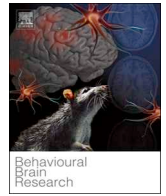




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Dynamic task observation: A gaze-mediated complement to traditional action observation treatment?

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ABSTRACT

Action observation elicits changes in primary motor cortex known as *motor resonance*, a phenomenon thought to underpin several functions, including our ability to understand and imitate others' actions. Motor resonance is modulated not only by the observer's motor expertise, but also their gaze behaviour. The aim of the present study was to investigate motor resonance and eye movements during observation of a dynamic goal-directed action, relative to an everyday one – a reach-grasp-lift (RGL) action, commonly used in action-observation-based neurorehabilitation protocols. Skilled and novice golfers watched videos of a golf swing and an RGL action as we recorded MEPs from three forearm muscles; gaze behaviour was concurrently monitored. Corticospinal excitability increased during golf swing observation, but it was not modulated by expertise, relative to baseline; no such changes were observed for the RGL task. MEP amplitudes were related to participants' gaze behaviour: in the RGL condition, target viewing was associated with lower MEP amplitudes; in the golf condition, MEP amplitudes were positively correlated with time spent looking at the effector or neighbouring regions. Viewing of a dynamic action such as the golf swing may enhance action observation treatment, especially when concurrent physical practice is not possible.

1. Introduction

A large body of evidence shows that observation, mental simulation and physical execution of an action share, at least in part, a common neural substrate [1–3]. Neurophysiological studies have shown that action observation (AO) and motor imagery (MI, i.e., motor simulation without overt movement) of an action elicit changes in the observer's motor system which resemble those that occur during execution of the action [4–6]. These changes are reflected in increased excitability of corticospinal motor pathways that innervate the muscles involved in the action, a phenomenon that has been referred to as *motor resonance* [7,8]. A recent meta-analysis of findings from neuroimaging studies [9] identified a set of motor and premotor areas – including the ventral and dorsal premotor cortices, the pre-supplementary motor area and the frontal part of the parietal cortex – which are consistently activated during action execution as well as during the covert states of AO and MI. However, AO has specifically been shown to recruit a small subset

of areas (i.e., the inferior frontal gyrus and the superior parietal cortex) which are regarded as the human homologue of area V5 of the macaque monkey's brain, where mirror neurons have clearly been identified [5,10]. These areas may thus represent core regions of the human action observation network [9,11]. As suggested by several theoretical accounts, the activity of this network serves not only the social function of understanding the actions and intentions of others, but it also plays a key role for imitation and learning of novel actions [12–14].

Repeated observation of an action modulates the formation of motor memories, leading to learning-related changes in the observer's motor system [15]. In this way, AO can enhance motor learning – although this enhancement may depend on individual differences in cortical function and structure [16] and the observer's somatosensory abilities [17]. Observational learning is thought to rely on covert activation of the same motor representations that are recruited during execution of the viewed action [13,18]; hence, AO can be regarded as a form of covert motor training. It has been shown that observational practice

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leads to improvements in performance of complex motor skills and their mental representation [19,20], and it is generally agreed that a combination of observational and physical practice is preferable to either type of practice independently [21–23]. Importantly, however, AO can lead to learning of a novel motor task even in the absence of physical practice [24,25].

AO is particularly beneficial in the case of patients suffering from motor deficits, and it is increasingly being incorporated into rehabilitation programmes aimed at promoting recovery of motor function. Studies have shown that repeated observation of an action can help improve, *inter alia*, upper limb motor function in children with cerebral palsy [26] and stroke patients [27], and it can aid motor recovery in postsurgical orthopaedic patients [28]. These improvements are reflected in increased activation of motor cortical areas, which suggests that the beneficial effects of *action-observation treatment* [29] are due to repeated activation of the same motor cortical representations that are involved in action production [27]. Typically, action observation treatment involves the observation of everyday actions, which are selected according to their ecological value to the patient. In each session, the patient repeatedly observes a single action which is divided into three to four motor acts, and is then required to perform it [29]. The actions selected are simple and target-directed, such as grasping and moving objects, opening and closing a jar, and writing with a pen [30], and they are typically confined to the upper limbs [29].

AO-based approaches to motor rehabilitation represent a form of covert motor training that is especially suited to aiding recovery in patients whose motor capacity is impaired. Since AO can facilitate motor re-learning by increasing CE in relation to the muscles actively involved in an observed action, it is conceivable that greater AO-induced corticospinal facilitation will promote motor recovery. Therefore, when designing AO-based interventions, it may be prudent to consider those factors which have been shown to modulate motor resonance. Motor resonance is attuned to the viewed action and its kinematics [31–34]. Alaerts and colleagues [35] showed participants videos of actors reaching for, grasping and lifting objects of different weights. Their results showed that MEP amplitudes recorded from the observer's hand and forearm muscles were modulated by the weight of the target object: observing the actor lift a heavy object elicited larger MEP amplitudes than when the object was light; similar results were reported by Senot and colleagues [36]. Weight-induced modulations of MEP amplitudes are present even when the target object is hidden from view [37]. Furthermore, there is evidence that lower back muscles, which have smaller and coarser cortical representations than hand or arm muscles, exhibit weight-related modulations of corticospinal excitability, or CE, [38]. Motor resonance is thus highly sensitive to subtle aspects of an observed action such as its force requirements. For example, it has been shown that observers are typically very accurate at estimating the weight of objects being lifted and the effort exerted in order to lift them [39]. Our visual perception of weight remains high even when actions are presented as a series of static images [40], and it can sometimes be more accurate than haptic perception [41].

Familiarity with the viewed action is another factor that could potentially modulate the AO-induced increases in CE, as neuroimaging studies consistently show greater motor resonance for actions which are already part of the observer's motor repertoire [42,43]. However, TMS evidence of expertise-dependent modulations in CE during the observation of complex actions is scarce and contradictory [44–46]. Hence, a logical line of inquiry is to investigate how familiarity with a complex action affects motor resonance during observation of that action.

Another important consideration for observational (re)-learning is the influence of visual attention. Gaze behaviour is an overt manifestation of information processing during both execution and observation of motor tasks. During the performance of everyday actions, individuals typically direct their eyes only to locations or objects which are relevant

to the task at hand, whereas irrelevant areas receive little attention [47,48]. Fixations are directed to the target of an action even before movement onset, which suggests that oculomotor plans are used to locate objects and guide and monitor movements [49]. These same oculomotor plans are also recruited during action observation. For instance, during the observation of transitive actions, the observer's gaze is coordinated with the actor's hand movements in a predictive manner: gaze tends to fixate on the action target before it is reached by the hand [50,51]. Through experience with our environment, we acquire visuo-motor representations of actions that are subsequently used to control and coordinate movement and to predict the future sensory state of events. This results in highly precise and predictive shifts of visual attention [52], which become more efficient with expertise [53,54].

