms), and visual stimulus type (action, shape) as factors. We also ran the same analysis using d-prime sensitivity values instead of accuracy. D-prime represents participants' ability to detect differences between stimuli (i.e., their sensitivity to the difference) relative to their general tendency to state that a difference was present. In addition, we calculated the response bias (criterion, 'c') for each condition, to determine whether there were significant biases in participants' responses (i.e., more 'same' or 'different' responses generally), or differences in bias between the conditions. The criterion values for each condition were submitted to a $2 \times 2 \times 3$ within-subject ANOVA, with the factors TMS site, stimulus type, and stimulation (300, 500, no stimulation). To follow-up significant interactions, we ran pairwise comparisons comparing the effect of stimulation at each *site*, for each stimulus type separately.

Difference scores were calculated to assess changes in RT compared to non-stimulation trials. These scores were then entered into a $2 \times 2 \times 2$ ANOVA. The analysis was run including all of the trial data, and also with values that were 3 standard deviations from the mean excluded. Both showed the same pattern of results, so the reported statistics are based on the full datasets with no data points removed.

3.1.6. Motor-evoked potentials

The amplitude of MEPs elicited by TMS over M1 was defined as the difference between the minimum and maximum values of the EMG signal in a 10–40 ms window following the stimulation pulse. For each participant, we calculated the mean amplitude of the EMG signal in the 100 ms preceding the TMS pulse, and excluded any trials for which the EMG amplitude during this period was more than 3 standard deviations away from the mean. This resulted in the exclusion of 3% of trials (similar rates of exclusion can be seen in other similar studies, e.g., Mahayana et al., 2014; Obhi, Hogeveen, & Pascual-Leone, 2011; Urgesi, Moro, Candidi, & Aglioti, 2006).

3.2. Results

3.2.1. Accuracy

Our 3-way ANOVA revealed a main effect of TMS site ($F(1,11) = 12.9$, $p = .004$, $\eta^2 = .540$), and a significant interaction between site and stimulus type ($F(1,11) = 6.51$, $p = 027$, $\eta^2 = .372$; Fig. 4). As the 3-way interaction between site, stimulus type, and time was not significant ($F(1,11) = .325$, $p = .580$, $\eta^2 = .029$), subsequent analyses were performed on data collapsed across the two stimulation time conditions. Paired-sample *t*-tests comparing the effect of TMS site for the action and shape conditions separately showed a significant difference between M1 and vertex stimulation for action trials ($t(11) = 3.96$, $p = .002$) but no difference between M1 and vertex trials for the shape condition ($t(11) = .531$, $p = .606$). One-sample *t*-tests comparing the difference scores against zero showed that accuracy was significantly impaired on action trials where TMS was delivered over M1 ($t(11) = 2.39$, $p = .036$), but not for shape trials or trials where TMS was applied over the vertex ($ps > .09$). As effects of stimulation over M1 on the action trials were predicted, corrections for multiple comparisons were not applied for these analyses. The main effect of site was driven by accuracy being significantly lower for M1 compared to vertex trials.

3.2.2. Sensitivity (d')

The ANOVA performed on the d-prime scores showed main effects of site and stimulus type. Post-hoc pairwise comparisons showed that the effects of stimulation were larger for M1 than vertex stimulation ($F(1,11) = 20.9$, $p = .001$, $\eta^2 = .655$), and for action than for shape trials ($F(1,11) = 6.05$, $p = .032$, $\eta^2 = .355$). Importantly, this analysis confirmed the significant interaction between stimulus type and site that was evident in the accuracy scores ($F(1,11) = 4.95$, $p = .048$, $\eta^2 = .310$). As we did for accuracy, paired-sample *t*-tests were conducted to compare the change in sensitivity for M1 versus vertex stimulation trials for each stimulus type. This revealed a larger decrease in sensitivity to the *action* stimuli following M1 stimulation compared to vertex stimulation ($t(11) = 3.83$, $p = .003$), but no difference between M1 and vertex for the shape condition ($t(11) = .655$, $p = .526$). Finally, one-sample *t*-tests performed to examine whether sensitivity was significantly different to baseline (i.e., no stimulation) showed that the only condition for which sensitivity was significantly different to no-stimulation was the action condition within the M1 stimulation block ($t(11) = 2.93$, $p = .014$). Thus, the sensitivity scores showed the same pattern of effects as the accuracy scores.

