Neurophysiological markers discriminate different forms of motor imagery during action observation

Abstract

The dual-action simulation hypothesis proposes that both an observed and an imagined action can be represented simultaneously in the observer's brain. These two sensorimotor streams would either merge or compete depending on their relative suitability for action planning. To test this hypothesis, three forms of combined action observation and motor imagery (AO+MI) instructions were used in this repeated-measures experiment. Participants observed index finger abduction-adduction movements while imagining the same action (*congruent AO+MI*), little finger abduction-adduction (*coordinative AO+MI*), or a static hand (*conflicting AO+MI*). Single-pulse transcranial magnetic stimulation was applied to the left primary motor cortex. The amplitude of motor evoked potential responses were recorded from both the first dorsal interosseous (FDI) and abductor digiti minimi (ADM) muscles of the right-hand while eye movements were tracked. When controlling for the influence of relevant eye movements, corticospinal excitability was facilitated relative to control conditions in the concurrently observed and imagined muscles for both *congruent* and *coordinative* AO+MI conditions. Eye-movement metrics and social validation data from post-experiment interviews provided insight into the cognitive mechanisms underlying these effects. The findings provide empirical support for the dual-action simulation hypothesis, indicating for the first time that it is possible to co-represent observed and imagined actions simultaneously.

Key words: motor imagery during action observation; dual-action simulation; transcranial magnetic stimulation; eye-tracking.

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1. Introduction

Action observation (AO) refers to the deliberate and structured observation of human movement (Neuman & Gray, 2013), whereas motor imagery (MI) involves the mental rehearsal of human movement, typically without accompanying body movement (Guillot & Collet, 2008). It is well-established that improvements in motor function, across rehabilitation and sporting contexts, can be obtained following both AO and MI interventions (e.g., de Vries & Mulder, 2007; Ste-Marie et al., 2012). Consequently, considerable research attention has been devoted to exploring the neurophysiological mechanisms that underpin the improved behavioral outcomes following AO and MI. According to Jeannerod's (2001) simulation theory, these two different forms of motor simulation are associated with activity in regions of the motor system that overlap, in part, with those involved in motor execution. This theory has been supported by neurophysiological research using a variety of techniques. For example, functional magnetic resonance imaging (fMRI) research has shown that several brain areas involved in motor planning and execution (e.g., supplementary motor area, premotor cortex, superior parietal lobe and the intraparietal sulcus) are also active during AO and MI (see Hardwick, Caspers, Eickhoff, & Swinnen, 2018 for a recent meta-analysis). Similarly, transcranial magnetic stimulation (TMS) research indicates that both AO and MI facilitate corticospinal excitability to a similar extent (e.g., Clark, Tremblay, & Ste-Marie, 2004; Williams, Pearce, Loporto, Morris, & Holmes, 2012). Given the similar neurophysiological and behavioral effects of independent AO and MI, recent research has started to explore the efficacy of combining the two motor simulation types (i.e., AO+MI; see

Eaves, Riach, Holmes, & Wright, 2016; Vogt, Di Rienzo, Collet, Collins, & Guillot, 2013 for reviews).

Vogt et al. (2013) proposed a spectrum of AO+MI states where MI can have different roles during AO when the two states are performed concurrently. At one end of the spectrum, an individual can perform *congruent* AO+MI, where s/he observes an action and imagines the kinesthetic sensations involved with performing an identical action. At the opposite end of the spectrum, an individual can perform *conflicting* AO+MI, where s/he observes an action whilst imagining the kinesthetic sensations involved with performing a different action that is unrelated to the observed action. Bridging the spectrum between *congruent* and *conflicting* AO+MI, an individual can perform forms of *coordinative* AO+MI, where s/he observes an action and imagines the kinesthetic sensations involved with performing an action that is different, but related to, the observed action. *Coordinative* AO+MI is not, therefore, a singular entity but, instead, a term that covers a broad range of AO+MI states that can vary in the level of congruency and conflict with the observed action. The extent of coordination depends on parameters including, but not limited to, the action, modality, agency, speed, and perspective for the two AO+MI components.

To further understand the spectrum of AO+MI states and the effect on motor performance and learning, researchers have become increasingly interested in *how* observed and imagined actions can be represented simultaneously. It has been suggested, for example, that both an observed and imagined action can, potentially, be represented as two parallel sensorimotor streams (i.e., dual-action simulation; see Eaves, Riach, et al., 2016). Cisek and Kalaska's (2010) affordance competition hypothesis provides a useful framework for conceptualizing dual-action simulation. Their model proposes that multiple sensorimotor representations are maintained in parallel as a set of action affordances, allowing for a selection process that involves different brain areas submitting 'votes' for relevant movement parameters that contribute towards actual movement execution. In the context of dual-action simulation for AO+MI, it is conceivable that concurrent representations of observed and imagined actions can be maintained simultaneously as two quasi-encapsulated sensorimotor streams. These two streams may either merge or compete based on their content and relevance towards ongoing action plans (Eaves, Turgeon, & Vogt, 2012; Eaves, Haythornthwaite, & Vogt, 2014; Eaves, Behmer, & Vogt, 2016). Whilst this conceptual hypothesis for dual-action simulation seems plausible, research has yet to establish whether it is possible to co-represent observed and imagined actions simultaneously, or explore possible neurophysiological mechanisms underlying dual-action simulation.

Understandably, empirical research investigating AO+MI to date has mainly focused on observing and imagining the same movement (i.e., *congruent* AO+MI; see Eaves, Riach, et al., 2016). Neurophysiological research using a range of different techniques has shown that cortico-motor activity is increased during *congruent* AO+MI of an action compared to independent AO or MI of the same action. This effect has been reported using fMRI (e.g., Macuga & Frey, 2012; Taube et al., 2015; Villiger et al., 2013), electroencephalography (EEG; e.g., Berends, Wolkorte, Ijzerman, & van Putten, 2013; Neuper, Scherer, Wriessnegger, & Pfurtscheller, 2009; Eaves, Behmer, et al., 2016) and transcranial magnetic stimulation (TMS; e.g., Mouthon, Ruffieux, Wälchli, Keller, & Taube, 2015; Sakamoto, Muraoka, Mizuguchi, & Kanosue, 2009; Wright, Williams, & Holmes, 2014). Taken together, this body of neuroscientific literature provides strong evidence for *congruent* AO+MI being associated with increased and more widespread activity in the motor system than either independent AO or MI. These findings have important implications for applied practice, where the use of *congruent* AO+MI may prove beneficial in reinforcing motor (re)learning. It is possible that increased neural activity during *congruent* AO+MI has the potential to support repetitive Hebbian modulation of intracortical and subcortical excitatory mechanisms through synaptic plasticity, in a similar manner to physical practice (Holmes & Calmels, 2008).

While the neurophysiological effects of *congruent* AO+MI are becoming increasingly well-established, few studies have investigated neurophysiological activity during *coordinative* and *conflicting* AO+MI. This is important in order to establish whether it is possible to co-represent different observed and imagined actions across the spectrum of AO+MI states. In one study to address this issue, Eaves, Behmer, et al. (2016) used EEG to examine possible electrophysiological differences between what they termed ‘synchronized’ AO+MI (an aggregation of *congruent* and *coordinative* AO+MI data) and *conflicting* AO+MI of rhythmical actions. They reported increased event-related desynchronization in the mu/alpha and beta frequency bands, indicative of increased activity, over the sensorimotor regions for their ‘synchronized’ AO+MI condition compared to independent AO or MI. There was, however, no difference in the extent of event-related desynchronization in these brain regions between their ‘synchronized’ and *conflicting* AO+MI conditions. In contrast, differences were reported in the left rostral prefrontal cortex, where for the ‘synchronized’ AO+MI condition there was increased activity compared to *conflicting* AO+MI. The rostral prefrontal cortex plays a role in routing attention between different information sources (Burgess, Simons, Dumontheil, & Gilbert, 2005). As such, the authors proposed that the increased activity in this region during their ‘synchronized’ AO+MI condition may reflect the shifting and reallocating of attentional resources between the observed and imagined actions. Consequently, it is currently unclear whether simultaneous co-representation of an observed and imagined action is possible in parallel, or whether shifts in attentional resources between observed and imagined content are required in order to maintain the representation of both actions.

To resolve this issue, it is essential to compare the neurophysiological correlates of AO+MI across the spectrum of AO+MI states (i.e., *congruent vs. coordinative vs. conflicting*), using a multi-modal approach to data collection. TMS is a suitable technique for exploring this issue. Using this technique, the activation of a muscle representation on the motor cortex produces a motor evoked potential (MEP) in the corresponding muscle(s); the amplitude of which provides a marker of corticospinal excitability (Naish, Houston-Price, Bremner, & Holmes, 2014; Rothwell, 1997). This technique is appropriate for exploring neurophysiological activity during different AO+MI states for several reasons. First, it is accepted that both independent AO and MI conditions facilitate corticospinal excitability compared to suitable control conditions (e.g., Clark et al., 2004; Williams et al., 2012). Second, particularly when targeting hand muscle representations, the topography of the motor cortex makes it possible to deliver TMS to a single scalp location and record MEP responses from multiple muscles (e.g., Boroojerdi et al., 1999; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). Third, the facilitation in corticospinal excitability reported during AO and MI is specific to the muscles involved in either the observed or the imagined action (see Naish et al., 2014; Grosprêtre, Ruffino, & Lebon, 2016), providing the opportunity to distinguish the contributions of AO and MI by studying muscle-specific effects during different AO+MI states.

Recently, researchers in the field of AO have begun to include the use of eye-tracking technology (e.g., D’Innocenzo, Gonzalez, Nowicky, Williams, & Bishop, 2017; Riach, Holmes, Franklin, & Wright, 2018; Wright, Wood, Franklin, et al., 2018) and social validation procedures (Riach, Wright, Franklin, & Holmes, 2018) as secondary data collection approaches in conjunction with TMS. The inclusion of these measures could prove beneficial in determining the extent to which simultaneous dual-action simulation is possible during different AO+MI states. For example, the use of eye-tracking provides the opportunity to explore visual attentional processes, based on the number and location of visual fixations (Causer, McCormick, & Holmes, 2013; Liversedge & Findlay, 2003). Examining eye movement behavior across the spectrum of AO+MI states could, therefore, provide an indication of whether simultaneous dual-action simulation is possible in parallel or whether a shifting of attentional resources is required between observed and imagined components of an action. Social validation procedures, such as post-experiment interviews and questionnaires, have also been used to explore participants' experiences of different experimental conditions in AO research. The use of these methods could provide valuable insight into the conscious cognitive processes of participants whilst they engage in different AO+MI states. It may be possible to determine how and why attention, intention, ease of engagement, and required effort may change across the spectrum of AO+MI states. Such information may help to explain possible differences found in the more objective neurophysiological markers of corticospinal excitability and visual attention.