Recent evidence suggests that appropriately directed point-of-gaze may increase information pickup during observational learning of a complex action [55]. Moreover, our gaze behaviour appears to modulate the resonance of our motor system during action observation. Leonetti and colleagues showed that the pattern of AO-induced facilitation in CE becomes coarser and loses its muscle specificity when actions are presented in the peripheral visual field [56], although covert attentional shifts may elicit comparable effects [57]. D'Innocenzo and colleagues [58] showed that, by asking participants to fixate their gaze on a location directly over the trajectory of a moving thumb, motor resonance in the corresponding muscle was maximized relative to a condition in which the eyes were free to move (i.e., natural viewing). Similarly, Wright and colleagues [59] showed participants videos of a ball pinching action, and asked them to observe the action naturally, or to focus their attention on either the ball or the index finger. Their results revealed that, by directing participant's gaze to the target, index finger MEP amplitudes were facilitated to a greater extent than under natural viewing conditions.

Gaze behaviour can thus modulate the way in which observed actions resonate with the observer's motor system [58,59]. Moreover, motor resonance is sensitive to subtle aspects of the action such as its force requirements, as shown by the weight- and effort-dependent modulations of MEP amplitudes during observation of lifting actions. Considering these observations, we used TMS to determine whether the complexity and force requirements of observed actions could modulate motor resonance and visual attention. We contrasted gaze behaviour and CE as participants observed a skilled model perform the full golf swing, a highly coordinative and dynamic action involving a large amount of force, with their gaze patterns and CE as they viewed a comparatively simple reach-grasp-lift (RGL) action. Since gaze behaviour appears to change, necessarily, as an observed complex action becomes more dynamic in nature, [55], we expected the two actions to elicit different gaze behaviours. We also expected the two actions to elicit different patterns of CE – specifically, that the RGL action would elicit lower facilitation relative to the considerably more forceful and dynamic golfing action. Finally, in line with recent evidence of a link between visual attention allocation and motor resonance [58], we hypothesised that the specific eye movement patterns adopted during action observation would be related to AO-induced modulations of CE. Both skilled golfers and novices were recruited, to determine whether familiarity with the observed action would modulate motor resonance.

2. Materials and methods

2.1. Participants

The study was approved on behalf of the Brunel University London Research Ethics Committee. Subsequent to providing their written informed consent, a total of 18 participants took part.² Of these, ten had

²The required sample size was determined based on the effect size of a previous study [[60]] which compared corticospinal facilitation during the

no previous experience of golf (6 males, 4 females; M age = 25.7 yrs, SD = 3.2 yrs); the remaining eight participants were skilled male golfers (M age = 28.25 yrs, SD = 14.8 yrs) with handicaps³ ranging from 0 to 15 (M = 6.75, SD = 4.56). Participants had normal or corrected-to-normal vision, and were all right-handed, as assessed using the Edinburgh Handedness Inventory [62], M = 83.6, SD = 17.5. Participants were screened prior to taking part to ensure that they had no contraindications to TMS, or any neurological, psychiatric or other medical problems [63,64]. None of them reported any discomfort or adverse effects during the TMS protocol.

2.2. Experimental design

The main aim of the study was to determine whether observation of a forceful and dynamic action can facilitate corticospinal excitability to a larger extent than observation of a comparatively simple everyday reach-grasp-lift (RGL) action. Following baseline measurement of corticospinal activity at rest, TMS-evoked MEPs were recorded from three forearm muscles (flexor carpi radialis [FCR]; flexor carpi ulnaris [FCU]; and extensor carpi radialis [ECR]) as participants watched videos of a RGL action and of a golf swing (GS). The responses recorded during observation of the two actions were then compared with those recorded during the resting baseline, as well as to each other.

There is evidence that motor resonance can be time-locked to a viewed action, and specific to the muscles involved in the execution of that action. For instance, during observation of RGL actions, the extent of activation recorded from forearm muscles typically peaks during the lifting phase, consistent with the higher force requirement for this phase [35,65,66]. Therefore, during observation of the RGL videos, TMS pulses were delivered during the lifting phase of the action. Motor resonance effects of observation of complex whole-body actions have not been studied extensively. Therefore, TMS stimulation timings for the golf swing action were selected according to evidence for muscle activation during execution of a golf swing action. Previous research has shown that FCR, FCU and ECR activity can be differentiated according to the phase of the swing [67]. Specifically, FCR and FCU activity peaks during the forward swing phase, but is comparatively lower in the acceleration, follow-through and backswing phases, in descending order. In contrast, maximal ECR activation occurs during the backswing phase, whereas activity is lower in the acceleration, forward swing and follow-through phases, again in descending order. We selected stimulation times to coincide with these peaks to determine whether the pattern of AO-induced facilitation followed the same time course of activation as that recorded during action execution.

Finally, the goal of the observation task has been shown to affect the

(footnote continued)

observation of healthy and dystonic handwriting across individuals who were visually familiar with both types of writing (i.e. clinicians) and individuals with no previous experience with dystonic writing (i.e. naïve subjects). Fiorio and colleagues found significant differences between the two groups in MEP amplitudes recorded from a hand muscle highly involved in the observed action (i.e. writing), during the observation of dystonic writing. This indicates that previous experience with the observed action affected CE as indexed by MEP amplitude. The means and SDs of the MEP amplitudes reported for the two groups were used to obtain a measure of the effect size, which was then used for the power calculations. These calculations (using G-power) revealed that the sample size should be 14 in total, or 7 participants per group.

³ In golf, the handicap represents a numerical measure of a golfer's potential ability; the lower a player's handicap, the greater his or her ability. The official handicap classification endorsed by the Council of National Golf Unions (CONGU; the national authorizing body for golf handicaps in Great Britain and Ireland) includes a total of six categories, each corresponding to a specific handicap band. In the present study, 7 golfers had handicaps between 0 and 12, which lie within the first and second categories, and can thus be regarded as *skilled players* [[61]]; one golfer had a handicap of 15, which lies in the third category, and can be considered an *intermediate player*.

degree to which mirror neuron areas are recruited [68]; notably, they are recruited to a larger extent when observing with the intention to imitate, when compared to passive viewing or action recognition tasks [69]. Thus, before engaging in the experimental conditions, participants were told that, upon completion of the observation task, they would be required to imitate the observed actions, matching their movements to those of the model as accurately as possible.