3.2.3. Response bias (criterion)

The results of our $2 \times 2 \times 3$ ANOVA showed a main effect of stimulation on response bias ($F(2,22) = 5.04$, $p = .016$, $\eta^2 = .314$), and an interaction between stimulation and stimulus type ($F(2,22) = 5.23$, $p = .014$, $\eta^2 = .322$). As no effects of TMS *site* were observed, subsequent analyses were conducted on data collapsed across M1 and vertex stimulation trials. Post-hoc pairwise comparisons between the stimulation conditions (to explore the main effect) showed the criterion value to be significantly smaller (representing *less bias*) when TMS was delivered at 300 ms compared to on 500 ms ($p = .046$) or no-stimulation trials ($p = .019$). The interaction between stimulation and stimulus type was followed up by running 15 exploratory paired *t*-tests. None of these pairwise differences were significant at a Bonferroni-corrected level of .003 ($ps > .010$). One-sample *t*-tests comparing criterion values against zero showed that participants had a significant bias towards judging stimuli as the 'same' on 500 ms and no-stimulation trials within the action condition (action/500 ms: $t(11) = 3.30$, $p = .007$; action/no-stimulation: $t(11) = 4.25$, $p = .001$). The bias for both conditions was significant after adjusting the alpha significance criterion for six comparisons. This analysis of bias was conducted to explore whether effects of M1 stimulation shown in the main analysis reflected differences in bias. As these data are not relevant for interpreting our central findings, they will not be discussed later in the manuscript.

3.2.4. Reaction times

Analysis of the RT difference scores revealed a significant interaction between TMS site and stimulation time ($F(1,11) = 5.94$, $p = .033$, $\eta^2 = .351$). This interaction was explored by collapsing across task (as the 3-way interaction was not significant; $p = .456$), and performing paired-samples *t*-tests to compare RT

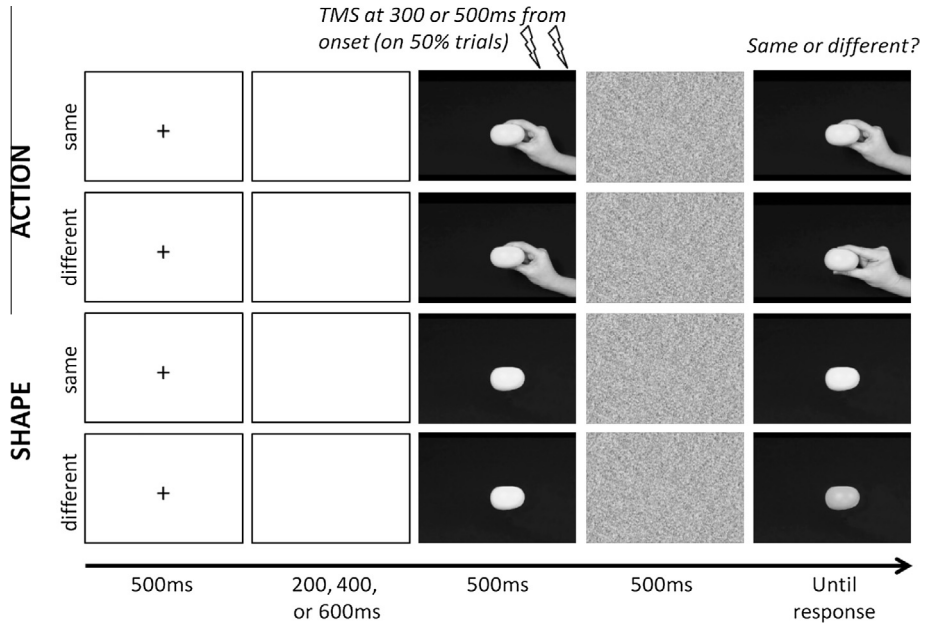

Fig. 3. Trial structure and example stimuli from Experiment 2. Note that all stimuli (Action and Shape, first and second presentations) were video clips.