The aim of the current experiment was to test the dual-action simulation hypothesis (Eaves, Riach, et al., 2016) by comparing neurophysiological markers of engaging in different states of AO+MI. This study aimed to compare corticospinal excitability for three AO+MI conditions, representative of the *congruent*, *coordinative* and *conflicting* AO+MI states proposed by Vogt et al. (2013). The first hypothesis was that *congruent* AO+MI would produce larger MEPs in the muscle primarily involved in the simultaneously observed and imagined action, compared to control conditions. The second hypothesis was that *coordinative* AO+MI would produce increased MEP amplitudes, compared to control conditions, in the two muscles involved in the different observed and imagined tasks. This would indicate that it is possible to simultaneously co-represent different, but related, observed and imagined actions, in line with the predictions of the dual-action simulation hypothesis (Eaves et al., 2012, 2014; Eaves, Behmer et al., 2016).. The third hypothesis was that MEP amplitudes would be significantly lower in both muscles during *conflicting* AO+MI compared to the *congruent* and *coordinative* AO+MI conditions due to the increased competition between MI and AO processes (Eaves et al., 2012). Eye movement markers of visual attention and post-experiment interviews and questionnaires were also used to identify attentional and cognitive mechanisms underlying the predicted changes in corticospinal excitability.

2. Material and methods

2.1. Participants

Based on previous AO+MI studies employing TMS (e.g., Wright et al., 2014), twenty-four healthy adults (16 male, 8 female) aged 20-39 years (mean age = 24.29 ± 4.96 years) participated in this study[1]. Prior to involvement in the experiment[2], all participants provided written informed consent and completed a survey pack including the TMS Adult Safety Screen (Keel, Smith, & Wassermann, 2001), Edinburgh Handedness Inventory (EHI; Oldfield, 1971), and the Vividness of Movement Imagery Questionnaire-2 (VMIQ-2; Roberts, Callow, Hardy, Markland, & Bringer, 2008). All individuals were eligible to participate in the experimental session based on their responses to the safety-screening questionnaire and no participants reported adverse effects either during or after completing the experiment. All participants were right-hand dominant (mean EHI laterality score 88.59 ± 8.62) and had normal or corrected-to-normal vision. Participant responses to the VMIQ-2 indicated that all participants were able to generate at least moderately clear and vivid internal (21.04 ± 9.11), external (23.75 ± 9.15), and kinesthetic (29.25 ± 11.41) imagery.

2.2. Experimental Design

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[1] We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

[2] No aspect of the study procedures or analyses were pre-registered prior to the research being conducted.

A repeated measure design was employed, which involved participants completing six conditions (see Figure 1). There were three control conditions: (i) a non-human baseline (BL_{NH}) condition where participants observed videos of a static white fixation-cross presented against a black screen; (ii) a human baseline (BL_{H}) condition where participants observed videos of a static right-hand in a pronated position; and (iii) an action observation (AO) condition where participants observed videos of a right-hand abducting and adducting the index finger in a pronated position. The three experimental conditions involved participants engaging in different AO+MI states: (i) a *congruent* AO+MI ($AO+MI_{CONG}$) condition where participants observed videos of a right-hand abducting and adducting the index finger whilst imagining simultaneously the feelings and sensations associated with performing the same movement with the index finger of their right-hand; (ii) a *coordinative* AO+MI ($AO+MI_{COOR}$) condition where participants observed videos of a right-hand abducting and adducting the index finger whilst imagining simultaneously the feelings and sensations associated with abducting and adducting the little finger of their right-hand; and (iii), a *conflicting* AO+MI ($AO+MI_{CONF}$) condition where participants observed videos of a right-hand abducting and adducting the index finger whilst imagining simultaneously the feelings and sensations associated with keeping their right hand in a still and relaxed position[3].

All participants completed the two baseline conditions (BL_{NH}, BL_{H}) first, with the order of these counterbalanced across the study sample. The AO condition was completed third for all participants. The three AO+MI state conditions ($AO+MI_{CONG}$, $AO+MI_{COOR}$, $AO+MI_{CONF}$) were completed last, with the order of these conditions counterbalanced across the study sample. This experimental order was adopted instead of a fully randomized design

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[3] All digital materials associated with this experiment, including video stimuli, presentation code, and analysis scripts, are archived in a publically available repository and accessible here: https://e-space.mmu.ac.uk/id/eprint/624008

to reduce the likelihood of prior imagery instructions (i.e., those provided prior to the three AO+MI state conditions) eliciting forms of spontaneous or deliberate imagery in experimental conditions where imagery was not instructed (BL_{NH}, BL_{H}, AO), whilst still maintaining a counterbalanced element to the study design. Similar designs have been used in previous TMS experiments investigating *congruent* AO+MI (e.g., Wright et al., 2014; Wright, McCormick, Williams, & Holmes, 2016; Wright, Wood, Eaves et al., 2018).

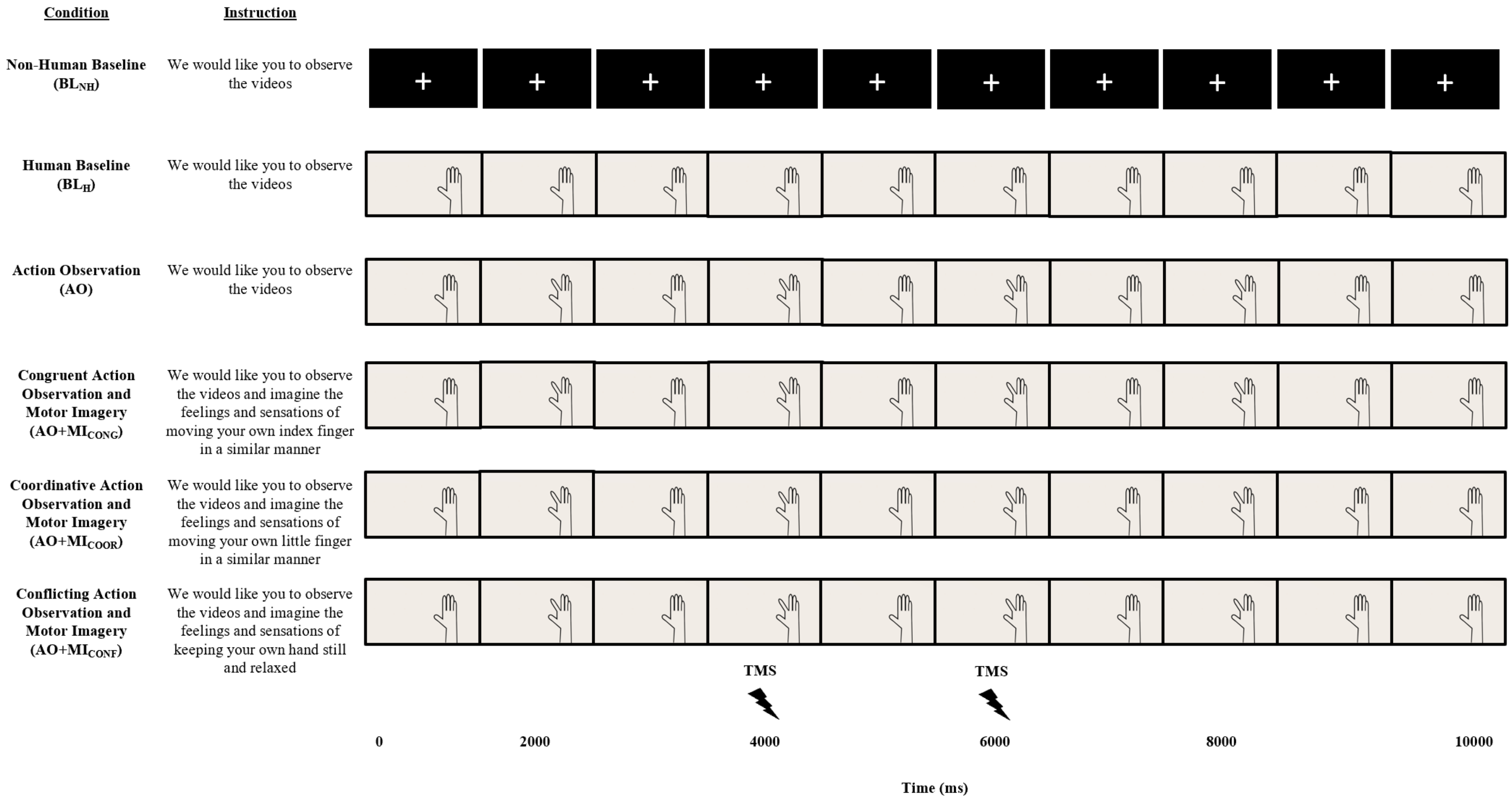

***Figure 1.* A visual representation of the six experimental conditions.** *Note:* For each trial, the stimulation was delivered at the point of maximum index finger abduction during either the second (4000 ms after video onset) or third (6000 ms after video onset) cycle for the

conditions displaying a moving hand, and at the same time-points during the static baseline conditions (BL_{NH}, BL_{H}), with the ordering of this randomized and counterbalanced across trials for each experimental block.

2.3. Procedure

2.3.1. Surface electromyography (EMG). EMG activity was recorded throughout the experiment from the first dorsal interosseous (FDI) and abductor digiti minimi (ADM) muscles of participants' right-hand using a Delsys Bagnoli 2-Channel EMG system. DE-2.1 bipolar single differential surface EMG electrodes (Delsys, Boston, MA, USA) were placed centrally on the skin overlying the muscle belly, with a reference electrode placed on the ulnar process of the right wrist. The EMG signal was processed using a Micro 1401-3 analogue-to-digital converter (Cambridge Electronic Design, Cambridge, UK) and recorded using Spike 2 (version 6.18) software with a sampling rate of 2 kHz, bandwidth of 20-450 kHz, 92 dB common mode rejection ratio and >1015 Ω input impedance.

2.3.2. Transcranial magnetic stimulation (TMS). Single-pulse TMS was delivered to the hand representation of the left primary motor cortex using a figure-of-eight shaped coil with 70mm diameter loops connected to a Magstim 200^2 magnetic stimulator (Magstim, Whitland, Dyfed, UK). The TMS coil was orientated at a 45° angle to the central line between the nasion and inion landmarks of the cranium (Brasil-Neto et al., 1992) and was held in place against the optimal scalp position (OSP) using a mechanical arm (Manfrotto™, Cassola, Italy). The OSP was located by delivering four stimulations at 60% maximum stimulator output to an initial scalp position 4 cm lateral to the centre of the head (i.e., 4 cm lateral from EEG electrode site Cz). This stimulation intensity was selected as it produces consistently large amplitude MEPs in most individuals (Loporto, Holmes, Wright, & McAllister, 2013) and has been used to establish the OSP in previous TMS experiments on *congruent* AO+MI (e.g., Wright et al., 2014, 2016; Wright, Wood, Eaves, et al., 2018). The coil was then moved around the initial scalp position in 1cm steps and the stimulation process was repeated until the site that produced MEPs with the largest and most consistent amplitudes in both muscles was found. This site was defined as the OSP and marked on a tightly fitting polyester cap worn by the participant. In most cases, the initial scalp position (4cm lateral, 0cm anterior from Cz) was identified as the OSP. The resting motor threshold (RMT) was then determined for each participant. This procedure involved gradually reducing or increasing the stimulation intensity to find the minimum stimulation intensity capable of producing MEP amplitudes in excess of 50 µV in 5 of 10 consecutive trials (see Rossini et al., 2015). Consistent with previous TMS research on AO+MI (e.g., Wright et al., 2014; Wright, Wood, Eaves, et al., 2018), the experimental stimulation intensity was set at 110% RMT for each participant to reduce direct wave stimulation (Loporto et al., 2013). The mean RMT was 46% (± 9.35) of the maximum stimulator output, and the mean experimental stimulation intensity was 51.21% (± 10.15).