2.3. Experimental stimuli

Videos were recorded using a Canon XF105 HD camcorder (Canon Inc., Tokyo, Japan). Golf swing (GS) videos displayed a whole-body view of the model (a 25-year-old skilled male golfer with a handicap of 4) from a third-person perspective, as viewed along the sagittal plane (Fig. 1, top). The reach-grasp-lift (RGL) videos displayed a side view of a model's forearm reaching for, grasping and lifting a 2-litre bottle full of coloured water, also viewed from a third-person perspective (Fig. 1, bottom). A 2-second grey screen preceded each video; each GS video lasted approximately 6 s, and each RGL video lasted approximately 8 s.

Experiment Builder software (SR Research Ltd, Ontario, Canada) was used to present videos and to trigger delivery of the TMS pulses. Videos were displayed on a 21-inch CRT monitor (100 Hz, screen resolution was set to 1024 × 768 pixels). Participants' eye movements were recorded using an SR Research EyeLink 1000 eye tracker (monocular, right eye, 1000 Hz; SR Research Ltd, Ontario, Canada). Viewing distance was 60 cm, and the participant's chin and forehead were positioned on a headrest to minimise head movements.

2.4. TMS

Motor-evoked potentials (MEPs) were recorded from the flexor carpi radialis (FCR), flexor carpi ulnaris (FCU) and extensor carpi radialis (ECR) of the right forearm using self-adhesive surface electrodes (Ag-AgCl, 1 cm diameter) placed over the muscle bellies. A reference electrode was placed over the styloid process of the radius. Signal software (v.6, Cambridge Electronic Design Limited, Cambridge, UK) was used to acquire electromyography (EMG) traces, which were band-pass filtered at 10–2000 Hz, digitized and displayed on a computer screen and stored on a PC for offline analysis.

Transcranial magnetic stimulation pulses were delivered using a Magstim 200 (Magstim Company Ltd., Whitland, UK) connected to a circular coil (130 mm outer diameter; 50 mm inner diameter). The coil was positioned over the scalp on the left hemisphere with side A visible so as to induce a posterior-to-anterior current flow, optimal to achieve stimulation of the left hemisphere [70]. Participants wore a tight-fitting swim cap. The distance between the inter-aural points and that between the nasion and inion were measured and the intersection between the lines connecting these points, which corresponded to the vertex (Cz), was marked on the cap. To locate the optimal scalp position (OSP) for eliciting MEPs in all three muscles of interest, the outer edge of the coil was placed over the vertex and it was systematically moved in steps of 1 cm. Once the OSP had been located, it was marked on the cap so as to ensure reliable placement of the coil; the experimenter continuously monitored the position of the coil relative to this mark throughout the study. Participants' resting motor threshold (rMT), defined as the lowest stimulation intensity required to elicit MEPs with an amplitude of ≥ 50 μ V from at least 5 out of 10 consecutive stimulations [71], was determined. Stimulation intensities used in the experimental trials corresponded to 120 % of the participant's rMT and ranged from 43 to 80 % of the maximum stimulator output (M = 61.4 %, SD = 11.6 %).

2.5. Experimental design, task and procedures

Participants sat on a padded chair facing the monitor screen, with their arms pronated on a table in front of them and their chin and forehead positioned on a support mounted on the table. Throughout the

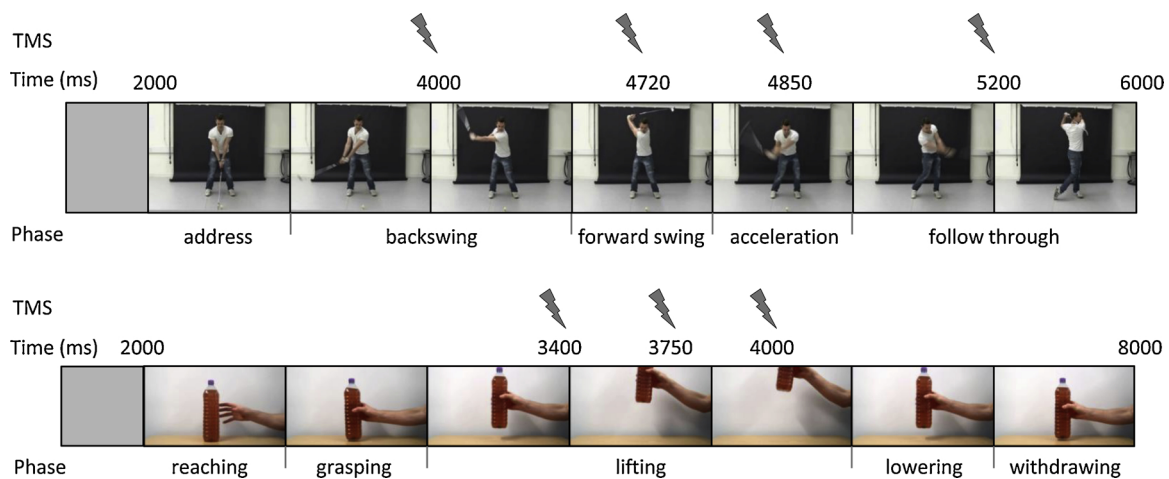


Fig. 1. The experimental conditions. GS condition (top timeline): TMS pulses were delivered at one of the stimulation times shown, for each of four sub-blocks. RGL condition (bottom timeline): pulses were delivered at one of the three stimulation times shown during the lifting phase.

protocol, the experimenter monitored EMG activity and reminded participants to relax their arms. Prior to commencing the experimental protocol, the rMT and optimal scalp position were determined as described above. The eye tracker was calibrated using a 13-point grid which appeared on the PC monitor facing the participant. In order to determine baseline levels of CE for the three muscles of interest, 10 MEPs were recorded while participants kept their eyes closed (baseline pre). A second baseline measurement was taken upon completion of the protocol, again with eyes closed (baseline post).

Participants completed two blocks, the order of which was counterbalanced. In one block, participants viewed 30 repetitions of the RGL video, and one TMS pulse was delivered during each video presentation. In line with previous studies, pulses were delivered during the lifting phase of the action [35]. The lifting phase began at 3260 ms from the onset of the RGL action, and it ended at 4220 ms. TMS pulses were delivered at one of three pseudo-random stimulation timings during observation of the lifting phase (i.e., 3400, 3750 or 4000 ms), so as to minimise participants' anticipation of the TMS pulses. A second block consisted of 120 iterations of the GS video, divided into four counterbalanced sub-blocks comprising 30 repetitions, each with a different stimulation time (see Fig. 1): i) 4000 ms, coinciding with the backswing phase of the action; ii) 4720 ms (forward swing); iii) 4850 ms (acceleration phase); and iii) 5200 ms (follow-through phase).

