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Observation of an action with a congruent contextual background facilitates corticospinal excitability: A combined TMS and eye-tracking experiment



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ABSTRACT

Keywords: Motor simulation Transcranial magnetic stimulation Motor-evoked potentials Visual context Action observation produces activity in similar regions of the brain to those involved in action execution and can offer an effective intervention for motor (re)learning, although optimal viewing conditions for such interventions remain to be established. In this experiment, single-pulse transcranial magnetic stimulation (TMS) and eyetracking were used simultaneously to investigate the effect of manipulating background context on both corticospinal excitability and visual attention during action observation. Twenty-four participants observed four different videos: (i) a static hand holding a sponge (control condition); and an index finger-thumb pinch of a sponge against (ii) a plain black background; (iii) a background containing objects that were incongruent with the observed action; and (iv) a background containing objects that were congruent with the observed action. TMS was delivered to the hand representation of the left primary motor cortex, and motor evoked potentials were recorded from the first dorsal interosseous and abductor digiti minimi muscles of the right hand. Eye movements were recorded throughout the experiment. Results indicated that corticospinal excitability was facilitated during the congruent context condition compared to both the static hand and plain black background conditions. In addition, the number of fixations and percentage of time participants spent fixating on the background scene were significantly greater during the incongruent and congruent conditions compared to the static hand and plain black background conditions. These results indicate that the provision of additional visual information that is congruent with the observed movement contributes to a facilitation of corticospinal excitability by providing the observer with information regarding the goal and intention of the observed action. Providing congruent contextual information may enhance the efficacy of action observation interventions for motor (re)learning.

1. Introduction

It is well-established that action observation produces activity in similar regions of the brain to those involved in action execution (Grèzes and Decety, 2001; Hardwick et al., 2017). This observation-execution matching mechanism is argued to be a central factor responsible for action observation contributing to improvements in motor function in motor (re)learning settings (see Buccino, 2014 for a review). As such, research has investigated the effect of different action observation conditions on activity in cortical motor regions in an attempt to identify optimal methods for designing and delivering action observation interventions for motor (re)learning (see Holmes and Wright, 2017 for a review).

The effect of action observation on activity in motor regions of the brain has been explored extensively using functional magnetic resonance imaging (fMRI; e.g., Iacoboni et al., 2005; Chong et al., 2008).

A recent meta-analysis by Hardwick et al. (2017) demonstrated that activity in premotor-parietal and somatosensory networks is elicited consistently during both action observation and action execution. This effect is well-established, however the manner in which action observation is delivered has been shown to modulate brain activity. One variable that appears to be important is the visual context in which the action is presented for observation. For example, Iacoboni et al. (2005) compared cortical activity during observation of grasping a cup against a blank background with two background scenes that provided context that was congruent with the observed action (i.e., reaching and grasping to either drink from or clean the cup). Iacoboni et al. (2005) reported a significant increase in activity in the premotor cortex and the inferior frontal gyrus when the observed action occurred within a contextually relevant background scene that provided additional visual information regarding the goal and intention of the movement, compared to the blank background that was devoid of additional visual

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information. This finding suggests that activity in the motor regions of the brain during action observation can be modulated by providing visual contextual information regarding the goal and intention of the observed action.

The importance of visual context during action observation has been explored further by research using transcranial magnetic stimulation (TMS). Since Fadiga et al. (1995) first demonstrated that action observation facilitates corticospinal excitability, researchers have investigated how this effect may be modulated by the manipulation of visual context during action observation. For example, Enticott et al. (2010) manipulated visual context by instructing participants to observe a grasping action that was either mimed or involved a hand-object interaction. Their results indicated that observing the hand-object interaction facilitated corticospinal excitability to a greater extent compared to when there was no object present to provide context to the observed movement. Similar findings have also been demonstrated by manipulating social context (Donne et al., 2011) and visual context (Amoruso and Urgesi, 2016). Taken together, this research indicates that corticospinal excitability is facilitated when observing actions within a scene that provides the observer with visual contextual information about the goal and intention of the observed movement. As such, the inclusion of this type of priming information within action observation interventions may benefit motor (re)learning.