2.3.3. Eye-tracking. An SMI Eye Tracking Glasses 2 Wireless system (SensoMotoric Instruments, Teltow, Germany) was used to record participants' eye movements (sampling rate of 60Hz) to monitor visual attention during the experiment. This mobile system required participants to wear eye-tracking glasses that record binocular eye movements using two infrared eye cameras projected into the participant's eyes, and the visual scene using a high-definition outward-facing camera. Each eye is illuminated by six infrared lighting sources and changes in corneal reflections of this infrared light are recorded using an infrared camera, which are then mapped on to the visual scene (recorded at 24 frames per second). The system uses a 3-point calibration check to ensure accuracy of the eye movement recordings and visual scene mapping. This calibration check was performed immediately prior to each experimental block and was monitored throughout the experiment via a laptop. The primary researcher validated the accuracy of the eye-tracking at two points during each experimental block (the inter-trial intervals between trials 10-11 and 20-21) by asking the participant to attend to different locations on the screen to clarify their on-screen gaze location. A 3-point recalibration was performed if necessary.

2.3.4. Experimental protocol. Participants were seated at a black wooden table in front of an LCD display (32-inch, DGM Model LTV-3203H) in a dimly lit room, with their head rested between an adjustable head-and-chin mount and the TMS coil. This maintained a consistent viewing position and minimized head movement for each participant, ensuring the accuracy of TMS coil placement and eye-tracking recordings within and across experimental blocks. The participants maintained a set position for all experimental blocks (see Figure 2), with their elbows flexed at 90° and their hands pronated in a relaxed position under a black-painted wooden casing on the table. The participants kept their right arm/hand positioned directly in front of them and their left arm/hand positioned across their body. The display was mounted horizontally to the table with a 15° inclination, meaning the centre of the screen was 60cm from the participants head position. The purpose of this was to ensure anatomical and perceptual congruency between the participant's hand and the observed hand (Riach, Holmes, et al., 2018). Blackout curtains were drawn alongside the experimental station to reduce the likelihood of visual distraction during data collection. Prior to beginning the experiment, participants were asked to read the on-screen instructions carefully, refrain from voluntary movement during the experimental blocks and to attend fully to the stimuli presented.

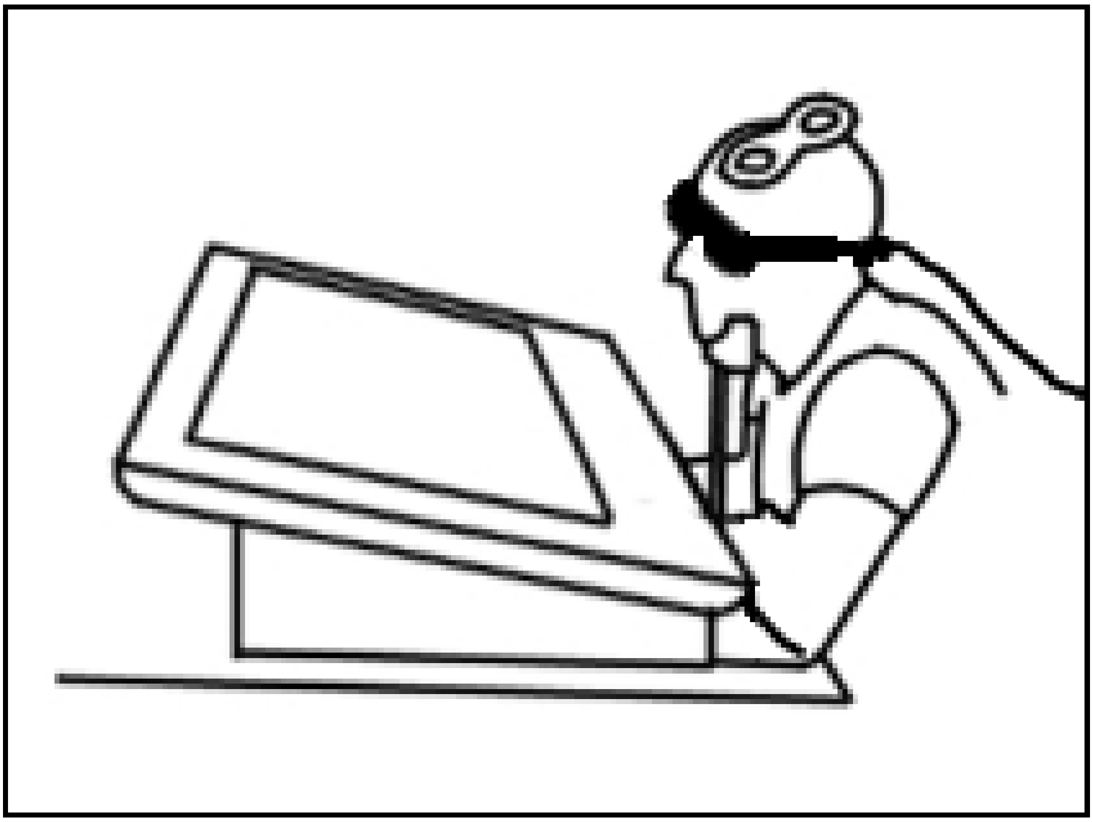

Figure 2. **A visual representation of the experimental setup including the screen position, TMS coil placement, and eye-tracking glasses.** *Note:* This figure was adapted, with permission, from a figure included in a previous paper by Riach, Wright, et al. (2018).

Participants completed the six experimental blocks consecutively within a single testing session, with each block lasting 7 minutes in total. A 3-minute rest period was included between blocks to prevent participant fatigue and discomfort, and to provide enough time to allow MEP amplitudes to return to baseline levels (Baldi, Perretti, Sannino, Marcantonio, & Santoro, 2002). All experimental blocks included 30 trials where the participant watched a 10-second video presented on the LCD display using DMASTR DMDX display software (Forster & Forster, 2003). Videos were recorded in high definition using a SONY CX405 Handycam (1920 x 1080/50p resolution) at a sampling frequency of 25 Hz. Participants were provided with written and verbal reminders of the specific instructions for each experimental block every 10 trials (see Figure 1). For the conditions involving the observation of human movement (AO, AO+MI$_{\text{CONG}}$, AO+MI$_{\text{COOR}}$, AO+MI$_{\text{CONF}}$), the video initially displayed a model hand at rest (1000 ms), followed by four repetitions of the hand abducting and adducting the index finger (2000 ms per cycle, 8000 ms per trial), before returning to the resting position (1000 ms). Using a bespoke script run through Spike 2 software, single-pulse TMS was delivered once per trial at the point of maximum index finger abduction as MEP amplitudes are greatest when stimulating at the point where the observed muscle contraction is maximal (Gangitano, Mottaghy, & Pascual-Leone, 2001). The stimulation was delivered during either the second (4000 ms after video onset) or third (6000 ms after video onset) cycle for the conditions displaying a moving hand, and at the same time-points during the static baseline conditions (BL$_{\text{NH}}$, BL$_{\text{H}}$). The ordering of the TMS delivery was randomized and counterbalanced across trials for each experimental block. Different stimulation timings were used to reduce the predictability of the stimulation and subsequent anticipatory behavior of the participants (Loporto, McAllister, Edwards, Wright, & Holmes, 2012). A 3-second transition period was adopted between trials to maintain an inter-stimulus interval greater than 10 seconds and allow the effects of the previous stimulation to subside (Chen et al., 1997). In total, 30 stimulations were administered per experimental condition to ensure a reliable measure of corticospinal excitability for all experimental conditions (Cuypers, Thijs, & Meesen, 2014; Goldsworthy, Hordacre, & Ridding, 2016).

2.3.5. Social validation. On finishing the experimental procedures, each participant was asked to “Rate the ease/difficulty with which you were able to imagine the efforts, feelings and sensations involved with…” using a 7-point scale between 1 (*Very easy to feel*) and 7 (*Very hard to feel*) for the AO+MI$_{\text{CONG}}$, AO+MI$_{\text{COOR}}$, and AO+MI$_{\text{CONF}}$ conditions. Following this, the primary researcher conducted a semi-structured social validation interview with each participant to check for compliance with the intended manipulations and gauge her/his experiences of the experimental conditions. Questions targeted overall effects, difficulty, attention (direction and level), applicability, and checks for spontaneous imagery during control conditions and imagery perspective during AO+MI conditions. The interview guide included 10 initial questions (e.g. “Do you have any comments on the difficulty of performing [insert AO+MI experimental task]?”). Multiple follow-up probes were listed for each question to gain the necessary detail from all participants (e.g., “What made this task difficult for you?”, “Was this task easier or harder than the other AO+MI experimental tasks, and why do you think this was the case?”).

2.4. Data Analysis

2.4.1. TMS data. MEP peak-to-peak amplitude was measured for the FDI and ADM muscles on a trial-by-trial basis and averaged across all trials for each experimental condition[4]. MEP amplitudes are reportedly increased for a target muscle if the EMG activity in that muscle is above resting state levels at, or immediately prior to, the time of stimulation (Devanne, Lavoie, & Capaday, 1997; Hess, Mills, & Murray, 1987). To avoid MEP contamination by volitional muscle activity, EMG activity was recorded in the 200 ms prior to each stimulation and any trials where the EMG amplitude exceeded average baseline values for that experimental block (mean +2.5 SD) were removed (e.g., Riach, Wright, et al., 2018; Wright et al., 2014; Wright, Wood, Eaves, et al., 2018). On average, 1.47 (± 1.64) trials were removed for the FDI muscle and 2.05 (± 2.20) trials were removed for the ADM muscle per experimental block. This resulted in the total number of included trials per muscle per

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[4] The conditions of our ethics approval do not permit public archiving of anonymized study data. Readers seeking access to the data should contact the corresponding author, Dr David Wright (d.j.wright@mmu.ac.uk) or the local ethics committee at the Faculty of Health Psychology and Social Care, Manchester Metropolitan University. Access will be granted to named individuals in accordance with ethical procedures governing the reuse of clinical data, including completion of a formal data sharing agreement and approval of the local ethics committee.

condition still being sufficient to provide a reliable estimate of corticospinal excitability (Cuypers et al., 2014). The raw MEP amplitude data of remaining trials was then normalized using the *z*-score transformation used commonly in similar experiments (e.g., Aglioti, Cesari, Romani, & Urgesi, 2008; Fadiga et al., 1995; Wright et al., 2014), to account for the large intra- and inter-participant variability in MEP amplitudes. This procedure involved standardizing the MEP amplitude value obtained in each trial against all other MEP amplitude values obtained across each condition in the experiment. This results in the mean amplitude for all trials being represented by a value of zero, and values for each experimental condition indicating by how many standard deviations a specific condition was above or below the mean of all conditions. Once normalized, the *z*-score MEP amplitude data from each muscle was analyzed with separate one-way repeated measures analysis of variance (ANOVA) tests with 6 levels (Condition: BL_{NH}, BL_{H}, AO, $AO+MI_{CONG}$, $AO+MI_{COOR}$, $AO+MI_{CONF}$). Bonferroni contrasts were used for post-hoc pairwise comparisons.