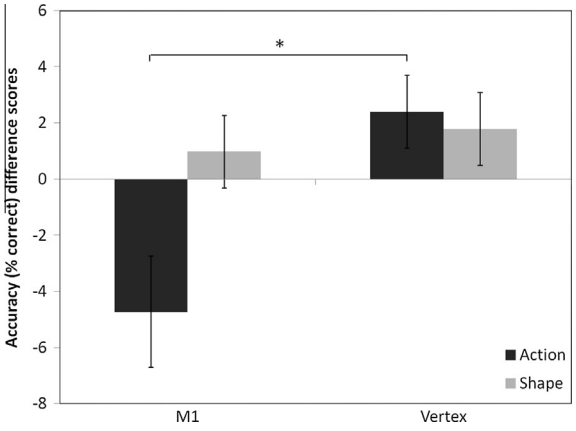

Fig. 4. Difference in accuracy (% correct) between stimulation and no-stimulation trials for each stimulus condition for each site (Experiment 2). Error bars represent standard error of the mean, and asterisks denote significant differences between conditions at the $p < .05$ level. Accuracy on action trials was significantly impaired when TMS was delivered over M1 compared to when no stimulation occurred (one-sample *t*-test comparing difference score against zero: $p = .036$).

difference scores between 300 and 500 ms for each site, and M1 versus vertex trials for each stimulation time. These tests showed a difference between the effect of stimulation delivered over M1 compared to the vertex within the 500 ms stimulation condition ($t(11) = 2.91$, $p = .014$); however this difference was not quite significant at the Bonferroni-corrected alpha level (significance criterion reduced to .013 to correct for four post-hoc comparisons).

To check for speed-accuracy trade-offs in both Experiments that could underlie the lower accuracy on action trials when TMS was applied over M1, we also ran paired-sample *t*-tests to compare RT for these trials (action, M1 stimulation) to RTs for action trials where TMS was not applied or was delivered over the vertex. The comparisons performed (for both Experiments 1 and 2) showed no RT differences, indicating that participants' lower accuracy when TMS was delivered over M1 was *not* a result of faster responding.

3.2.5. Motor-evoked potentials

A paired-samples *t*-test showed no significant difference in the size of MEPs elicited during action trials ($M = .484$, $SD = .557$) compared to shape trials ($M = .475$, $SD = .564$; $t(11) = 1.07$, $p = .309$). The analysis was also performed after excluding trials on which MEP amplitude fell 3 standard deviations away from the mean MEP size for the participant, which revealed the same pattern of results.

3.3. Discussion

Experiment 2 built on the findings of Experiment 1 to further explore the role of the motor system in the offline recognition of previously-viewed action. Single-pulse TMS was applied over the hand region of the motor cortex as participants watched hand actions, and participants were required to judge whether a video clip displayed 500 ms later depicted the same or a different action. Consistent with Experiment 1, we found that TMS applied over M1 impaired recognition of the action stimulus compared to when no stimulation was applied. Furthermore, performance on the effector recognition task when TMS was delivered over M1 was significantly impaired relative to (a) performance on the effector recognition task when TMS was delivered over the vertex, and (b) performance on the *shape* task when TMS was delivered over M1. Thus, we can infer that the impairment of effector recognition associated with stimulation over M1 did not reflect an effect of non-specific cortical stimulation, or a general disruption of visual processing or recognition memory.

Interestingly, there was no difference between effects of TMS delivered at 300 ms and 500 ms (action offset). This shows that the effects of stimulation over M1 demonstrated in these two experiments are not specific to action offset; stimulating over M1 and then viewing a further 200 ms of action disrupted recognition to the same extent as did stimulation applied at the end of the action. This finding supports two possible conclusions about the role played by the motor cortex in action recognition: (1) M1 is involved exclusively in action *retention*, or (2) it is involved in both the retention and encoding of the stimulus. We assume that the motor cortex plays a role at least in *retaining* a motor representation of action for the following reasons. In both Decloe and

Obhi's study (2013) and Experiment 1 of the current paper, the impairment that arose from stimulation over M1 was relative to recognition accuracy when actions were viewed – uninterrupted by TMS – for either 300 (Experiment 1) or 400 ms (Decloe & Obhi, 2013). This indicates that whatever motor representation was disrupted by TMS must be formed by 300 ms, leaving recognition relatively unimpaired on trials where no TMS was applied. Based on this, the current finding that stimulation at 500 ms impaired action recognition strongly implies that TMS at this time point interfered with *retention* of the action rather than encoding (as encoding should have been complete by this time point).