Despite evidence that the context in which an action is observed can modulate activity in the motor regions of the brain, some aspects of the relationship require further investigation. Iacoboni et al. (2005) only examined the effect of action observation with a blank background compared to action observation with background scenes that were related to the observed reach and grasp. Based on this, the authors claimed that action observation with a meaningful visual context modulates activity in the brain. It is possible, however, that the reported changes in neurophysiological activity were due to the presence of additional visual information in the background, rather than the congruence of that information to the observed action. Amoruso and Urgesi (2016) have provided some initial evidence that the congruency of the context contributes to a facilitation of corticospinal excitability during action observation. It may be beneficial, therefore, to explore this effect further using TMS and eye-tracking techniques simultaneously in order to understand better how the manipulation of context influences visual attention and corticospinal excitability.

The manipulation of background contexts in action observation experiments may also modulate participants' visual attention, which may be associated with changes in corticospinal excitability (Conte et al., 2007). An emerging body of research has begun to investigate how eye-movement behaviour may influence corticospinal excitability during action observation (e.g., Donaldson et al., 2015; Leonetti et al., 2015; D'Innocenzo et al., 2017; Wright et al., 2018). Specifically, corticospinal excitability is facilitated in a muscle-specific manner when actions are observed in central compared to peripheral vision (Leonetti et al., 2015), and when there are more fixations on hand-object interactions compared to non-action-related areas of the video (Donaldson et al., 2015). In addition, directing participants' visual attention explicitly towards task-relevant features of an observed action has been shown to modulate corticospinal excitability to a greater extent than passive observation conditions (D'Innocenzo et al., 2017; Wright et al., 2018). These findings indicate that visual fixation location is an important factor in the modulation of corticospinal excitability during action observation.

The aim of this experiment was to determine the effect of background context on corticospinal excitability and visual attention during action observation. It was hypothesised that: (i) corticospinal excitability would be facilitated during action observation conditions compared to a control condition; (ii) the facilitation effect would be specific to the muscles involved in the execution of the observed action; (iii) the facilitation of corticospinal excitability would be greater when an action is observed against a congruent contextual background compared to either a plain black background or an incongruent contextual background; and (iv) both the number of fixations and the percentage of time spent fixating on the background scene would be greater during action observation conditions with a congruent or incongruent contextual background compared to action observation with a plain black background.

2. Method

2.1. Participants

Based on an *a priori* power analysis conducted using G*Power, twenty-four volunteers (16 male, 8 female) aged 19–32 years (mean age 22.42 \pm 3.23 years) participated in the experiment. Twenty-one participants were right-handed and three were left-handed, as measured by the Edinburgh Handedness Inventory (Oldfield, 1971). The TMS Adult Safety Screen (Keel et al., 2001) was used to ensure that no participants were predisposed to possible adverse effects of the stimulation. No participants were excluded according to these criteria and none reported discomfort or negative reactions to the stimulation during the experiment. All participants provided full written informed consent prior to participation. The protocol was granted ethical approval by the local ethics committee and was conducted in accordance with the Declaration of Helsinki (World Medical Association, 2013).

2.2. Electromyography and transcranial magnetic stimulation protocol

2.2.1. Electromyography

Electromyographic (EMG) recordings were collected from the first dorsal interosseous (FDI) and abductor digiti minimi (ADM) muscles of the right hand. These muscles were selected as experimental and control muscles due to their respective involvement and lack of involvement in the execution of the observed movement. Bipolar, single differential surface electrodes (DE-2.1, Delsys Inc, Boston, MA) were attached on the mid-point of the muscle belly of both muscles, and a reference electrode was attached over the right ulnar process. Alcohol wipes were used to clean the electrode sites prior to electrode attachment. EMG signals were recorded using Spike2 v6.18 software (Cambridge Electronic Design, Cambridge, UK) via a Micro 1401–3 analogue-to-digital converter (Cambridge Electronic Design, Cambridge, UK), with a sampling rate of 2 kHz, bandwidth of 20 Hz to 450 kHz, 92 dB common mode rejection ratio and $> 10^{15} \Omega$ input impedance.