2.4.2. Eye-tracking data. To compare eye movement markers of visual attention between the AO+MI state conditions, eye movements were recorded during the AO+MI experimental blocks (i.e., $AO+MI_{CONG}$, $AO+MI_{COOR}$, $AO+MI_{CONF}$). The eye movement data was analyzed on a trial-by-trial basis using SMI BeGaze analysis software (SensoMotoric Instruments, Teltow, Germany). BeGaze software automatically detected fixations, defined as gaze that remained stable (± 1° visual angle) for more than 99.9 ms (Vickers, 1996), and these were semantically mapped onto the visual scene. Dynamic areas of interest (AOI) were drawn around the index finger, little finger, and other parts of the hand (see Figure 3), with all other background regions in the visual scene classified as a fourth AOI for analysis purposes. Eye movement metrics (total number of fixations and total duration of fixations) were calculated for each AOI across the three AO+MI experimental blocks. A one-way ANOVA with four levels (AOI: index finger, little finger, other hand areas, background) was used to compare eye-movement data for the different AOI separately within each of the three AO+MI conditions (AO+MI$_{\text{CONG}}$, AO+MI$_{\text{COOR}}$, AO+MI$_{\text{CONF}}$). Separate analyses were conducted for the total number of fixations and total duration of fixations data. Bonferroni contrasts were used for post-hoc pairwise comparisons.

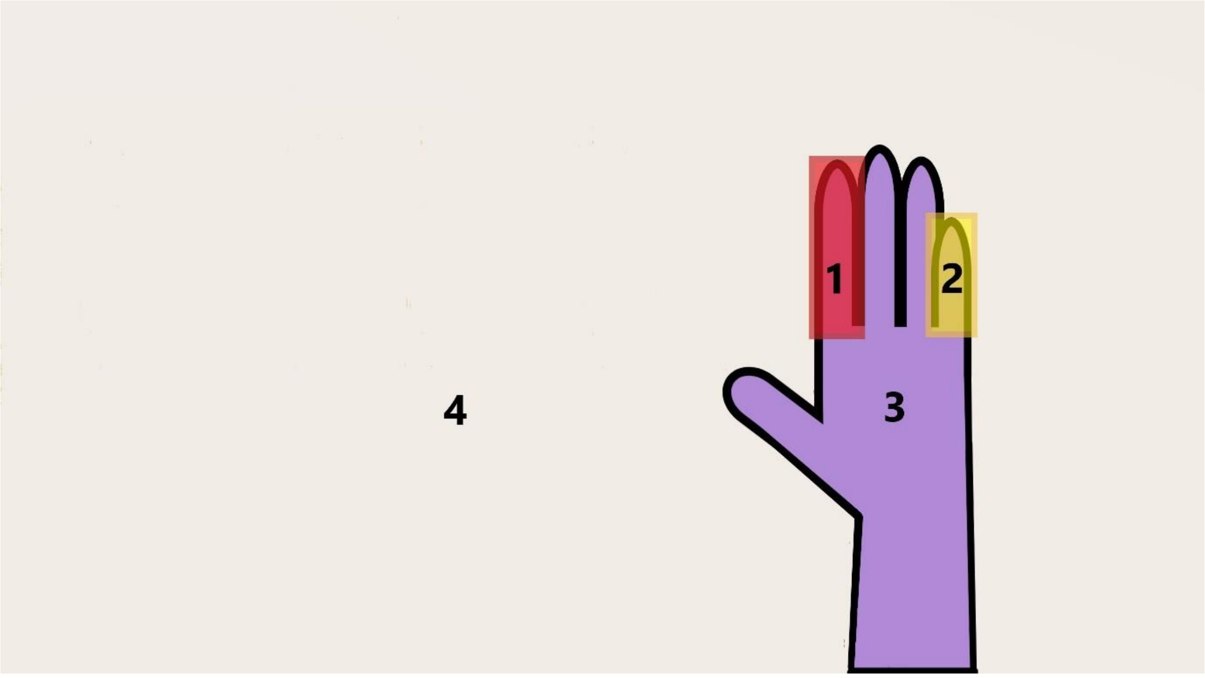

Figure 3. **A visual representation of the areas of interest utilized for the eye-tracking analyses during the AO+MI experimental conditions.** Dynamic areas of interest were used to cover the (1) index finger, (2) little finger, (3) other hand areas, and (4) the background for trials in AO+MI experimental conditions.

2.4.3. TMS data: Controlling for eye-tracking data as a covariate. Previous research by D’Innocenzo et al. (2017) and Wright, Wood, Franklin, et al. (2018) reported significant increases in MEP amplitude for specific muscles during AO when participants attended to that muscle in action, compared to when they attended elsewhere in the display. In the present study it was, therefore, important to control for eye movement data recorded within the predetermined AOIs when comparing MEP amplitudes across the experimental conditions. Based on previous findings (D’Innocenzo et al.; Wright, Wood, Franklin, et al.), the eye movement metrics obtained for the index finger AOI were deemed crucial variables that could moderate MEP amplitudes in the FDI muscle. Consequently, a one-way repeated measures analysis of covariance (ANCOVA) with five levels (Condition: BL_H, AO, $AO+MI_{CONG}$, $AO+MI_{COOR}$, $AO+MI_{CONF}$) was run on the FDI muscle *z*-score MEP amplitude data to account for the influence of both the total number of fixations and total duration of fixations recorded in the index finger AOI on MEP amplitude in this muscle. Similarly, the eye movement metrics recorded in the little finger AOI were defined as moderator variables when assessing MEP amplitudes in the ADM muscle. Thus, a one-way repeated measures ANCOVA with five levels (Condition: BL_H, AO, $AO+MI_{CONG}$, $AO+MI_{COOR}$, $AO+MI_{CONF}$) was run on the ADM muscle *z*-score MEP amplitude data to account for the influence of both the total number of fixations and total duration of fixations recorded in the little finger AOI on MEP amplitudes in this muscle. Bonferroni contrasts were used for post-hoc pairwise comparisons.

2.4.4. Social validation data. A one-way repeated measures ANOVA with three levels (Condition: $AO+MI_{CONG}$, $AO+MI_{COOR}$, $AO+MI_{CONF}$) was used to examine differences in participants ratings for perceived ease/difficulty of kinesthetic image generation during experimental conditions where imagery was instructed. Bonferroni contrasts were used for post-hoc pairwise comparisons. Social validation interview data was interpreted using Braun and Clarke’s (2006) six-step thematic analytical procedures. The data analysis involved: (1) familiarization with the data, (2) transcription of the audio recorded interviews, (3) identification of the initial codes, (4) identification of themes, (5) naming, reorganizing and completing the themes, (6) theme comparison and write-up with reference to existing research regarding AO+MI (e.g., Taube, Lorch, Zeiter, & Keller, 2014; Vogt et al., 2013; Wright et al., 2014).

3. Results

3.1. TMS Data

In the FDI muscle, the one-way repeated measures ANOVA on the *z*-score MEP amplitude data revealed a significant effect of experimental condition, $F_{(5,115)} = 7.46$, $p < .001$, $\eta_p^2 = .25$. Pairwise comparisons (Figure 4) showed that MEP amplitudes were larger in the AO+MI$_{\mathrm{CONG}}$ condition compared to the BL$_{\mathrm{NH}}$ ($p = .003$), BL$_{\mathrm{H}}$ ($p < .001$), and AO+MI$_{\mathrm{CONF}}$ ($p = .001$) conditions, and approached a significantly larger score in the AO+MI$_{\mathrm{COOR}}$ condition compared to the BL$_{\mathrm{H}}$ ($p = .13$) and AO+MI$_{\mathrm{CONF}}$ conditions ($p = .11$). In the ADM muscle, the one-way repeated measures ANOVA revealed a significant effect of experimental condition, $F_{(5,115)} = 9.71$, $p < .001$, $\eta_p^2 = .30$. Pairwise comparisons (Figure 4) indicated that MEP amplitudes were larger in the AO+MI$_{\mathrm{COOR}}$ condition compared to the BL$_{\mathrm{NH}}$ ($p = .003$), BL$_{\mathrm{H}}$ ($p < .001$), AO ($p < .001$), AO+MI$_{\mathrm{CONG}}$ ($p = .03$), and AO+MI$_{\mathrm{CONF}}$ conditions ($p = .009$). No other significant differences were reported for pairwise comparisons in either muscle.

***Table 1.* Mean, standard error (SE), confidence interval (CI), and alpha values (*p*) for focal post-hoc pairwise comparisons between MEP amplitudes from the FDI and ADM muscles, displayed as z-scores, for the six experimental conditions.** BL$_{NH}$ – non-human baseline; BL$_{H}$ – human baseline; AO – action observation; AO+MI$_{CONG}$ – congruent action observation and motor imagery; AO+MI$_{COOR}$ – coordinative action observation and motor imagery; AO+MI$_{CONF}$ – conflicting action observation and motor imagery.