In order to promote participants' attention to the task, a small number of novel videos were interspersed within each of the GS conditions; these videos were created by flipping the original video about its vertical axis, using video editing software (Avidemux v.2.4.1). Participants were instructed to count the number of flipped videos they saw, and to report this number upon completion of each condition.

We considered the possible confounds which can arise from participants' engagement in the mental simulation, or motor imagery, of the viewed action. Motor imagery recruits similar processes to those involved in action observation and execution [1], and there is evidence that concurrent motor imagery and action observation can facilitate CE to a greater extent than when the two processes are employed separately [72,73]. In order to control for this, participants were asked to fill in a brief questionnaire after each block, to determine their engagement with imagery during video viewing. Specifically, participants answered the following questions: *When you were watching the videos, did you imagine yourself performing the observed action? If so, then for what percentage of the clips do you recall doing this? If you did imagine yourself, then: i) How intensely, on average, did you FEEL yourself performing the movement? Please provide a rating from 1 (no sensation) to 5 (as intense as executing the action); ii) How vividly, on average, did you SEE yourself performing the movement? Please provide a rating from 1 (no image) to 5*

(image as clear as seeing).

Participants were given a ten-minute break between blocks, and five-minute breaks between golf conditions. Each testing session lasted approximately 1.5 h. The experimenter regularly monitored the participants' comfort, attentiveness and alertness throughout the protocol.

2.6. Data processing and analysis

2.6.1. Motor-evoked potentials

EMG data were analysed using data acquisition software (Signal v. 4.11, Cambridge Electronic Design Limited, Cambridge, UK). The root mean square of the background EMG (bEMG) occurring in the 90 ms preceding the onset of the TMS stimulus was calculated; trials in which this value was greater than 100 μ V were excluded from the analyses. Offline analyses revealed that none of the data met this criterion.

Peak-to-peak amplitudes were measured, in millivolts, for each MEP and then averaged across baseline, the reach-grasp-lift block, and each of the four golf observation conditions. Averaged MEP amplitudes recorded during baseline pre were compared to those recorded during baseline post using separate repeated measures t-tests for each of the muscles of interest; these tests revealed no significant differences (all $p > 0.05$), indicating that there was no overall change in CE over time. Thus, amplitudes recorded in the two baseline periods were averaged to yield a total baseline measure of CE. The averaged amplitudes recorded during the golf and the reach-grasp-lift videos were normalised to the averaged baseline values and expressed as a percentage of change from baseline as per the following equation: $X = (a - b) / b * 100$, where X is the normalised amplitude, a is the averaged amplitude recorded in a given condition, and b is the mean amplitude of the averaged baseline.

2.6.2. Gaze data

Gaze data were analysed using Data Viewer software (SR Research Ltd., Ontario, Canada). Fixations were defined as eye movements with velocities of less than 30°/s and accelerations below 8000°/s²; eye movements with velocities and accelerations above these parameters were defined as saccades. For analysis purposes, the GS video was subdivided into two interest periods (IPs): a static IP, which began with the onset of the video and ended immediately prior to backswing initiation, and a dynamic IP, which comprised the entirety of the action thereafter (cf. D'Innocenzo et al., 2016). Dynamic interest areas (IAs) were superimposed over the different elements of the videos. For the GS videos, a total of nine IAs were superimposed over the corresponding areas of the display: the model's head, hands, arms, torso (*centre IA*), legs, shoulders and feet; the ball; and the club. An additional IA was superimposed over the area corresponding to the path of the golf club

for the dynamic IP. For the RGL videos, IAs were superimposed over the model's hand, his forearm and the bottle.

Two low-level gaze metrics were analysed: *average fixation duration* and *average saccadic amplitude*. In addition, dwell times on all IAs, expressed as a percentage of the total dwell time in a specific trial, were averaged across trials and included in the analyses.

2.7. Statistical analyses

Data were analysed using IBM SPSS Statistics software (v. 20; IBM, Armonk, NY). For statistical analyses, Significance levels were set at $p < 0.05$, and they were adjusted using Bonferroni correction in case of multiple post-hoc comparisons. Where the assumption of sphericity was violated, degrees of freedom are reported using Greenhouse-Geisser correction. Tables with descriptive statistics are reported in the appendix.

3. Results

3.1. Motor-evoked potentials

3.1.1. Facilitatory effects of action observation

Raw MEP amplitudes recorded across the four stimulation times during observation of the GS videos were averaged to obtain a total raw MEP amplitude for each of the muscles of interest. A Group (Skilled/Novice) x Condition (Baseline/Golf/RGL) x Muscle (FCR/FCU/ECR) mixed ANOVA was conducted on the raw MEP amplitudes to determine whether observation of the two actions differentially affected CE, and whether this differed across the two expertise groups (Fig. 2). The results revealed a significant main effect of Condition, $F(2, 32) = 9.36$, $p = .001$, $\eta_p^2 = .37$. Pairwise comparisons using Bonferroni correction indicated that overall, raw MEP amplitudes during the GS observation condition ($M = .29$, $SEM = .03$, 95 % CI [.23, .35]) were higher than those recorded during the baseline condition ($M = .21$, $SEM = .02$, 95 % CI [.16, .27]) $p = .001$; there were no differences in MEP amplitudes between the RGL observation condition ($M = .26$, $SEM = .02$, 95 % CI [.21, .30]) and baseline. There were no main effects of Group or Muscle, and no significant interactions.

3.1.2. Golf videos

A Group (Skilled/Novice) x Muscle (FCR/FCU/ECR) x Stimulation Time (Backswing/Forward swing/Acceleration/Follow-through) ANOVA was conducted to assess whether normalised MEP amplitudes recorded from the three muscles differed across the four stimulation times; skilled-novice comparisons were also made. No significant main effects or interactions emerged.