2.2.2. Transcranial magnetic stimulation

A figure-of-eight coil (two 70 mm diameter loops) was used to deliver single-pulse TMS from a Magstim 200² magnetic stimulator (Magstim Co., Whitland, Dyfed, UK), delivering monophasic pulses with a maximum field strength of 2.2 T. The TMS procedure followed the published guidelines of Loporto, McAllister, Williams, Hardwick, and Holmes (2011). The coil was fixed in place over the hand representation of the left motor cortex throughout the experiment with a mechanical arm (Manfrotto™, Cassola, Italy) and was orientated for the induced current to flow in a posterior-anterior direction by positioning the coil at a 45° angle to the midline between nasion and inion landmarks of the skull. This coil orientation was used to achieve indirect trans-synaptic activation and optimal MEP amplitudes (Opitz et al., 2013; Sakai et al., 1997). The optimal scalp position (OSP) was found by stimulating the approximate area of the motor cortex for the FDI muscle of the right hand at an intensity of 60% maximal stimulator output (Clark, Tremblay, and Ste-Marie, 2003). The coil was then moved in 1 cm steps around this area until the site that produced MEPs of largest amplitude in the FDI muscle, and of consistent amplitude in the ADM muscle, was found. This area was then marked on a tightlyfitting cap worn by the participants to ensure consistent coil placement throughout the experiment. The modal location of the OSP was 4 cm

lateral and 1.5 cm anterior from Cz. After determining the OSP, the resting motor threshold (RMT) was determined by gradually adjusting the stimulation intensity until peak-to-peak MEP amplitudes of 50μ V or more were found in 5 out of 10 trials (Rossini et al., 2015). This stimulation intensity plus 1% maximum stimulator output was defined as the RMT (Rossini et al., 2015). The experimental stimulation intensity was then set at 110% RMT to reduce direct wave stimulation (Loporto et al., 2013). Experimental stimulator output (mean intensity 52.17 ± 8.95).

2.3. Eye-tracking protocol

Each participant's eye movements were recorded throughout the experiment using ETG 2w eye-tracking glasses and iView ETG 2.7 software (SensoMotoric Instruments, Teltow, Germany) at a sampling rate of 60 Hz. The eye-tracking glasses contained two cameras directed towards the participant's eyes and projected six infrared lights onto both of the participant's eyes to record eye movements. A circular cursor indicated the location of gaze in the visual scene recorded from a forward-facing camera to an accuracy of 0.5°. To calibrate the glasses prior to beginning the experiment, a three-point calibration system was used on a five-point grid displayed on-screen in front of the participant at a distance of 90 cm. Calibration was monitored throughout the experiment and, if necessary, adjusted before the onset of the following block of trials or *post-hoc* using BeGaze 3.7 software (SensoMotoric Instruments, Teltow, Germany).

2.4. Procedure

Participants were seated at a distance of 90 cm in front of a vertical 32" LED screen (Samsung U32E850R) with their elbows flexed at 90° and their hands pronated in a relaxed position on a table directly in front of them. A chinrest and headrest was used to reduce head movements. Participants were asked to refrain from any voluntary movement during each condition and to attend fully to the stimuli presented on the screen. Blackout curtains were drawn alongside the screen and table setup to eliminate distracting visual stimuli in the surrounding environment.

Each participant observed four conditions: a static right hand holding a sponge between the index finger and thumb against a plain black background (Fig. 1a); and a right hand performing two index finger-thumb pinches of a sponge against either a plain black



Fig. 1. Still images from (a) the control condition, and the three experimental conditions; (b) a plain black background, (c) a contextually incongruent background, and (d) a contextually congruent background.

background (Fig. 1b), a background containing objects that were incongruent with the activity of daily living of pinching a sponge to wash dishes, such as a cardboard box, tools, and pens (Fig. 1c), or a background containing objects that were congruent with the activity of daily living of pinching a sponge to wash dishes, such as a sink, plates, and cutlery (Fig. 1d). The location of the background objects were kept similar, though the object features differed to ensure no overlap of the background context between conditions. Additionally, an index fingerthumb pinch was used over a possibly more ecologically-valid whole hand squeeze to explore the muscle-specificity effect between visible experimental and control muscles. Kinematic equivalence across conditions was not measured, but the recorded actions were matched visually to keep the movement consistent across all conditions. The experiment was split into four blocks of 32 trials, with each block containing eight trials of each condition presented in a random order.