Muscle	Condition	Mean	SE	95% CI	vs	Condition	Mean	SE	95% CI	*p*
FDI	AO+MI$_{CONG}$	0.39	0.08	[0.23, 0.56]	vs	BL$_{NH}$	-0.06	0.06	[-0.19, 0.07]	.003
					vs	BL$_{H}$	-0.22	0.06	[-0.34, -0.10]	< .001
					vs	AO+MI$_{CONF}$	-0.22	0.08	[-0.38, -0.07]	.001
	AO+MI$_{COOR}$	0.12	0.08	[-0.05, 0.28]	vs	BL$_{H}$	-0.22	0.06	[-0.34, -0.10]	.13
					vs	AO+MI$_{CONF}$	-0.22	0.08	[-0.38, -0.07]	.11
ADM	AO+MI$_{COOR}$	0.51	0.10	[0.31, 0.71]	vs	BL$_{NH}$	-0.06	0.07	[-0.20, 0.08]	.003
					vs	BL$_{H}$	-0.16	0.06	[-0.28, -0.04]	< .001
					vs	AO	-0.22	0.07	[-0.37, -0.07]	< .001
					vs	AO+MI$_{CONG}$	-0.03	0.09	[-0.22, 0.17]	.03
					vs	AO+MI$_{CONF}$	-0.04	0.07	[-0.18, 0.09]	.009

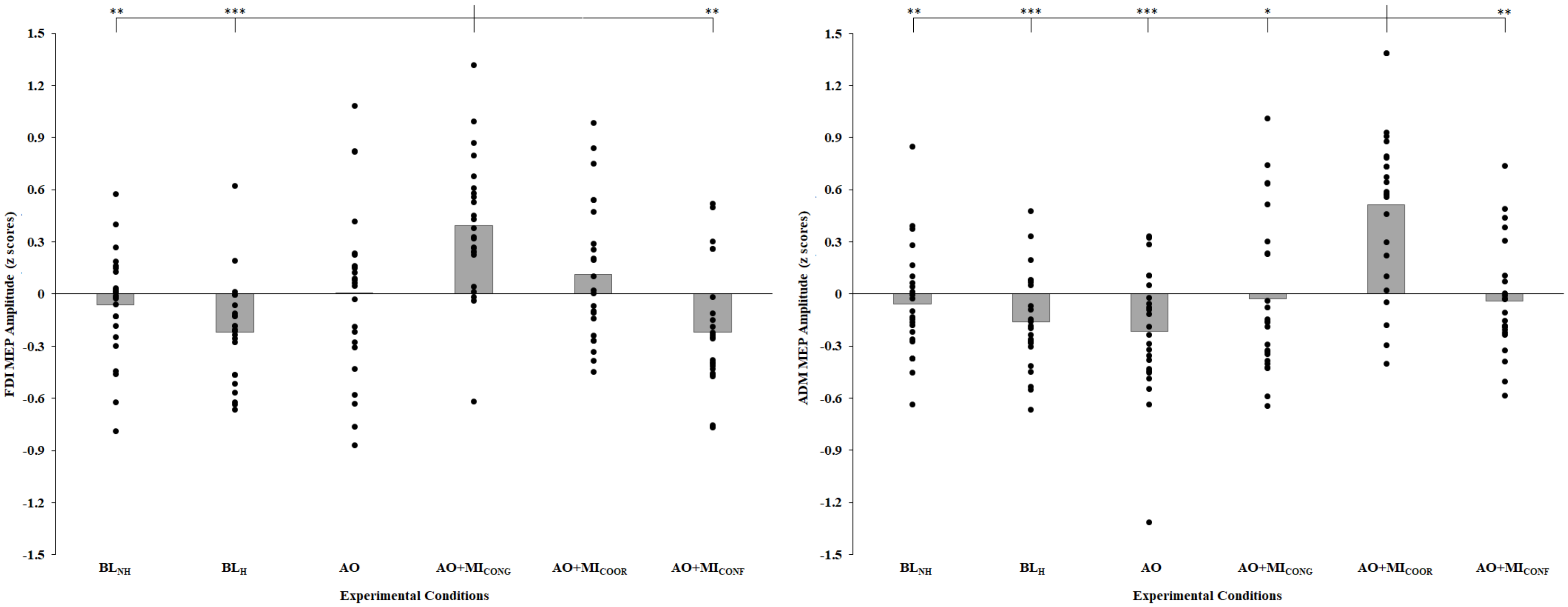

Figure 4. **MEP amplitudes from the FDI and ADM muscles, displayed as z-scores, for the six experimental conditions.** BL$_{NH}$ – non-human baseline; BL$_{H}$ – human baseline; AO – action observation; AO+MI$_{CONG}$ – congruent action observation and motor imagery; AO+MI$_{COOR}$ – coordinative action observation and motor imagery; AO+MI$_{CONF}$ – conflicting action observation and motor imagery. The mean value for each condition is displayed as the column, with values for all participants displayed as markers. Positive z-score values indicate that the MEP amplitude in that condition was greater than the mean MEP amplitude in that muscle across all conditions. Negative z-score values indicate that the MEP amplitude in that condition was less than the mean MEP amplitude in that muscle across all conditions. *Note:* ****p* <.001, ***p* <.01, **p* <.05.

3.2. Eye-Tracking Data

3.2.1. Total number of fixations. The one-way repeated measures ANOVA for the $AO+MI_{CONG}$ condition showed a significant effect of AOI, $F_{(1.47,33.76)} = 43.33$, $p < .001$, $\eta_p^2 = .65$. Pairwise comparisons revealed that in this condition there were more fixations on the index finger compared to the little finger ($p < .001$), other hand areas ($p < .001$), and background AOI ($p < .001$). The one-way repeated measures ANOVA for the $AO+MI_{COOR}$ condition also showed a significant effect of AOI, $F_{(3,69)} = 5.43$, $p = .002$, $\eta_p^2 = .19$. Pairwise comparisons revealed that in this condition there was no difference in the number of fixations on the index finger compared to the little finger ($p = .67$), but there were more fixations on the little finger compared to the background AOI ($p = .006$). Finally, the one-way repeated measures ANOVA for the $AO+MI_{CONF}$ condition showed a significant effect of AOI, $F_{(1.96,45.15)} = 10.28$, $p < .001$, $\eta_p^2 = .31$. Pairwise comparisons revealed that in this condition there were more fixations on the index finger and other hand areas compared to the little finger AOI ($p < .001$).

***Table 2.* Mean, standard error (SE), confidence interval (CI), and alpha values (*p*) for focal post-hoc pairwise comparisons between mean number of fixations recorded in each area of interest for the AO+MI experimental conditions.** AO+MI$_{\text{CONG}}$ – congruent action observation and motor imagery; AO+MI$_{\text{COOR}}$ – coordinative action observation and motor imagery; AO+MI$_{\text{CONF}}$ – conflicting action observation and motor imagery.

Condition	**AOI**	**Mean**	**SE**	**95% CI**	**vs**	**Condition**	**Mean**	**SE**	**95% CI**	***p***
AO+MI$_{\text{CONG}}$	Index finger	307.13	29.49	[246.13, 368.12]	vs	Little finger	1.46	0.72	[-0.20, 2.94]	< .001
					vs	Other hand areas	93.00	18.08	[55.61, 130.40]	< .001
					vs	Background	58.54	15.37	[26.74, 90.34]	< .001
AO+MI$_{\text{COOR}}$	Index finger	87.92	21.41	[43.62, 132.21]	vs	Little finger	151.33	21.62	[106.62, 196.05]	.67
	Little finger	151.33	21.62	[106.62, 196.05]	vs	Background	53.67	11.69	[29.49, 77.85]	.006
AO+MI$_{\text{CONF}}$	Index finger	160.71	30.71	[97.18, 224.24]	vs	Little finger	6.25	3.20	[-0.37, 12.87]	< .001
	Other hand areas	173.25	22.04	[127.65, 218.89]	vs	Little finger	6.25	3.20	[-0.37, 12.87]	< .001

3.2.2. Total duration of fixations. In the AO+MI$_{\text{CONG}}$ condition, the one-way repeated measures ANOVA showed a significant effect of AOI, $F_{(1.34,30.71)} = 60.44$, $p < .001$, $\eta_p^2 = .72$. Pairwise comparisons revealed that in this condition participants spent more time fixated on the index finger compared to the little finger ($p < .001$), other hand areas ($p < .001$), and background AOI ($p < .001$). In the AO+MI$_{\text{COOR}}$ condition, the one-way repeated measures ANOVA showed a significant effect of AOI, $F_{(1.98,45.59)} = 6.45$, $p = .004$, $\eta_p^2 = .22$. Pairwise comparisons revealed that there were no differences in the time participants spent fixated on the index finger compared to the little finger AOI ($p = .27$), but participants spent more time fixated on the little finger compared to the background AOI ($p = .001$). In the AO+MI$_{\text{CONF}}$ condition, the one-way repeated measures ANOVA showed a significant effect of AOI, $F_{(1.66,38.19)} = 15.36$, $p < .001$, $\eta_p^2 = .40$. Pairwise comparisons revealed that participants spent more time fixated on the index finger compared to the little finger ($p < .001$) and background AOI ($p = .01$). Participants also spent more time fixated on the other hand areas compared to the little finger ($p < .001$) and background AOI ($p = .001$).

***Table 3.* Mean, standard error (SE), confidence interval (CI), and alpha values (*p*) for focal post-hoc pairwise comparisons between mean duration of fixations recorded in each area of interest for the AO+MI experimental conditions.** AO+MI$_{\text{CONG}}$ – congruent action observation and motor imagery; AO+MI$_{\text{COOR}}$ – coordinative action observation and motor imagery; AO+MI$_{\text{CONF}}$ – conflicting action observation and motor imagery.

Condition	AOI	Mean	SE	95% CI	vs	Condition	Mean	SE	95% CI	*p*
AO+MI$_{\text{CONG}}$	Index finger	179.39	14.80	[148.77, 210.01]	vs	Little finger	0.40	0.19	[0.01, 0.80]	< .001
						Other hand areas	44.07	9.14	[25.16, 62.98]	< .001
						Background	24.19	5.93	[11.92, 36.46]	< .001
AO+MI$_{\text{COOR}}$	Index finger	47.11	13.91	[18.34, 75.88]	vs	Little finger	106.09	17.13	[70.65, 141.53]	.27
	Little finger	106.09	17.13	[70.65, 141.53]	vs	Background	22.57	5.43	[11.35, 33.80]	.001
AO+MI$_{\text{CONF}}$	Index finger	99.49	16.66	[65.02, 133.96]	vs	Little finger	3.41	2.15	[-1.03, 7.85]	< .001
					vs	Background	26.81	9.07	[8.05, 45.57]	.01
	Other hand areas	123.38	17.11	[87.98, 158.78]	vs	Little finger	3.41	2.15	[-1.03, 7.85]	< .001
						Background	26.81	9.07	[8.05, 45.57]	.001