It is less clear whether encoding of the action would have been complete by *300 ms*, and therefore whether stimulation at this time point is likely to have disrupted the encoding or retention of the action. The results of previous studies using TMS indicate that corticospinal excitability is modulated in a muscle-specific manner from around 200 ms during action observation (for a review, see Naish, Houston-Price, Bremner, & Holmes, 2014). This suggests that a motor representation of the observed action should have been formed before the 300 ms stimulation in the present study. However, the relationship between corticospinal excitability changes and action encoding is not presently known. That is, although previous work suggests that 200 ms is long enough for muscle-specific representations of action to be formed, we do not know whether the representations evident at this *peripheral* level reflect representations that can be used in subsequent action (or effector) recognition. It might be that further processing time is required for a stable representation to be formed. Indeed, the MEP data collected in Experiment 2 indicate no difference in corticospinal excitability between the action and the shape condition; however, we did find differences in the *behavioural* effects of stimulation. In other words, the difference in recognition memory does not seem to map onto a difference in MEP modulation. The lack of difference between MEPs elicited in the action and shape condition is discussed further in the General Discussion.

In considering whether the motor system is involved in encoding as well as retention, we must also take into account the timings used by Decloe and Obhi (2013), and their findings. In Decloe and Obhi's study, stimulation delivered at 100 ms into a 400 ms movie clip significantly impaired delayed recognition of the object involved in the action. If motor cortex were involved *exclusively* in retention of action-related stimuli, then this finding of disruption 100 ms into a 400 ms action clip would mean two things: (1) a representation of the object (that could be used to aid recognition) was formed within the first 100 ms of action observation, and (2) a new representation was *not* formed in the remaining 300 ms action observation period that followed the pulse. Previous research has found that passive observation of a graspable object facilitates motor excitability (in a seemingly muscle-specific manner) by 120 ms from stimulus onset (Franca et al., 2012). In Franca et al. (2012) study, 120 ms was the earliest stimulation time point, so it is possible that representation is formed even earlier than this (i.e., by 100 ms). However, as with representations of observed action, we do not know whether representations formed at this point are sufficient to contribute to subsequent object recognition. In the case of both action and object representations, further exposure time might be required for formation of a lasting representation. It is possible that in Decloe and Obhi's study, encoding and retention of the object representation took longer than 100 ms, and that TMS disrupted a critical point in this process. That is, perhaps the encoding/retention process continued in the remaining 300 ms, but the part of the process that is critical for recognition was disrupted by TMS and not compensated for later in the process.

A final consideration when discussing the stage of processing affected by TMS is that stimulation might have affected processing in the period *after* the pulse. Indeed, if 100 ms of observation *is* long enough for a representation of an object to be formed, then the TMS pulse in Decloe and Obhi's experiment must have disturbed motor activity in the 300 ms following the pulse, such that a new representation of the object could *not* be formed. Although motor excitability measured in the muscle typically returns to its (pre-pulse) baseline within around 100 ms, effects at the cortical level might last considerably longer (e.g., Shitara, Shinozaki, Takagishi, Honda, & Hanakawa, 2011; Siebner, Hartwigsen, Kassuba, & Rothwell, 2009). Therefore, it is feasible that the stimulation delivered at 100 ms into a 400 ms clip (Decloe & Obhi, 2013), or at 300 ms into a 500 ms action clip (current study), could have affected encoding or retention processes for several hundred milliseconds following the pulse (i.e., the remaining action observation period). To explore further the time-course of motor cortex involvement in recognition of action-related stimuli, and the mechanism by which TMS disrupts recognition, future work should examine the effects of disrupting motor processing at a wider range of time points in the 500 ms following the onset of action observation.