The videos showed a Caucasian male's right hand and forearm filmed from a first-person visual perspective, with the hand positioned to the right of the screen to enhance anatomical congruence and perception of ownership (Riach et al., 2018). All videos were seven seconds in duration, and the action observation videos contained two pinches at a rate of approximately 0.3 Hz. For the three experimental conditions, one stimulation was delivered per trial at the point of maximal contraction of the FDI muscle during either the first or second sponge pinch (either 1700 ms or 4900 ms after video onset). Two stimulation timings were used to reduce the predictability of the stimulation (Loporto et al., 2012). Participants were given a break of approximately 2 min between each block.

2.5. Data analysis

2.5.1. TMS

As increased pre-stimulation EMG activity can facilitate the amplitude of the resulting MEP artificially (Devanne et al., 1997; Hess et al., 1987), background EMG activity in both muscles was examined to identify trials in which the MEP may have been influenced by muscular contraction prior to the stimulation. Trials in which peak-to-peak amplitude of the baseline EMG activity was 2.5 standard deviations greater than the mean baseline in the 200 ms preceding the stimulation were discarded from further analysis (Loporto et al., 2012). Separate 2 (muscle: FDI, ADM) x 4 (condition: static hand, plain black background, incongruent context background, congruent context background) repeated measures ANOVAs were used to check for differences in the number of rejected trials per condition, and the remaining average peak-to-peak EMG baseline amplitude between conditions.

To account for biological interindividual variability in MEP amplitudes, all participants' raw MEP data were transformed into z-scores (Aglioti et al., 2008; Fadiga et al., 1995; Loporto et al., 2012) prior to analysis with a 2 (muscle) x 4 (condition) repeated measures ANOVA.

2.5.2. Eye-tracking

Individual trials were analysed using two separate dynamic areas of interest (AOI) for the sponge and hand. A third dynamic AOI was defined as the remaining background scene to cover all elements relating to the congruency of the background context (i.e., the backdrop and all background objects; Fig. 2). A process of manual fixation-by-fixation mapping of fixation locations to the different AOIs on a reference image was utilised to ensure that fixations were assigned to the appropriate AOI. The dynamic nature of the AOIs accounted for both the hand movement, and the resulting change in size and shape of the AOIs relative to the contextual cues that they cover throughout the pinch action (Kang et al., 2016). The number of fixations and percentage fixation duration were calculated within each AOI using BeGaze 3.7 software (SensoMotoric Instruments, Teltow, Germany). A fixation was defined as any gaze that remained within $1^{\circ} \pm 0.5^{\circ}$ of visual angle for a minimum duration of 100 ms (Salvucci and Goldberg, 2000). Percentage fixation duration was defined as the percentage of time spent



Fig. 2. Dynamic areas of interest were used to cover the (1) sponge, (2) hand, and (3) remaining background scene on the (a) static hand, (b) plain black background, (c) incongruent context background, and (d) congruent context background conditions.

fixating within a particular AOI. The number of fixations and percentage fixation duration data was analysed using separate 3 (AOI: sponge, hand, background) \times 4 (condition) repeated measures ANOVAs.

For both TMS and eye-tracking analyses, where Mauchly's test indicated that the assumption of sphericity was violated, the Greenhouse-Geisser method was used to correct the degrees of freedom. The alpha level for statistical significance was set at p < 0.05 and *post-hoc* pairwise comparisons with Bonferroni corrections were performed on significant results. Effect sizes are reported using Cohen's *d*.