Pearson's correlation was thus used to determine the relationship between the participant's engagement in motor imagery during

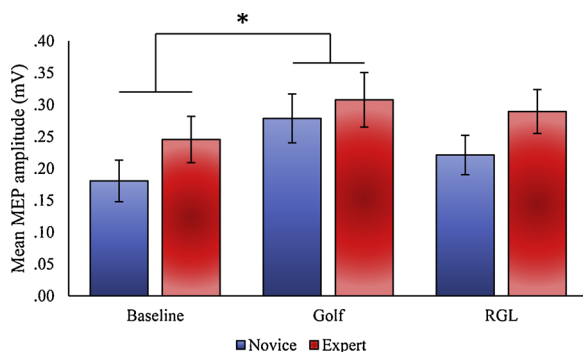


Fig. 2. Mean raw MEP amplitudes – collapsed across the three muscles – recorded during rest, during observation of the golf videos and during observation of the RGL videos. Error bars represent standard error of the means; * $p = 0.001$.

observation of the GS – as indexed by the percentage of clips during which participants had engaged in motor imagery of the golf swing, the vividness of the visual image and the intensity of the feeling – and the normalised MEP amplitudes recorded from each of the target muscles. Results revealed no significant correlations.

3.1.3. RGL videos

A Group (Skilled/Novice) x Muscle (FCR, FCU, ECR) mixed ANOVA was conducted to assess whether there were any differences between novices and skilled golfers' normalised MEPs amplitudes recorded from the three muscles. This revealed no significant main effects or interactions.

Pearson's correlation revealed no significant relationship between normalised amplitudes recorded during observation of the RGL videos and any of the motor imagery variables investigated.

3.2. Gaze data

Fixation durations and saccadic amplitudes were analysed using two separate Group (skilled/novice) x Condition (RGL/golf) mixed ANOVAs. For fixation duration (Fig. 3A), there was a significant main effect of Condition, $F(1, 16) = 7.83$, $p = .013$, $\eta_p^2 = .33$: overall, fixation durations were significantly longer in the RGL condition ($M = 434.13$, $SEM = 40.98$, 95 % CI [347.26, 521.01]) than they were in the GS condition ($M = 334.24$, $SEM = 17.68$, 95 % CI [296.77, 371.71]). As can be seen in Fig. 3A, novices tended to show shorter fixation durations in the RGL condition relative to the GS condition compared to golfers, but this interaction did not reach significance. The main effect of Group was not significant. For saccadic amplitude (Fig. 3B), the ANOVA did not reveal any significant main effects or interactions.

Two additional Phase (Static/Dynamic) x Group (Skilled /Novice) mixed ANOVAs were conducted to determine whether the duration of the fixations and the amplitude of the saccades recorded during observation of the GS videos were affected by the phase of the swing. For average fixation duration (Fig. 3C), the ANOVA revealed a significant main effect of Phase, $F(1, 16) = 11.87$, $p = .003$, $\eta_p^2 = .43$: durations were longer during the dynamic phase ($M = 346.17$, $SEM = 20.32$, 95 % CI [303.09, 389.25]) than during the static phase ($M = 289.67$, $SEM = 12.55$, 95 % CI [263.08, 316.27]), for all participants. The main effect of Group and the Group x Phase interaction were not significant. The ANOVA conducted on the average saccadic amplitude revealed no significant main effects or interactions; however, amplitudes tended to be smaller during the dynamic phase than the static phase (Fig. 3D).

Dwell times on the interest areas were analysed separately for the RGL and the GS conditions using two Group x IA mixed ANOVAs. For the RGL videos (Fig. 4), results revealed a significant main effect of IA, $F(1.33, 21.27) = 44.48$, $p < .001$, $\eta_p^2 = .74$: irrespective of group, participants spent considerably longer looking at the bottle than they did at the hand or the forearm, both $p < .001$. In addition, dwell time was significantly longer on the hand than it was on the forearm, $p = .028$. There was no main effect of Group, nor a Group x IA interaction.

For the GS videos, given the changes in low-level gaze metrics across the two phases of the swing, a Group (Skilled /Novice) x IA (Head/Hands/Arms/Shoulders/Centre/Legs/Feet/Ball/Club) x Phase (Static/Dynamic) ANOVA was used to determine whether golfers' and novices' dwell times on the various IAs differed according to the phase of the swing. The ANOVA revealed a significant main effect of IA, $F(3.38, 54.05) = 15.62$, $p < .001$, $\eta_p^2 = .49$, as well as a significant Phase x IA interaction, $F(3.13, 50.09) = 40.59$, $p < .001$, $\eta_p^2 = .72$. Since the Group factor did not show any significant main effect or interactions, dwell times were collapsed across groups. Separate paired samples t-tests were then used to compare the extent to which dwell times for each IA differed across the two phases of the swing (Bonferroni corrected threshold = .006). Results revealed significant differences between the two phases of the swing for dwell times on all

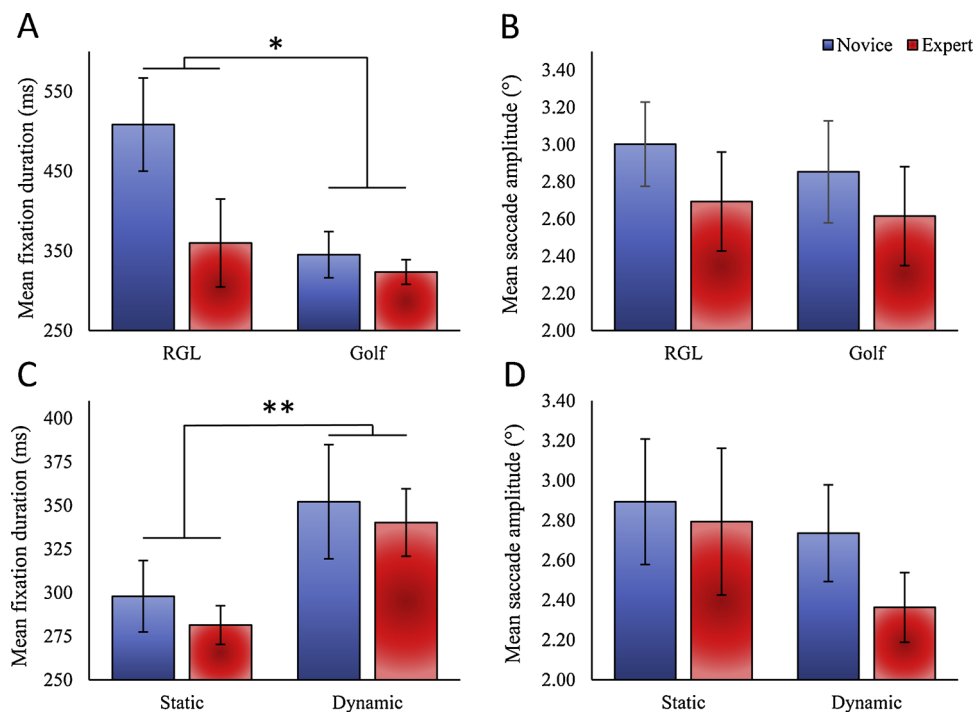


Fig. 3. Mean fixation duration (in ms) across the two conditions (A) and the two phases of the golf condition (C); mean saccadic amplitude (in degrees of visual angle) across the two conditions (B) and the two phases of the golf condition (D). Error bars represent standard error of the means; * $p < 0.05$, ** $p < 0.005$.