4. General discussion

Most investigations of modulation of motor activity during action observation have focused on characteristics of this modulation at the time of action observation, and have not examined possible functional significance beyond this period. To the extent that motor modulation during action observation ('MMAO') is an automatic phenomenon (Hogeveen & Obhi, 2013), understanding its functional significance is crucial. In human cultures (and indeed some non-human primate 'cultures'), social learning is often achieved via observation of conspecifics performing actions. Being able to understand the action being performed in real time is certainly useful, but being able to form and maintain a representation of the observed action for later use is presumably critical for effective social learning. Here we investigated the notion that motor cortex is involved in this purported "offline" function.

In the two experiments reported in this paper, we applied transcranial magnetic stimulation (TMS) over the motor region of the cortex, with the aim of briefly disrupting cortical activity in the hand region of the motor cortex as participants watched hand actions. The results of both experiments suggest that stimulation over M1 influences effector recognition, with recognition accuracy being impaired relative to when no stimulation occurred. In contrast, we found no effects of stimulation applied over the *vertex* during or at the end of action observation, suggesting that the effects on effector recognition are specific to stimulation over motor cortex. Furthermore, there were no effects of M1 stimulation on recognition of a still hand or dot configuration (Experiment 1) or the colour of a moving shape (Experiment 2). Therefore, it is not the case that motor cortex stimulation disrupted memory or recall of *any* visual stimulus.

The results reported here are complementary to the findings of Decloe and Obhi (2013), which suggested that motor processing during observation of object-directed actions is linked to forming object representations that are retained beyond the observation period. However, it was unclear from these data whether motor cortex forms or stores representations of the object only, or whether it also stores a representation of the wider action context. Taking together the current findings with those of Decloe and Obhi (2013), we suggest that the motor system encodes *both the object and the effector* acting on the object during action observation, leading to a representation (or representations) of both of these components that endure beyond the action observation period. It remains unclear, however, whether a representation of the *action*

itself – i.e., its kinematic profile – is stored. Activation associated with movement appears to occur even when a visual stimulus implies action but no visible effector or object is present. For example, mu suppression (a putative index of mirror activation) occurs when individuals view point light displays of human movement (Ulloa & Pineda, 2007). If this activation occurs when an action is perceived, in the absence of direct observation of either an object or the acting effector, it is possible that a representation of action itself is stored by motor cortex and used to recognise later actions.

The mechanism by which TMS over M1 affects subsequent object and effector recognition is not clear at this stage. An important feature of the current study is that it rules out one possible explanation of Decloe and Obhi's study that stimulation exerted its effects by drawing attention *away* from the to-be-recognised part of the stimulus. Specifically, it is possible that stimulating over M1 impaired object recognition by enhancing attention to the part of the stimulus with the most motion (i.e., the hand) and therefore shifting attention away from the object. The present finding that stimulation over M1 disrupted recognition of the effector itself speaks against this conclusion, and suggests that this stimulation over motor regions affects recognition of action components in another way. We suggest that stimulation over M1 interfered with the modulation of the motor system occurring when the action was viewed (MMAO). However, the characteristics of this MMAO itself are unclear (Naish et al., 2014). Many studies have shown that excitability measured at the level of the *muscle* is increased during action observation; however, the pattern of cortical and spinal excitatory and inhibitory processes that lead to this final output is not known. There is evidence from monkeys, for example, of corticospinal *inhibition* during action observation (e.g., Kraskov, Dancause, Quallo, Shepherd, & Lemon, 2009). This inhibition might arise to suppress overt imitation of viewed movement. The effects of stimulation on effector recognition could be due to disruption of either, or both, excitatory or inhibitory processes that occur during action observation. Further studies using techniques such as paired-pulse TMS and peripheral nerve stimulation would be required to explore the exact processes being influenced by stimulation in these studies.