3. Results

3.1. Preliminary analyses

The 2 (muscle) × 4 (condition) repeated measures ANOVA on the number of rejected trials showed a significant main effect for muscle, $F_{(1,23)} = 7.09$, p = 0.01, d = 0.49, with significantly more trials rejected from the ADM muscle (2.52 ± 0.65) compared to the FDI muscle (1.03 ± 0.24). There was no significant main effect for condition, $F_{(2.19,50.35)} = 2.18$, p = 0.50, and no significant muscle x condition interaction effect, $F_{(3,69)} = 1.60$, p = 0.26.

The 2 (muscle) × 4 (condition) repeated measures ANOVA on the pre-stimulation baseline EMG data of the remaining trials showed no significant main effect for muscle, $F_{(1,23)} = 0.09$, p = 0.77, or condition, $F_{(1.67,38.29)} = 0.13$, p = 0.84. In addition, there was no significant muscle x condition interaction effect, $F_{(1,70,39,10)} = 2.05$, p = 0.15.

3.2. Main analyses

3.2.1. TMS data

Raw MEP amplitudes recorded from the FDI and ADM muscles for each of the conditions are reported in Table 1. The 2 (muscle) × 4 (condition) repeated measures ANOVA on the *z*-score MEP amplitude data showed a significant muscle × condition interaction effect, $F_{(3,69)}$ = 4.80, p < 0.001. Pairwise comparisons showed that MEPs recorded from the FDI muscle were significantly larger during the congruent context condition than MEPs recorded from both the static hand (p = 0.02, d = 0.65) and plain black background (p = 0.02, d = 0.65) conditions (Fig. 3). In addition, MEPs recorded from the ADM muscle were significantly larger during the static hand condition compared to the plain black background condition (p = 0.01, d = 0.74; Fig. 3).

Table 1

Raw MEP amplitudes recorded from the FDI and ADM muscles for each condition.

	Raw MEP amplitude (µV)	
	FDI	ADM
Static hand Plain black background Incongruent context Congruent context	$1423.60 (\pm 221.9) 1470.17 (\pm 229.2) 1548.85 (\pm 261.05) 1604.49 (\pm 255.28) $	914.85 (± 174.95) 769.42 (± 143.3) 805.41 (± 161) 801.23 (± 145.19)

3.2.2. Eye-tracking data

A 3 (AOI) x 4 (condition) repeated measures ANOVA on the number of fixations data showed a significant AOI x condition interaction, $F_{(3.92.90.04)} = 25.12, p < 0.001$. Pairwise comparisons revealed that more fixations were made on the sponge compared to both the hand and background AOIs during all conditions (all $p \le 0.004$, all d from 0.76 to 2.28; see Fig. 4). In addition, more fixations were made on the background during both the congruent and incongruent context conditions compared to the static hand (p < 0.001, d = 1.02 and 1.23 respectively) and plain black background (p < 0.001, d = 1.03 and 1.19 respectively) conditions (see Fig. 4). The difference between the number of fixations on the background during the incongruent and congruent context conditions approached significance (p = 0.08, d =0.54). Significantly more fixations were made on both the static hand and incongruent context conditions compared to both the plain black background and congruent context conditions (all $p \leq 0.02$, all d from 0.27 to 0.53; see Fig. 4).

A 3 (AOI) \times 4 (condition) repeated measures ANOVA on the percentage fixation duration data showed a significant AOI \times condition interaction, $F_{(4.14,95.13)} = 8.69$, p < 0.001. Pairwise comparisons revealed that participants spent a greater percentage of time fixating on the sponge compared to both the hand and background AOIs during all conditions (all p < 0.001, all d from 1.33 to 3.14; see Fig. 5). In addition, participants spent a greater percentage of time fixating on the background during both the congruent and incongruent context conditions compared to the static hand (both $p \le 0.001$, d = 0.94 and 0.98 respectively) and plain black background (both $p \le 0.001$, d = 0.92and 1.03 respectively) conditions (see Fig. 5). No significant difference was found in the percentage fixation duration on the background during the incongruent and congruent context conditions (p = 1.00, d= 0.12). A greater percentage of time was spent fixating on the hand during the congruent context compared to the incongruent context condition (p = 0.004, d = 0.81; see Fig. 5).