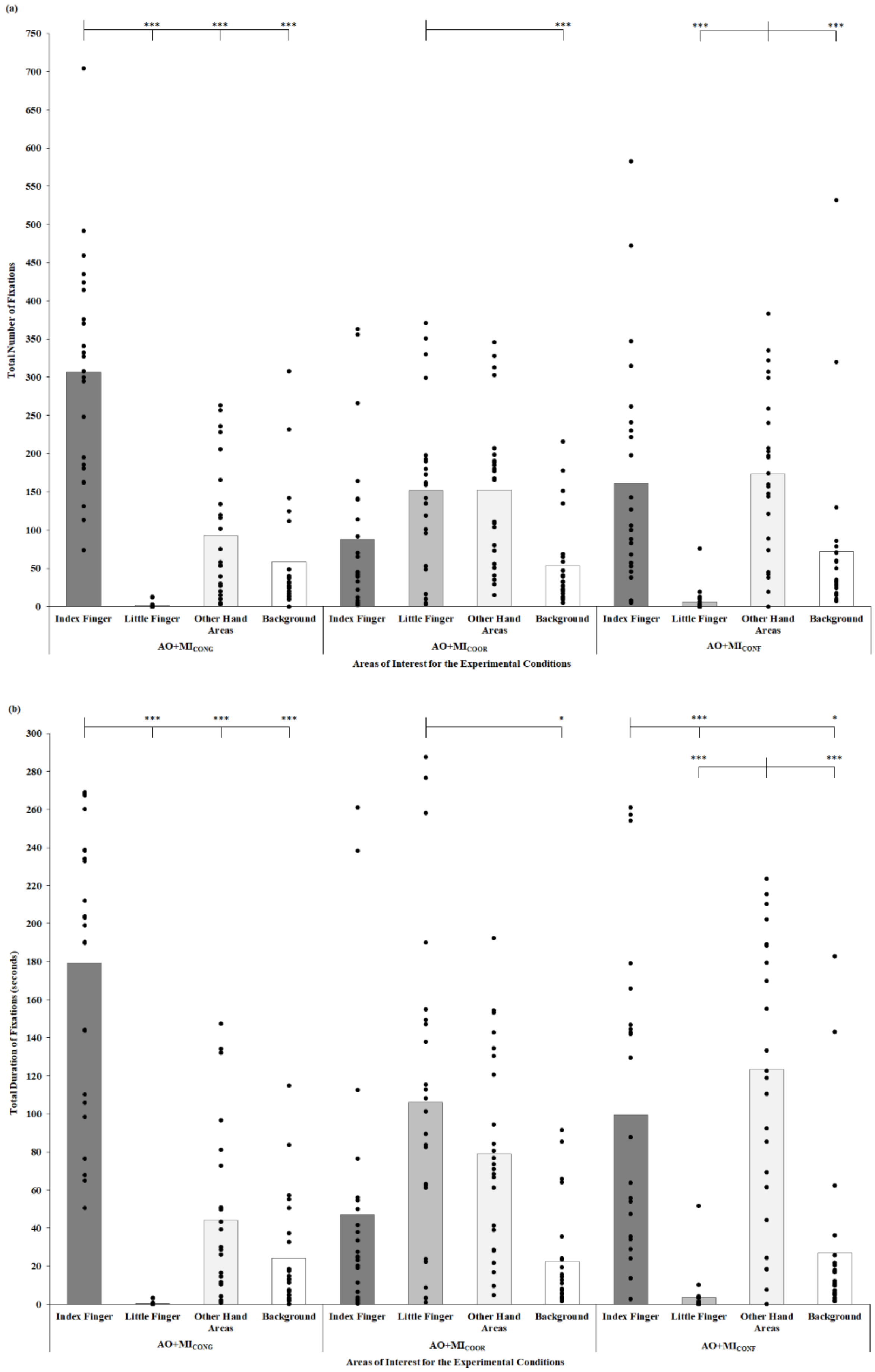
(a)
Total Number of Fixations
750
700
650
600
550
500
450
400
350
300
250
200
150
100
50
0
***
***
***
***
***
***
Index Finger
Little Finger
Other Hand Areas
Background
AO+MI$_{CONG}$
AO+MI$_{COOR}$
AO+MI$_{CONF}$
Areas of Interest for the Experimental Conditions
(b)
Total Duration of Fixations (seconds)
300
280
260
240
220
200
180
160
140
120
100
80
60
40
20
0
***
***
***
*
***
*
***
***
Index Finger
Little Finger
Other Hand Areas
Background
AO+MI$_{CONG}$
AO+MI$_{COOR}$
AO+MI$_{CONF}$
Areas of Interest for the Experimental Conditions

Figure 5. **Mean number (a) and duration (b) of fixations recorded in each area of interest for the AO+MI experimental conditions.** AO+MI$_{\text{CONG}}$ – congruent action observation and motor imagery; AO+MI$_{\text{COOR}}$ – coordinative action observation and motor imagery; AO+MI$_{\text{CONF}}$ – conflicting action observation and motor imagery. The mean value for each condition is displayed as the column, with values for all participants displayed as markers. *Note:* ***p <.001, *p <.05.

3.3. TMS Data: Controlling for Eye-Tracking Data as a Covariate

For the FDI data, the one-way ANCOVA revealed a significant effect of experimental condition on the z-score MEP amplitude data after controlling for both eye movement metrics (total number of fixations and total duration of fixations) in the index finger AOI, $F_{(4,113)} = 8.35$, $p < .001$, $\eta_p^2 = .23$. Pairwise comparisons showed MEP amplitudes were larger in the FDI muscle for the AO+MI$_{\text{CONG}}$ condition compared to the BL$_{\text{H}}$ ($p < .001$), AO ($p = .01$) and AO+MI$_{\text{CONF}}$ conditions ($p < .001$). MEP amplitudes were also larger in the AO+MI$_{\text{COOR}}$ condition compared to the BL$_{\text{H}}$ ($p = .03$), and AO+MI$_{\text{CONF}}$ ($p = .04$) conditions. For the ADM data, the one-way ANCOVA revealed a significant effect of experimental condition on z-score MEP amplitude data after controlling for both eye movement variables in the little finger AOI, $F_{(4,113)} = 6.74$, $p < .001$, $\eta_p^2 = .19$. Pairwise comparisons showed MEP amplitudes were larger in the AO+MI$_{\text{COOR}}$ condition compared to the BL$_{\text{H}}$ ($p < .001$), AO ($p < .001$), AO+MI$_{\text{CONG}}$ ($p = .004$), and AO+MI$_{\text{CONF}}$ conditions ($p = .002$).

Table 4. **Mean, standard error (SE), confidence interval (CI), and alpha values (*p*) for focal post-hoc pairwise comparisons between MEP amplitudes from the FDI and ADM muscles, displayed as z-scores, after controlling for both eye movement metrics (total number and duration of fixations) for the index finger and little finger AOI, respectively.** BL_H – human baseline; AO – action observation; $AO+MI_{CONG}$ – congruent action observation and motor imagery; $AO+MI_{COOR}$ – coordinative action observation and motor imagery; $AO+MI_{CONF}$ – conflicting action observation and motor imagery.

Muscle	Condition	Adjusted Mean	SE	95% CI	vs	Condition	Adjusted Mean	SE	95% CI	*p*
FDI	$AO+MI_{CONG}$	0.36	0.09	[0.19, 0.54]	vs	BL_H	-0.20	0.08	[-0.37, -0.04]	< .001
					vs	AO	-.014	0.08	[-0.18, 0.15]	.01
					vs	$AO+MI_{CONF}$	-0.22	0.08	[-0.38, -0.05]	< .001
	$AO+MI_{COOR}$	0.15	0.09	[-0.03, 0.32]	vs	BL_H	-0.20	0.08	[-0.37, -0.04]	.03
					vs	$AO+MI_{CONF}$	-0.22	0.08	[-0.38, -0.05]	.04
ADM	$AO+MI_{COOR}$	0.58	0.13	[0.33, 0.83]	vs	BL_H	-0.17	0.08	[-0.34, -0.01]	< .001
					vs	AO	-0.24	0.08	[-0.40, -0.07]	< .001
					vs	$AO+MI_{CONG}$	-0.05	0.09	[-0.22, 0.13]	.004
					vs	$AO+MI_{CONF}$	-0.06	0.08	[-0.22, 0.11]	.002

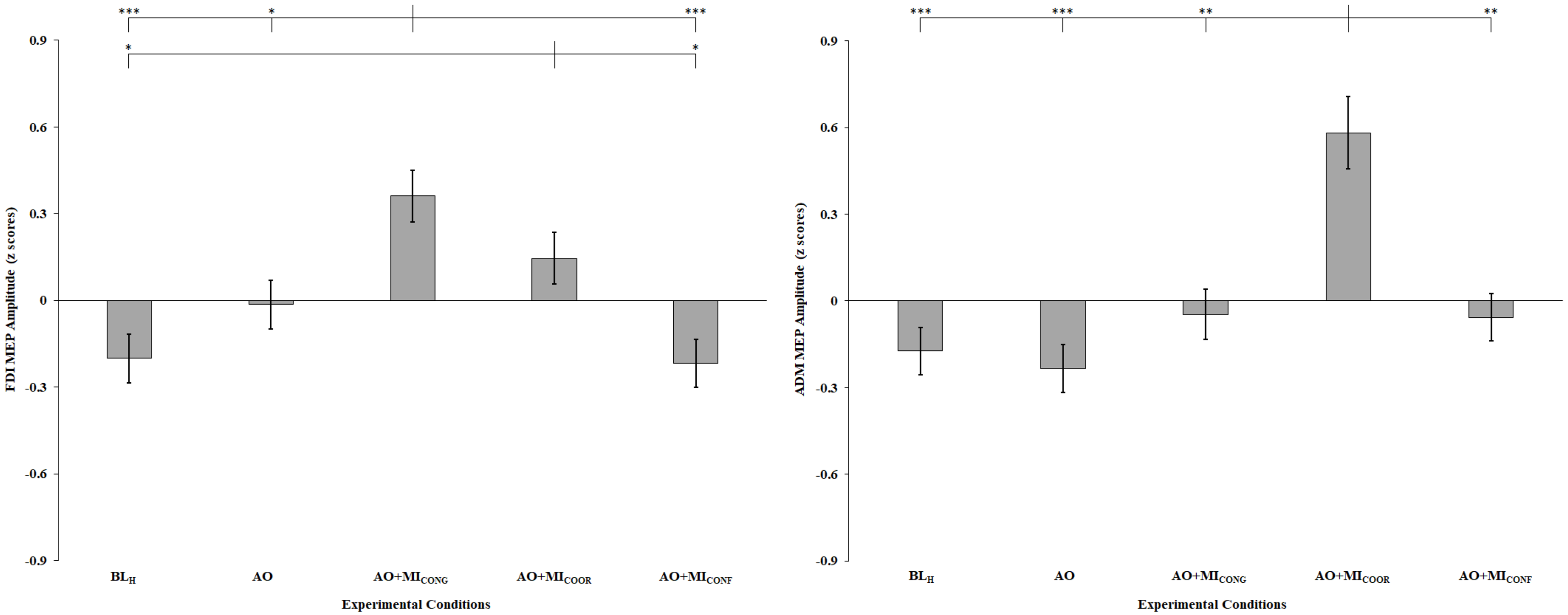

***Figure 6.* Mean MEP amplitudes from the FDI and ADM muscles, displayed as z-scores, after controlling for both eye movement metrics (total number and duration of fixations) for the index finger and little finger AOI, respectively.** BL$_H$ – human baseline; AO – action observation; AO+MI$_{CONG}$ – congruent action observation and motor imagery; AO+MI$_{COOR}$ – coordinative action observation and motor imagery; AO+MI$_{CONF}$ – conflicting action observation and motor imagery. Positive z-score values indicate that the MEP amplitude in that condition was greater than the mean MEP amplitude in that muscle across all conditions. Negative z-score values indicate that the MEP amplitude in that condition was less than the mean MEP amplitude in that muscle across all conditions. Error bars represent standard error values for the condition. *Note:* ***p <.001, **p <.01, *p <.05.