The lack of impairment of hand recognition in the still hand condition (in Experiment 1) is especially interesting, as it suggests that the processes or representations that are affected by stimulation over M1 are formed specifically by *action* observation, rather than the observation of a hand alone. It would be interesting in future work to examine whether recognition of a still hand embedded in a full action context (e.g., a static image of the hand squeezing a ball) would also be disrupted by motor cortex stimulation, or whether the observed *movement* itself is required for the motor representation to be formed. Our still hand condition showed the hand in a grasping posture, so it could be argued that these stimuli depicted implied action. Urgesi et al. (2006) found MEP facilitation when participants viewed static images of a hand performing a precision grip compared to when the hand was not acting, which suggests that implied motion – in the absence of an object – influences responses of the motor system. However, other work has found that object presence *is* important. In Enticott, Kennedy, Bradshaw, Rinehart, and Fitzgerald (2010) study, only stimuli showing a hand grasping a cup facilitated MEPs, while viewing a hand grasping without the cup – or even seeing the hand grasping next to (but not acting towards) the cup – had no effect on motor excitability compared to viewing a hand at rest. Villiger, Chandrasekharan, and Welsh (2011) also found that motor responses elicited during action observation were larger when an object was present in the action scene compared to when it was absent. Comparing the effects of TMS over M1 on recall of a moving action stimulus versus a static action stimuli (both with object present) would tell us whether observed motion is a crucial component of M1's involvement in hand recognition. Our finding (Experiment 1) that still hand recognition was not affected by stimulation over M1 is more in keeping with the findings of Urgesi et al. (2006) and Villiger and colleagues, as it indicates that observing implied action does not affect the motor system in the same way as does observing actual movement.

Although our task control condition in Experiment 2 involved a moving shape, and was designed to visually match the action condition in all respects apart from the presence of the acting hand, it must be noted that the control task itself was a judgement of *colour* and not movement. Therefore, we cannot infer from these results whether stimulation over M1 disrupts recognition of human action specifically. Had we requested participants to recognise the compression of the shape (which was actually the ball being squeezed without a hand shown), we may have found that participants' performance on this task was impaired by stimulation over M1. In fact, the finding that MEP amplitude did not differ between the action and moving shape condition could indicate that recognition of the *motion* of the shape would have been disrupted by stimulation over M1. Unfortunately, our lack of a low-level baseline condition (such as a fixation cross) in this experiment is a limitation, as we cannot infer whether corticospinal excitability was facilitated in both or neither condition. It is possible that viewing the shape – which was actually the ball being compressed – elicited an association with action. If participants perceived the shape as the ball, then there are at least two reasons why this condition could have facilitated motor excitability comparably to action observation. First, participants might have attributed a squeezing action to the compression that they saw, such that the implied action of an "invisible hand" squeezing the ball elicited a resonance response (e.g., Urgesi et al., 2006). Alternatively, the object itself (if indeed perceived as an object) might have elicited motor facilitation due to object affordances (e.g., Franca et al., 2012). To better understand the processes that are being affected by stimulation over M1, future work should investigate the effects of motor cortex stimulation, not only on the recognition of biological motion, but also on recognition of the movement of non-biological stimuli. There are different levels of non-biological stimuli that could be explored. In particular, it would be useful to compare a moving stimulus that affords no action at all and is similar to the hand action only in the fact that it moves, with a goal-directed movement performed by a non-biological entity such as a robotic hand. Previous work has shown motor facilitation occurs for both robot and human action observation (Gazzola, Rizzolatti, Wicker, & Keysers, 2007; Hogeveen & Obhi, 2012), so it might be the case that stimulation of the motor cortex during movement observation would affect recognition of any movement to which a goal can be attributed.

Our experiments so far have examined the recognition of simple object-directed actions, but it seems important to investigate how recognition of *socially-relevant* actions is influenced by interference with motor processing. In work by Sartori and colleagues (e.g., Sartori, Bucchioni, & Castiello, 2013; Sartori, Cavallo, Bucchioni, & Castiello, 2012), it has been found that observing an action that invites a complementary non-identical response induces a pattern of covert muscle activity reflecting the complementary action. For example, it was found that observing an actor perform a whole hand grasp to lift a flask led initially to a pattern of motor activation that reflected the observed grasp, but that when the actor's movement became a request for the observer to perform a precision grip, the motor activation reflected that associated with precision grip (Sartori et al., 2013). That is, when the appropriate reciprocal action was different to the observed action, the MMAO no longer reflected what was being observed, but reflected the motor activation necessary to *respond* to the observed action. Based on this work by Sartori and colleagues, we might predict that

the specific motor representation that would be disrupted at different points of such movements would differ, such that stimulating over M1 at the very start of action observation would disrupt a representation of the observed movement itself, but stimulation occurring later into the movement observation period would disrupt a representation of the planned, reciprocal action. On this basis, it is possible that recognition of an action that warrants a non-imitative response might in fact be *poorer* than recognition of a movement not associated with an alternative movement (e.g., intransitive movements), because the motor representations formed and stored when the former is observed would not reflect that movement exclusively.