4. Discussion

The aim of this experiment was to determine whether the visual context in which an action is observed modulates corticospinal excitability and visual attention during action observation. The findings indicate that action observation presented with a congruent contextual background produces a facilitation of corticospinal excitability compared to the control condition. This effect was only present in the FDI muscle that would be involved in the execution of the observed action, providing support for the well-established muscle-specificity effect during action observation (Naish et al., 2014). In contrast, action observation presented with an incongruent contextual background or a background devoid of contextual information did not significantly facilitate corticospinal excitability relative to the control condition. Furthermore, the presence of the congruent context facilitated corticospinal excitability to a greater extent than action observation with a plain black background, indicating that the presence of contextually relevant information enhances the facilitation of corticospinal excitability during action observation. The preliminary analyses confirm that these differences between conditions cannot be accounted for by increased



Fig. 3. MEP amplitudes recorded from the FDI and ADM muscles during each condition. *p = 0.02, **p = 0.01.



Fig. 4. The average number of fixations per trial recorded in each AOI during each condition. * indicates significantly more fixations on the sponge AOI compared to the hand and background AOIs in each condition ($p \le 0.004$). ** indicates significantly more fixations on the background AOI in the incongruent and congruent conditions compared to the static hand and plain black background conditions (p < 0.001). *** indicates significantly greater total number of fixations during both the static hand and incongruent context conditions compared to both the plain black background and congruent context conditions (all $p \le 0.02$).

muscle activity prior to stimulation and, therefore, can be attributed to the manipulation of the visual contextual information.

These findings indicate that corticospinal excitability was only facilitated during action observation with a congruent context and not for action observation with a plain black background or with an incongruent context. Previous studies have reported that the observation of actions perceived to be meaningful by the individual are more likely to produce a facilitation of corticospinal excitability, compared to actions perceived to be less meaningful (Donne et al., 2011; Enticott et al., 2010). In the present experiment, it can be suggested that only the congruent context condition provided contextually meaningful information to the participants to allow them to infer the goal and intention of the observed action. The presence of this information may enable the observer to utilise attentional and comparator cognitive mechanisms underlying motor simulation, allowing for the accurate selection of appropriate motor representations required for action execution (Jeannerod, 2004; O'Shea and Moran, 2017) which would be expected to reflect as a facilitated MEP profile. This may explain why only the congruent context condition resulted in a facilitation of corticospinal excitability in comparison to the control condition. These findings support Iacoboni et al.'s (2005) results by demonstrating that the facilitation of corticospinal excitability only occurred when the action was observed with a congruent context abackground. The lack of facilitation effect in the incongruent context condition also extends the findings of Iacoboni et al. (2005) by confirming that it is the congruency of the context to the observed action that produces the facilitation effect, not just the presence of additional visual information in the background scene. Additionally, the findings of the present



Fig. 5. The percentage fixation duration recorded on each AOI during each condition. * indicates significantly greater percentage fixation duration on the sponge AOI compared to the hand and background AOIs in each condition (p < 0.001). ** indicates significantly greater percentage fixation duration on the background AOI in the incongruent and congruent conditions compared to the static hand and plain black background conditions ($p \le 0.001$). *** indicates significantly greater percentage fixation duration on the background AOI in the congruent condition on the hand AOI in the congruent condition compared to the incongruent condition (p = 0.004).

experiment support and extend the findings of Amoruso and Urgesi (2016) by demonstrating that action observation with a congruent, but not an incongruent, context facilitates corticospinal excitability. These findings highlight the need to consider contextual meaning in both research and applied settings.