3.4. Social Validation Data

3.4.1. Imagery. No participants reported engaging in any form of imagery for the two control conditions, suggesting instead that they purely observed the stimuli presented (e.g., “I don’t think I imagined anything, but focused on keeping my hand limp and inhibited anything apart from just looking at the hand” (participant 5)). Sixteen participants (66.67%) suggested they did not imagine their own hand moving during the AO condition, whilst eight participants (33.33%) experienced some spontaneous imagery in this condition, although they noted that this was not as frequent or vivid as in the AO+MI experimental blocks (e.g., “maybe a tiny bit of imagery, but not purposefully as I was trying to inhibit it and I found focusing on the timing of the movement helped me do this” (participant 9)).

All participants used first-person perspective imagery during the AO+MI conditions, suggesting that this seemed natural. They indicated that their use of a first-person perspective was triggered by the perspective used in the AO stimuli and the screen orientation on which the stimuli was presented. They also reported that the use of this MI perspective allowed them to control their images and generate the associated feelings and sensations more accurately (e.g., “I saw it through my own eyes in first-person. The way the video was presented, it felt easy to do this as I could imagine my own arm and hand replacing the one on-screen as they were aligned” (participant 12)).

The one-way repeated measures ANOVA results for perceived ease of motor imagery during AO+MI conditions, $F_{(2,46)} = 16.95$, $p < .001$, $\eta_p^2 = .42$ showed that participants perceived MI to be easier in the AO+MI$_{\text{CONG}}$ condition compared to the AO+MI$_{\text{COOR}}$ ($p = .002$) and AO+MI$_{\text{CONF}}$ conditions ($p < .001$). Interview data suggested that participants found the AO+MI$_{\text{CONG}}$ task easier to imagine as it increased the perception of hand ownership, was more natural and required less concentration to perform. It was also reported that the two components facilitated one another more than the other AO+MI tasks (e.g., “[It was] easy because I find it is more of a natural movement, as I move that finger more than others in everyday life and because the person in the video was doing it, so I could imagine doing it in time with the video" (participant 3)). However, participants found the AO+MI$_{\text{COOR}}$ and AO+MI$_{\text{CONF}}$ conditions to be more difficult as there were greater cognitive processing demands in these conditions compared to the AO+MI$_{\text{CONG}}$ condition (e.g., *"this [AO+MI$_{\text{CONF}}$] was the hardest because I had to concentrate more when keeping it still. Watching what they were doing [index finger movement] whilst imagining doing the opposite [keeping hand still] was difficult as it split my attention throughout"* (participant 17)).

3.4.2. Attention. For the AO+MI$_{\text{CONG}}$ condition, eye-tracking data revealed that participants directed their visual attention primarily to the index finger. Interview data indicated that all participants looked at the moving finger as this allowed pick-up of the movement timing and speed information (looking at second knuckle and fingertips) and the sensations involved with moving the finger (looking at the first knuckle and muscle) to generate accurate images of their own index finger moving (e.g., "I was looking at the muscle for the moving finger and imagining the feelings of my own finger moving. This helped me feel what I think it would feel like in my own hand" (participant 4)).

For the AO+MI$_{\text{COOR}}$ condition, eye-tracking data indicated that participants split their attention between the little finger and other hand areas. Conversely, interview data suggested that most participants (62.50%) reported attending to both the index finger and the little finger, switching between the two fingers to facilitate MI of the little finger movement. This allowed participants to monitor directly or peripherally the index finger movement while simultaneously imagining little finger movement (e.g., "I tended to shift, sometimes at the index-finger and then the little-finger, then back to the index-finger again because it was moving. I guess, because I was trying to imagine moving the little-finger, fixating on it allowed me to generate the sensations involved with that finger" (participant 11)).

In the AO+MI$_{\text{CONF}}$ condition, the eye-tracking data indicated that participants directed their visual attention primarily towards the index finger and other hand areas. This was reflected in the interview data as most participants (62.50%) reported switching between the moving finger and still parts of the hand to help them imagine their own hand being still whilst observing some movement (e.g., "I guess I was mainly fixating towards those two fingers [middle and fourth fingers] but was shifting towards the other parts of the hand, but it was more towards the movement. Again, because I was trying to focus on remaining still it made sense to look at parts of the hand that were still" (participant 11)). However, nine participants (37.50%) reported looking at the moving finger peripherally and focusing on still parts of the hand (other fingers, top of the hand, and/or the wrist) to facilitate imagery of their hand staying in a still and relaxed position (e.g., "I think it [my attention] fell onto the knuckles quite central to the hand again. This helped me block out the index finger movement and imagine my hand being still" (participant 14)).

4. Discussion

The aim of this experiment was to test the dual-action simulation hypothesis (Eaves, Riach, et al., 2016). To test this hypothesis corticospinal excitability was measured across three different AO+MI states, representative of the *congruent, coordinative* and *conflicting* AO+MI states proposed by Vogt et al. (2013). Eye-tracking and social validation data were also collected, respectively, as markers of attentional and cognitive processes underlying these neurophysiological responses. This study represents the first investigation of neurophysiological markers across the spectrum of AO+MI states. In the following sections, the key findings for each of the three AO+MI states tested in this experiment will be discussed in relation to relevant literature and the dual-action simulation hypothesis.

4.1. Congruent AO+MI

In this condition, findings supported the first hypothesis as MEP amplitudes were significantly larger in the FDI muscle during *congruent* AO+MI, compared to the control conditions and the *conflicting* AO+MI condition. Furthermore, when controlling for visual fixations on the index finger in the ANCOVA, corticospinal excitability was also facilitated in the FDI for the *congruent* AO+MI condition compared to the AO condition. This finding is consistent with the growing body of research indicating that corticospinal excitability is facilitated to a greater extent during *congruent* AO+MI, compared to independent AO, MI, or control conditions (e.g., Sakamoto et al., 2009; Wright et al., 2014; see Eaves, Riach et al., 2016 for a review).

The current study extends previous work by providing the first evidence of the attentional and cognitive processes involved in *congruent* AO+MI. The eye-tracking data indicates that visual attention was directed predominantly towards the index finger in this condition. Intuitively this makes sense, as the action of this finger was directly relevant to the simultaneously observed and imagined task, and there is evidence that visual attention is typically drawn to the most task-relevant aspects of a display in situations where visual attention is not directed explicitly (Wright, Wood, Franklin, et al., 2018). The interview data indicated that participants directed their visual attention to the index finger to increase the ease with which they could complete the *congruent* AO+MI task by helping them to both imagine the feelings associated with themselves executing the observed action and synchronize the timing of their imagery to the observed stimuli.

Conceptually, the findings reported for *congruent* AO+MI provide support for the dual-action simulation hypothesis. This hypothesis proposes that concurrent representations of observed and imagined actions can be maintained simultaneously as two quasi-encapsulated sensorimotor streams, which may either merge or compete based on their content and relevance towards ongoing action plans (Eaves et al., 2012, 2014; Eaves, Behmer, et al., 2016). Presumably during *congruent* AO+MI, the identical content for the AO and MI tasks resulted in the merging of the two sensorimotor streams representing the observed and imagined actions. The merging of these two sensorimotor streams would likely have produced more widespread activity in the premotor cortex (see Filimon et al., 2015) than the control, AO and *conflicting* AO+MI conditions, contributing to an increased MEP amplitude via cortico-cortical connections linking premotor and motor cortices (Fadiga, Craighero, & Olivier, 2005).

The findings reported here for *congruent* AO+MI have important implications for motor (re)learning across settings such as neurorehabilitation and sport. Increased activity in premotor and motor cortices associated with repeated engagement in *congruent* AO+MI may promote Hebbian modulation of intracortical and subcortical excitatory mechanisms through similar synaptic plasticity mechanisms to those observed following physical practice of the same task (Holmes & Calmels, 2008). Consequently, researchers have advocated the use of *congruent* AO+MI interventions to improve motor function (e.g., Emerson, Binks, Scott, Kenny, & Eaves, 2019; Holmes & Wright, 2017). Current behavioral evidence supports the efficacy of using *congruent* AO+MI for this purpose across a range of settings and outcomes, including improving strength (Sun, Wei, Luo, Gan, & Hu, 2016; Scott, Taylor, Chesterton, Vogt, & Eaves, 2017), balancing (Taube et al., 2014), aiming (Romano-Smith, Wood, Wright, & Wakefield, 2018) and motor control (Scott, Emerson, Dixon, Tayler, & Eaves, 2019). Longitudinal research incorporating both neurophysiological and behavioral measures is now required to verify the extent to which *congruent* AO+MI promotes functional connectivity and plasticity within the brain that may underpin the associated motor performance and learning improvements.

4.2. Coordinative AO+MI

In the *coordinative* AO+MI condition, the findings are broadly supportive of the second hypothesis. In the initial analysis of the data, MEP amplitude was facilitated relative to control conditions in the ADM muscle, which was associated with the MI component of the coordinative task. There was a trend for a similar effect in the FDI muscle, but this effect only became significant when visual attention on the index finger was controlled in the ANCOVA analysis. Consequently, the results provide support for the experimental hypothesis, but it appears that attentional mechanisms may influence the extent to which simultaneous dual-action simulation is possible.

The eye-tracking data indicate that participants directed their visual attention similarly to the observed index finger movement, the imagined little finger movement and other areas of the hand, with no differences in number and duration of fixations across these three areas of interest. In addition, in the interviews, most participants reported adopting a strategy where they alternated between directing their attention to the index and little fingers in order to maintain both aspects of the task. This was reported to be an effortful and cognitively demanding strategy as participants rated the *coordinative* AO+MI task as more difficult to complete than the *congruent* task. In the only previous study to explore the neurophysiological effects of *coordinative* AO+MI, Eaves, Behmer, et al. (2016) reported increased event-related desynchronization in alpha and beta frequency bands in the left rostral prefrontal cortex. This activity was interpreted to represent the continual reallocation of attentional resources between the observed and imagined tasks, and the eye-tracking and interview findings reported here are consistent with this interpretation.

In the context of the dual-action simulation hypothesis (Eaves, Riach, et al., 2016), the requirement to co-represent two related, but not identical, movements during *coordinative* AO+MI resulted in competition between the observed and imagined actions. This competition may explain the switching of visual attention between the observed and imagined stimuli, as different premotor regions involved in imagery and observation contributed ‘votes’ to prioritize the respective motor simulations based on their relevance to the ongoing task. Despite this competition between the two sensorimotor streams, the similarities between the AO and MI stimuli in relation to movement timing and kinematics likely permitted dual-action simulation of the different observed and imagined actions when attentional factors were controlled. This dual-action simulation for *coordinative* AO+MI would likely be associated with activity in a wider network of premotor regions when engaging in AO and MI components simultaneously (Filimon et al., 2015),facilitating corticospinal excitability in both FDI and ADM muscles via cortico-cortical connections between premotor and motor cortices (Fadiga et al., 2005).