Our suggestion that MMAO is a fundamental process concerned with action memory is in line with a recent suggestion that sensorimotor resonance during action observation can serve to keep a seen action "on hold" – thus serving a type of working memory function for action – while an appropriate response is prepared (Sartori & Betti, 2015). Indeed, our results provide neurophysiological evidence for this working memory role as we show that disrupting MMAO impairs later recognition of seen actions.

The present results demonstrated that MMAO is involved in offline recognition of actions after a very brief delay; however, depending on how long these action representations are retained, it could play a role in longer-term learning. Support for this notion comes from the work of Brown, Wilson, and Gribble (2009), who applied repetitive TMS (rTMS) to M1 after participants watched an actor learn to perform a movement under novel force conditions. Specifically, the participants watched, and then later performed, reaching under the influence of a clockwise or counter-clockwise force-field imposed by a robotic arm. In previous work (Mattar & Gribble, 2005), it was shown that watching someone learn to reach in the clockwise force-field condition improved the observer's own later performance on the task in the same (i.e., clockwise) force environment, but impaired performance on reaching under the opposite (counter-clockwise) condition. Brown et al. (2009) found that administering 15 minutes of 1 Hz rTMS to M1 in the interval between observing and performing the task affected both the beneficial and detrimental effects of observation. Specifically, rTMS reduced the improvement resulting from viewing the movement in the same force condition, and eliminated the detrimental effect of viewing the movement being learned under the opposite force condition. Brown and colleagues' findings suggest that the motor cortex is causally involved in motor learning by observation, thus suggesting that MMAO has a role beyond real-time action processing and short-term action and effector recognition.

As stated, the vast majority of previous work on MMAO has focused on its possible role in real-time functions such as understanding the intention of the person performing the action. Based on the present results and previous research (e.g., Brown et al., 2009; Decloe & Obhi, 2013), we propose that MMAO plays a role in later recognition of actions and possibly response preparation (for example, to facilitate the execution of complementary actions). The retention of motor representations of observed actions could contribute to social cognition on at least two levels. First, it might lead to a faster recognition of the action when it is encountered again, thus conferring a processing speed and action understanding advantage compared to if a representation of the observed action had not been stored. Second, retaining a representation of action might allow the observer to replicate the movement themselves at a later time point (i.e., observational learning). Although a prominent theory focused around MMAO is that it is involved in action imitation (e.g., Rizzolatti, Fogassi, & Gallese, 2001), the exact mechanism behind this is unclear. Studies of behavioural mimicry have often associated mimicry with MMAO. However, such mimicry is often defined as any imitation of a given movement occurring during the interaction period, or within a certain time window *after* the original (imitated) movement occurs (e.g., Hogeveen & Obhi, 2012; Lakin & Chartrand, 2003). This supposition implies that MMAO affects action execution after a delay, but how this might occur has not been explained. The present findings provide some of the first evidence that the effects of MMAO are not restricted to the movement observation period, and thus provide tentative support for the notion that this modulation of motor activity *could* be involved in delayed action imitation.

To summarise, in the present study we demonstrated that interfering with motor activity induced by action observation – either during or at the offset of action observation – affects subsequent offline recognition of the effector involved in that action. Together with the findings of Decloe and Obhi (2013), these results indicate that the motor system retains a representation of the observed object and effector, which may be used recognise the action (or at least the components of the action) at a later time point. Further work is necessary to establish how long the formed motor representations of observed actions are retained for, and whether this is affected by factors related to the action, the observer, or the actor. Addressing these questions will bring us closer to determining the role of MMAO in social cognitive functions such as observational learning, action imitation, and motor response preparation.

Significance statement

These experiments provide seminal causal evidence that motor cortical processing during action observation is functionally significant for the later recognition of the effector involved in the action. This novel finding suggests that the motor representations formed during action observation are retained and serve a cognitive function beyond the processing of an action in real time.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.cognition.2016.01.008.

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