The eye-tracking data in this experiment provides further support for the explanation that the congruence of the background scene facilitated corticospinal excitability. The data revealed that, across all conditions, participants made more fixations and spent a greater percentage of time fixating on the sponge compared to the hand or the background scene. This indicates that visual attention may have been drawn towards understanding the interaction element of the observed action (Wright et al., 2018). To generate a motor response to an observed action, individuals use observable information such as objects and movements to understand the observed stimuli, though the sponge alone may not have been sufficient (Manthey et al., 2003). Additional information that may have provided further understanding of the observed action was present in the congruent and incongruent context conditions. This resulted in participants making more fixations and spending more time fixating on the background scene during both the congruent and incongruent context conditions compared to the static hand and plain black background conditions. This indicates that the presence of objects in the background scene altered participants' visual attention during action observation, diverting visual attention towards elements of the stimuli that could provide higher understanding of the observed action. As the videos were presented in a random order, it is conceivable that participants fixated more and for longer on the background scene in the congruent and incongruent conditions in an attempt to identify and extract this additional information about the goal and intention of the observed movement for each individual video (Kelly and Wheaton, 2013). One explanation, therefore, for why corticospinal excitability may have been facilitated in the congruent context condition and not the incongruent context condition could be that participants were able to understand the action better when fixating on

the congruent background, but not when fixating on the incongruent background (Wurm and Schubotz, 2017). The congruent context condition provided the additional information relating to the action goal (i.e., washing dishes) that the incongruent context condition did not provide. Such information is required for motor planning and provides complete access to motor representations in a similar manner to action execution (Jeannerod, 2004), and to high-level contextual representations (Amoruso et al., 2016), which may have contributed to the facilitation of corticospinal excitability in this condition.

Participants spent similar lengths of time fixating on the background during the congruent and incongruent context conditions, but there was a trend (p = 0.08) for more fixations on the background during the incongruent, compared to the congruent, condition. This enabled participants to fixate longer on the movement itself, with significantly greater lengths of time spent fixating on the hand AOI during the congruent context compared to the incongruent context condition. This could indicate that participants had to search actively for visual information regarding the goal and intention of the observed movement during the incongruent context condition. As they may not have been able to extract this information from the visual scene, the additional fixations distracted visual attention away from the movement itself. As this information was not directly identifiable in the incongruent or plain black background conditions, the visual features of the observed actions may have been analysed and interpreted inferentially (Molenberghs et al., 2012). Inferring the goal and intention of an action to access appropriate motor representations is possible when context congruent with the goal and intention is provided, even when an incomplete action is shown (Amoruso and Urgesi, 2016). With such important task-relevant information being inaccessible to the observer during action observation in the incongruent or plain black background conditions, however, incomplete, or even incorrect, selection of motor representations may have occurred, even though the complete action was observed. This may be due to the lack of congruency between the observed action and the objects displayed in the background scene

(Kelly and Wheaton, 2013; Ocampo and Kritikos, 2010; Wurm and Schubotz, 2017). Additionally, a greater total number of fixations were made during the static hand and incongruent context conditions compared to both the plain black background and congruent context conditions. Increased eye movement has been shown to result in a reduction in corticospinal excitability (D'Innocenzo et al., 2017). The behavioural response of increased fixations on the incongruent background context may explain why corticospinal excitability was not facilitated when actions were observed with an incongruent contextual background.

Kelly and Wheaton (2013) postulated that both contextual and physical knowledge is required to understand hand-object interactions. As the observed task was a common activity of daily living, it is likely that the physical knowledge of the observed action was available to participants in all three action observation conditions of this experiment (e.g., how the object is typically used, the weight and texture of the sponge). The importance of this knowledge is demonstrated in the eye-tracking data, as participants fixated on the sponge AOI a greater number of times than the hand and background AOIs across all conditions. Contextual knowledge, however, is still required for a better understanding of the observed action. In the present experiment, only the congruent context condition would have provided sufficient and appropriate contextual information for each participant to understand the action and infer the goal of the observed action (Kelly and Wheaton, 2013).