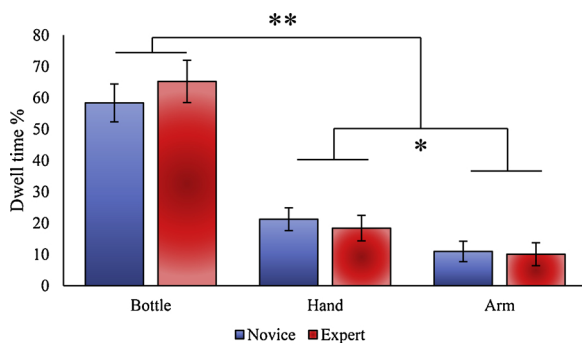


Fig. 4. Mean dwell time (as percentage of total dwell time) on the interest areas during viewing of the RGL videos. Error bars represent standard error of the means; * $p = 0.03$, ** $p < 0.001$.

IAs except for the feet. Specifically, participants tended to direct their gaze to more central areas of the display such as the head and centre during the dynamic phase than they did during the static phase (see Fig. 5).

3.3. Correlations between MEPs and gaze

Pearson's correlation was used to determine whether participants' gaze behaviour was related to MEP amplitudes, as such a relationship has been demonstrated previously (D'Innocenzo et al., 2017).

For the RGL videos, dwell time on the bottle was negatively related to amplitudes recorded from the FCU, $r = -.47$, $p = .025$, and the ECR, $r = -.45$, $p = .03$, and dwell time on the forearm was positively related to ECR MEP amplitudes, $r = .52$, $p = .014$. MEP amplitudes were not significantly correlated to fixation duration or saccadic amplitude.

A similar relationship between gaze location and MEP amplitude was also found for the golf videos. Results revealed a positive correlation between FCR amplitudes and dwell time on the shoulders, $r = .57$,

$p = .007$; and between FCU amplitudes and dwell time on the arms, $r = .46$, $p = .026$, and on the centre, $r = .50$, $p = .018$. No significant correlations were found between fixation duration or saccadic amplitude and MEP amplitudes.

4. Discussion

In the present study, we examined motor resonance in skilled and novice golfers as they observed two actions - one highly dynamic (GS) and one more mundane (RGL). We expected the two actions to differentially modulate CE - notably, greater increases for the dynamic task. In addition, we expected observation of the two actions to elicit different gaze behaviours, and we aimed to determine whether eye movement patterns would modulate motor resonance.

4.1. Motor resonance during observation of complex versus simple actions

Observation of the golf swing significantly facilitated MEPs from baseline. In contrast, no difference was found between amplitudes recorded during observation of the RGL action and those recorded at baseline. This is in contrast to some previous studies, as increased activation of areas comprising the action-observation network [74] and facilitation of CE [75,76] have often been found during the observation of such actions. However, the idea that action observation can either facilitate or inhibit AON activity is gaining support in the literature [77-79]. Although facilitation of CE still seems to be the predominant finding [65], there is also evidence that observed or implied actions can induce a suppression of mirror activity [80-82]. Hannah and colleagues [79] recently showed that engaging in observation of a pinch grip action resulted in a non-specific, arousal-related facilitation of CE which was reflected in higher MEP amplitudes during an intra-task baseline compared to the pre-task baseline. However, observing the action did not facilitate CE from the intra-task baseline levels - instead, over 60 % of participants showed inhibition of MEP amplitudes during AO.