It should be noted that the current study only tested one form of *coordinative* AO+MI. *Coordinative* AO+MI is a collective term for AO+MI states spanning from *congruent* to *conflicting* AO+MI. The MI component of the *coordinative* AO+MI task in this experiment shared similarities with the AO component in terms of movement kinematics and timing, but differed based on the effector muscle (ADM vs. FDI) and moving body part (little finger vs. index finger) that was imagined. The extent to which attentional shifts are required between MI and AO components of a *coordinative* AO+MI task may depend on the level of congruence between the different simulation components of the task. For example, attentional shifts may be less necessary in a more closely coupled *coordinative* AO+MI task such as imagining the sensations associated with flexion-extension of the right index finger whilst observing right index finger abduction-adduction. Future research should, therefore, seek to identify the neurophysiological, attentional and cognitive markers for different *coordinative* tasks across the spectrum of AO+MI states.

The findings reported for *coordinative* AO+MI have implications for motor (re)learning. Whilst *congruent* AO+MI training may be the current optimal simulation-based approach for (re)learning a specific action, *coordinative* AO+MI may prove beneficial in supporting the (re)learning of joint actions. Forms of *coordinative* AO+MI may provide a viable complementary training method to physical therapy in rehabilitation settings and may promote the (re)learning of actions that are currently impaired or missing from a person's motor repertoire. For example, a post-stroke patient may benefit from observing videos of themselves accurately performing reach and grasp actions with their non-affected limb, whilst simultaneously imagining the feelings and sensations associated with performing that action with their impaired limb. In such cases, *coordinative* AO+MI could support motor (re)learning by promoting Hebbian plasticity in a similar manner to that described above for *congruent* AO+MI. With the possibility of dual-action simulation of *coordinative* AO+MI states confirmed in this study, future research should begin to explore the efficacy of *coordinative* AO+MI interventions for improving behavioral outcomes across settings such as sport and neurorehabilitation.

4.3. Conflicting AO+MI

In the *conflicting* AO+MI condition, the findings are consistent with the third hypothesis, as MEP amplitude was significantly lower compared to the *congruent* AO+MI condition in the FDI muscle and compared to the *coordinative* AO+MI condition in the ADM muscle. Additionally, when controlling for eye-movements in the ANCOVA, MEP amplitude was lower in the FDI muscle in the *conflicting* AO+MI condition compared to the *coordinative* AO+MI condition.

The eye-tracking and interview data provide a possible explanation for the reduction in corticospinal excitability in this condition, compared to the *congruent* and *coordinative* AO+MI conditions. The eye-tracking data indicates that during the *conflicting* AO+MI condition, participants directed their visual attention towards the index finger and other stationary areas of the hand. The interview data indicates that participants tended to adopt a strategy of either (i) shifting attention between the index finger movement and stationary parts of the hand to help them complete both parts of the task, or (ii) attending predominantly to stationary parts of the hand in an attempt to block out the observed movement and facilitate MI of their hand in a still and relaxed position. This highlights the difficulty of co-representing conflicting observed and imagined stimuli simultaneously, with participants rating *conflicting* AO+MI as more difficult than the *congruent* AO+MI task.

In relation to the dual-action simulation hypothesis, the data presented in this experiment for *conflicting* AO+MI indicates that it may not be possible to co-represent *conflicting* AO+MI states simultaneously. The instruction to imagine an action that is in complete conflict with an observed action may have led to increased competition between the two sensorimotor streams representing the observed and imagined tasks. Participants appear to have attempted to resolve this conflict by making a conscious effort to switch attentional resources between the two tasks, or prioritize MI at the expense of the AO component. Despite these conscious attempts to maintain dual-action simulation of the conflicting AO+MI components, premotor brain regions involved in the AO and MI tasks may have submitted 'votes' for conflicting processes that, in effect, nullified each other, suppressing corticospinal excitability.

It is important to note that the findings reported here for *conflicting* AO+MI differ to those reported by Eaves, Behmer, et al. (2016) in the only previous neurophysiological experiment to compare *conflicting* AO+MI against other AO+MI states. They reported comparable levels of event-related desynchronization in the alpha and beta frequency bands over the sensorimotor region in their 'synchronized' and *conflicting* AO+MI conditions, yet in this experiment corticospinal excitability was reduced during *conflicting* AO+MI, compared to both *congruent* and *coordinative* AO+MI. This discrepancy can be explained by the different origins of the activity detected by EEG and TMS measures. Mu and alpha activity over sensorimotor areas during AO and MI originate in the somatosensory cortex and so reflect primarily sensory, rather than motoric, aspects of the task (Lepage et al., 2008). Conversely, the facilitation of corticospinal excitability when TMS is delivered to the motor cortex during AO and/or MI conditions is generally assumed to be indicative of increased activity that originates in the premotor cortex (Fadiga et al., 2005) and, therefore, reflects primarily motoric aspects of the task. In the current study, there was a lack of motoric content in the MI instruction to imagine the kinesthetic sensations associated with keeping the hand still and relaxed, which would likely have contributed to the suppression in MEP amplitude in the *conflicting* AO+MI condition. In contrast, the EEG measure used by Eaves Behmer, et al. may have reflected more sensory aspects of the MI task, which would still be present with the static MI component of their *conflicting* AO+MI condition.

The findings reported here indicate that *conflicting* AO+MI may not be useful as an intervention for motor (re)learning, based on the plasticity mechanisms explained above for *congruent* and *coordinative* AO+MI. Rather than contribute to motor (re)learning, it is feasible that *conflicting* AO+MI training could provide a useful method for training individuals to ignore unnecessary and/or distracting stimuli during movement execution. For example, in sport, a soccer goalkeeper could benefit from observing videos of a penalty taker feigning the kicking action and imagining the feelings and sensations associated with her/himself remaining still in the center of the goal. This could potentially reduce the likelihood of unwanted reactions to deceptive movements and benefit anticipation skills in such scenarios. These suggestions are tentative at this stage, but further research could test the efficacy of *conflicting* AO+MI in such settings.

4.4. Limitations

This study is the first of its kind to investigate the neurophysiological, attentional and cognitive mechanisms associated with three different AO+MI states, but it is important to acknowledge possible limitations associated with the experiment. First, whilst TMS allowed the contributions of each simulation state to be distinguished by examining the effects of different AO+MI instructions on MEP responses in separate muscles, this technique only provides an indication of activity within the motor and premotor cortices of the brain. Neurophysiological activity associated with different AO+MI states in other brain regions (e.g., rostral prefrontal cortex; Eaves, Behmer, et al., 2016) would, therefore, not have been represented in the MEP response in this experiment. Consequently, there is a need to explore the precise anatomical substrates involved in different AO+MI states using neuroscientific methods with increased spatial resolution. FMRI research employing multi-voxel pattern analysis has shown it is possible to distinguish between different actions for MI and execution (Pilgramm et al., 2016; Zabicki et al., 2016). Applying this analysis to fMRI data for different AO+MI states could further advance the understanding of the neural mechanisms underpinning AO+MI and the dual-action simulation hypothesis (Eaves, Riach, et al., 2016).

Second, the MEP data reported in this experiment reflects the allocation of visual attention during the AO+MI conditions. During the AO+MI$_{\text{CONG}}$ condition, MEP amplitudes were increased in the FDI muscle and visual attention was directed predominantly to the index finger. During the AO+MI$_{\text{COOR}}$ condition, MEP amplitudes were increased in the FDI and ADM muscles and visual attention was split between the index and little fingers. During the AO+MI$_{\text{CONF}}$ condition, MEP amplitudes were lower in both FDI and ADM muscles and visual attention was often directed away from the two fingers to static parts of the hand. Consequently, a potential alternative explanation is that the results represent the allocation of visual attention, rather than support for the dual-action simulation hypothesis. Participants were allowed to view each condition with unrestricted eye-movements to maintain the ecological validity of the experiment and increase understanding of the natural gaze behaviors associated with the different forms of AO+MI. We then controlled for the influence of visual attention by including fixations on predetermined AOIs as covariates in the ANCOVA analysis, wherein the results supported the dual-action simulation hypothesis. However, there is a need to further test the dual-action simulation hypothesis when controlling attentional factors experimentally. For example, future research could control for this potential confound by instructing participants to direct their visual attention to a fixation cross placed in a standardized position during different AO+MI conditions, thus matching visual attentional requirements when comparing these different forms of AO+MI.

Third, this study did not employ a fully counterbalanced design. Partial counterbalancing was instead used to reduce the likelihood of prior imagery instructions (i.e., those provided prior to the three AO+MI state conditions) eliciting forms of spontaneous or deliberate MI in experimental conditions where MI was not instructed (BL_{NH}, BL_{H}, AO). Similar designs have been used in previous TMS experiments investigating *congruent* AO+MI (e.g., Wright et al., 2014, 2016; Wright, Wood, Eaves et al., 2018). Although social validation interview data revealed that eight participants experienced some spontaneous MI during the AO condition, all noted that this was not as frequent or vivid as in the AO+MI state conditions. Despite our data suggesting that spontaneous MI was apparent in this experiment, our results align with predictions based on the dual-action simulation hypothesis and so it is unlikely that this is an issue in this study. Moreover, this problem is inherent in decades of research into AO processes (Vogt et al., 2013), so we recommend researchers consider the issue of spontaneous MI when designing future experiments on motor simulation processes and employ manipulation checks and social validation procedures to, at least, acknowledge this potential confound.

5. Conclusions

The main finding of this experiment is that concurrent representations of observed and imagined actions can be maintained simultaneously when the observed and imagined states are either congruent or coordinative. Co-representation of observed and imagined actions does not, however, appear to be possible when the observed and imagined actions conflict with each other. These results provide an important advancement in the literature on action simulation as they go beyond Jeannerod's (2001) seminal assertions that AO and MI are functionally equivalent to one another and show that they can in fact co-occur. In doing so, these findings also provide the most concrete evidence to date in support of the dual-action simulation hypothesis (see Eaves, Riach, et al., 2016). Now that the possibility of dual-action simulation has been demonstrated for both *congruent* and *coordinative* AO+MI, future research should seek to further explore the underlying mechanisms and subsequent consequences of these types of interventions. It would be worthwhile to identify the neurophysiological, attentional and cognitive markers of a range of different *coordinative* AO+MI states to better understand the full spectrum of AO+MI states. In addition, future research should seek to explore the efficacy of *congruent* and *coordinative* AO+MI interventions for improving movement kinematics and behavioral outcomes across a range of different populations and motor actions.

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