A mechanistic explanation for the findings in this experiment is that distinct but connected neural substrates are involved in processing observed objects, actions and context (Epstein, 2005; Schubotz et al., 2014). The strength of the association between the three sources of information affects the strength and likelihood of co-occurring activation within the substrates (Wurm and Schubotz, 2017). The congruent context condition in the present experiment presented each participant with strong visual associations between the object, the action, and the context. This may have allowed for more efficient processing of the observed action in the ventral processing stream by encouraging preactivation of action information, including the goal of the action (Bar, 2004; Ganis and Kutas, 2003; Wurm et al., 2012; Wurm and Schubotz, 2017). This initial expedited understanding of the observed action through the ventral stream may then have manifested as enhanced dorsal stream processing during observation of the action and a facilitation in corticospinal excitability as this stream terminates in a key area of the human action observation matching system. When one of the three sources of information are missing, it is still possible that information regarding the absent source can be predicted from two remaining sources (Wurm and Schubotz, 2017). Consequently, an increased prediction error becomes apparent throughout the ventral processing stream; the extent to which is dependent on the type of action information (Kilner et al., 2007). The prediction error could explain why corticospinal excitability was not facilitated during the incongruent and plain black background conditions, as incomplete information (i.e., missing valuable contextual information) resulted in reduced goal and intention-related cognition. Specifically for the incongruent context condition, it is possible that the incongruence of the context misled the observers' expectations of the action (Wurm and Schubotz, 2012), resulting in slower action recognition through the ventral stream and, therefore, diminished utilisation of the dorsal processing stream and interference in the motor response. This would be expected to reflect in the lack of facilitation of corticospinal excitability found in the present experiment.

The finding that corticospinal excitability was facilitated in the ADM muscle during the static hand condition compared to the plain black background condition was unexpected. A possible explanation for this could relate to the spontaneous use of motor imagery in this condition for some participants. It is possible that the image of a static hand holding the sponge may have contained *implied* movement information (Kourtzi and Kanwisher, 2000; Pavan et al., 2011; Proverbio et al.,

2009) and encouraged participants to spontaneously imagine performing a sponge squeeze action that included flexion of all the fingers. Due to the randomisation of the conditions, only 25% of the videos observed within each block showed no movement. Although this randomisation was included to control for coil movement across conditions, a consequence may have been that participants expected to observe a movement during static hand trials. This may have resulted in participants unintentionally engaging in motor imagery of a wholehand squeeze whilst observing the static hand. Such spontaneous use of motor imagery in this condition may have resulted in a facilitation of corticospinal excitability in the ADM muscle during the static hand condition (Fadiga et al., 1998; Stinear et al., 2006). This phenomenon would not be expected during the other three action observation conditions, where the limited involvement of the ADM muscle is more obvious and when, due to the observation of an action, motor resonance becomes stronger. Further research is required to test this speculation.

It is likely that the reported findings are due to the visual contextual information provided and the congruency of the context to the action. It is possible, however, that other issues could have influenced the results to some extent. For example, as each video was filmed independently over the backgrounds, kinematic equivalence could not be matched exactly. Differences in the kinematic profiles of an observed action (Aihara et al., 2015; Mc Cabe et al., 2014), including the force used to perform an observed action (Alaerts et al., 2010), can modulate corticospinal excitability. Careful attempts were made to match the movement visually for each video as closely as possible to minimise the possible confounding effect that this could have had on the results. In addition, due to the different backgrounds, each video may have generated different levels of interest for the participant. This may have altered attention from observing the goal of the action to the background based on the participant's interest, resulting in modulated corticospinal excitability. This appears unlikely, however, as a greater number of fixations and a greater percentage of time spent fixating on the sponge AOI compared to the hand and background AOIs was observed across all conditions.

Action observation interventions have been shown to contribute to improvements in motor (re)learning (see Buccino, 2014). Holmes and Wright (2017) suggested that interventions that elicit increased activity in the extended motor system may indicate more optimal intervention methods. The findings of the current experiment indicate that including congruent contextual information in action observation interventions can promote increased activity in the motor system. Provision of such information may, therefore, contribute to more effective action observation interventions for motor (re)learning, and future research should establish the veracity of this claim.

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M. Riach et al.

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