These findings are consistent with the discovery of a class of cells

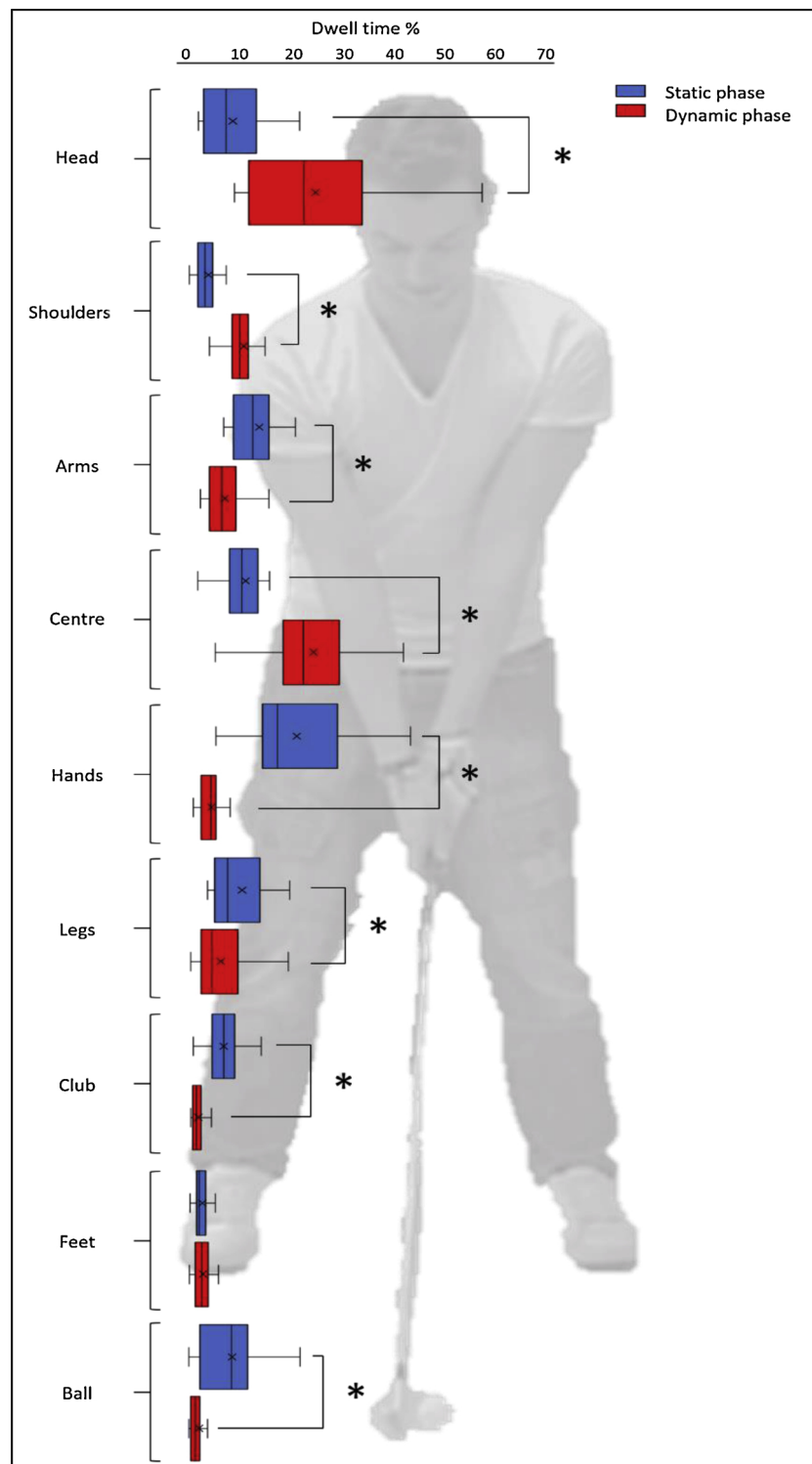


Fig. 5. Box plots showing dwell times on the IAs (expressed as a percentage of the total dwell time) across the static and dynamic phases. Whiskers represent the lowest and highest values; vertical lines represent the medians; x symbols represent the means; * $p < 0.001$.

that are present both in the monkey's [83] and in the human brain [84], which show inhibitory responses to action observation. These cells may play the key functional role of distinguishing between the actions of others and those of the self, and of inhibiting unwanted self-movement resulting from observation-execution matching processes [83,84]. Such inhibitory mechanisms are thought to play a fundamental role for

selective imitation during action observation [85] by preventing the activated motor representations from reaching the threshold at which they are overtly executed [86].

Asking participants to refrain from moving and to maintain a comfortable and relaxed position, as is typically done in TMS studies, may increase the need to suppress subliminal muscle activation,

resulting in a modulation of the AO-induced effects on the excitability of the target muscles [87,88]. Consistent with this, Bruno and colleagues [89] recently showed that, during motor imagery of finger-thumb opposition, participants who were not given any specific instruction pertaining to the production of overt movement showed facilitation of CE; in contrast, those who were instructed to refrain from moving showed inhibition, reflected in a decrease of MEP amplitudes from baseline. Finally, when observers adopt a posture that is congruent with that of the model there is a stronger activation of the corresponding motor representation – reflected in larger MEP amplitudes – compared to when the observer and model's postures are incongruent [90,91]. In the present study, the RGL video had been filmed while the actor was sitting down in front of the table – a posture congruent with that of our participants. This may have further facilitated activation of the motor representations for the observed action, enhancing the need to counteract these excitatory mechanisms with inhibition to prevent overt imitation of the action. In contrast, the GS video displayed a full-body view of the golfer, whose posture and freedom to move were very different from that of our participants. It is likely that, as a result, observation of the golf swing resulted in a facilitation of CE which could not possibly reach the high threshold for overt execution. The modulations in MEP amplitudes recorded during this condition were not enough to trigger inhibitory mechanisms – which was consequently reflected in facilitation of CE.

4.2. Modulatory effects of gaze behaviour on motor resonance

Our findings also suggest that the patterns of CE modulations observed in our two conditions were affected by the participant's gaze behaviour. In the RGL condition, participants predominantly looked at the target of the action, as is typically found in natural contexts involving the viewing and performance of transitive actions [50,92], and this did not facilitate MEP amplitudes. In contrast, during observation of the dynamic phase of the GS condition, CE was significantly facilitated – and gaze was directed mainly towards the model's head and the centre of his body. Visual attention plays a key modulatory role in the activity of the AON [93], and attending to relevant aspects of an action can facilitate learning [55]. Recently, it has been shown that, by asking observers to fixate their gaze on a point close to the main effector, CE can be maximised [58,59], suggesting that foveation on or close to the effector may be preferable for activating the cortical representations of a movement [56,94]. Our results may be explained as follows: foveal vision occupies the central portion of the visual field, estimated to be between 2° and 3°, whereas parafoveal vision extends up to 5° on either side of fixation [95,96]. Since our RGL video displayed a side view of the action that occupied the entire visual display, the forearm was at an eccentricity of 12° from the centre of the target. When the participant was fixating on the target, the forearm could thus only be perceived through peripheral vision, potentially moderating motor resonance. In contrast, the GS videos displayed a full-body view of the golfer, whereby the distances between the golfer's forearms and his head or the centre of his body were always inferior to 3.8° and 5° of visual angle, respectively. Therefore, when the participant was looking at areas of the golfer's body such as the centre and the head, the arms were always within the field of parafoveal vision, with visual acuity approaching that of the fovea, thereby facilitating CE. Our results indicate that foveation on – or close to – the effector of an action can facilitate motor resonance. Our findings also suggest that this type of gaze behaviour is more likely to occur during observation of a complex, whole-body action, when there are multiple moving elements that need to be monitored, than during viewing of many everyday target-directed actions, where gaze is typically drawn to the target.

4.3. Gaze behaviour during complex versus simple action observation

In line with our predictions, eye movement patterns were modulated by the characteristics of the action. When observing the simple, single-limb task in the RGL video, participants adopted naturalistic gaze behaviour which consisted of long-duration fixations directed to the action target and concurrent monitoring of the single-limb action in peripheral vision. The GS videos, in contrast, displayed a very complex action, in which the arms, and legs to a far lesser extent, moved simultaneously in a highly dynamic and coordinated manner. Since peripheral vision may not allow effective monitoring of all relevant information, participants resorted to using a gaze pattern that comprised short-duration fixations to multiple areas, enabling them to extract information about the absolute and relative positioning of the model's body and limbs. Therefore, they did not exhibit the target-looking behaviour which is typically found during natural observation of transitive actions. As illustrated in Fig. 5, gaze also became more centralised as the action progressed from the static phase to the dynamic phase; this corroborates the fixation duration data and is in line with our previous findings [55].

The present study does not allow us to determine the relative contributions of gaze and inhibitory mechanisms to the observed changes in CE. However, it is likely that both factors are important in determining the extent of AO-induced modulations. Increased excitability during observation of simple transitive actions still seems to be a prevalent finding in the literature. Since target-looking is a prepotent behavioural tendency, we might assume that participants in other AO studies in which increased facilitation was found, were also looking at the target of the action. It therefore seems likely that suppression mechanisms are responsible for our findings. Nevertheless, we did find evidence of a relationship between MEPs and gaze: MEPs tended to be larger when gaze was directed to the main effector, or areas close to it. This reinforces the notion that gaze behaviour can modulate the automatic effects of action observation.

4.4. Expertise-related modulations of motor resonance

Finally, contrary to findings from previous studies [42–44], we did not find evidence for expertise-related modulations in AO-induced corticospinal facilitation. Regardless of the participant's familiarity with golf, modulations in CE during observation of golf were found to be non-muscle-specific and not time-locked to the action, in that they did not match the pattern of muscular activation observed during action execution [97]. The degree of phase-locked facilitation may depend on the complexity of the observed action [98] and on the specific target muscles which are selected. Typically, studies which have found phase-specific effects of motor resonance during action observation have employed very simple and common actions consisting of single-limb movements [65]. However, unlike the fine-grained motor representation of the highly specialised finger muscles, the representation of the forearm muscles may be too coarse to manifest fine phase-specific modulations of MEP amplitude, which may explain the lack of expertise-related modulations observed by others [44].

4.5. Practical implications

The findings of the present study show that observation of a forceful, dynamic action facilitates motor resonance to a greater extent than viewing of a simple, single limb action, and that this occurs regardless of the observer's familiarity with the action. Our results also suggest that this effect may be due to the different gaze behaviours elicited by the two actions. In the RGL condition, participants predominantly directed gaze to the target and away from the effector, and this was associated with no facilitation of corticospinal excitability. In

contrast, significant facilitation was observed in the GS condition, when gaze was largely fixated close to the main effectors. This indicates that eye movements may influence motor resonance processes, potentially determining whether the motor representations that are subliminally activated during AO reach the threshold for overt execution, and whether suppression mechanisms arise.

Our results have important implications for AO-based approaches for motor function recovery. Approaches such as action observation treatment [29] are based on the notion that observational learning is achieved through repeated activation of the motor representations which are recruited during action execution [13,18,27], and thus aim at increasing CE in the observer's motor system. In the present study, we found that the extent of motor facilitation elicited by AO is modulated by the characteristics of the viewed action as well as by the observer's gaze behaviour. AO-based rehabilitation programmes may therefore benefit from incorporating instructions designed to direct the patient's gaze away from the target and towards the effector muscles for the observed action, as such a gaze strategy may enhance CE. In addition, observation of a dynamic task may be more effective than viewing simple actions, for eliciting corticospinal facilitation. Therefore, action observation treatment should consider including the presentation of such actions; doing so may not only increase the amount of covert motor activation (with beneficial effects for motor rehabilitation), but may also naturally result in optimal effector-directed gaze behaviour – without the cognitive load associated with verbal instructions. The implications of our findings can also be extended to the learning of novel motor skills: demonstrations and observational practice are widely used in motor skill acquisition settings as a form of covert motor training, and greater levels of motor resonance are in some cases associated with physical proficiency with an action [42,43]. Therefore, directing visual attention so that corticospinal excitability during AO is maximised may also enhance formation of the motor representation in the observer's motor system, thereby accelerating skill acquisition.

4.6. Limitations and future directions

The present study had some limitations. During collection of the baseline MEPs, we asked participants to keep their eyes closed. However, it has been argued that, in order to obtain a representative measure of the baseline levels of CE and rule out any changes in excitability due to differences in visual input per se, visual stimulation during baseline conditions should be as similar as possible to that in experimental conditions [59,99]. It may also have been preferable to include other baseline measurements of excitability by recording MEPs during observation of static images of the GS and RGL actions; however, we decided not to do so, to avoid increasing the number of TMS pulses delivered. In addition, it would have been preferable to acquire recordings of EMG activity during action execution itself, to act as a reference point for subsequent assessments of corticospinal facilitation during AO. It should also be noted that the two videos employed in the present study differed from one another in several ways. The GS video comprised a large amount of visual information. In contrast, the RGL video only showed a side view of the actor's hand and arm, and the target. It would have been beneficial to include an additional condition comprising a whole-body view of the actor performing the RGL action. This would have allowed us to determine whether the differences in the visual display affected motor resonance and gaze behaviour – something that should be addressed in future research.

Our selection of the TMS stimulation timings may also be

considered as a limitation; in the RGL condition, pulses were delivered during the lifting phase, based on previous evidence that this phase of the action elicits the largest increases in CE [35,66]. Although stimulation timings always corresponded to the lifting phase, they were pseudo-randomised to in an effort to reduce participants' anticipation of the TMS pulses. This may have acted as a confound; since motor resonance has often been shown to be finely tuned to the temporal evolution of an action [33,34], had we used a single stimulation time corresponding to the late lifting phase of the RGL action, we may have found greater levels of CE [65].

In contrast with previous studies [44–46], we did not find any expertise-dependent modulation of MEP amplitudes. A factor that may have prevented the emergence of skill-related differences can be found in our presentation of the action. Jola and Grosbras [45] showed novice dance spectators videoed and live dance performances and found that observing live performances resulted in higher normalised amplitudes compared to video-modelled performances. This effect may be due, at least in part, to the size of the stimulus, as a whole-body action presented on a PC monitor spans a smaller visual angle than a live action. If we had used a life-size projection, or even a live model, then the skilled players' motor system might have been more finely tuned to the observed act, allowing potential skill-related differences to emerge. This possibility also warrants further investigation. It should also be noted that our skilled sample included individuals with varying levels of golfing expertise, which may also have contributed to the lack of expertise effects. This could be determined in future studies by adopting a stricter selection criterion for the skilled group, or by selecting a larger sample of players and dividing them into smaller categories based on their handicap ratings in order to compare the effects of action observation across different skill groups.

4.7. Conclusion

The current study advances existing work on the relationship between gaze behaviour and neurophysiological changes during action observation. We demonstrated that observation of a dynamic whole-body task increased motor resonance in the observer, more so than viewing a mundane upper limb task. We also demonstrated that this was somewhat mediated by the observer's gaze – but not by their familiarity with the task. Taken together, these findings suggest that AO-based approaches to promote motor rehabilitation may benefit from the inclusion of more varied and complex actions, and that gaze should be directed appropriately in order to maximise motor resonance.

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Declaration of Competing Interest

None.

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Appendix A

See Tables A1–Table A6

Table A1
Raw MEP Amplitudes (mV) – Descriptive Statistics.

Muscle	Group	Condition	<i>M</i>	<i>SEM</i>	<i>SD</i>	<i>Min</i>	<i>Max</i>
FCR	Novice	Baseline	0.17	0.03	0.08	0.05	0.30
		Golf	0.26	0.05	0.14	0.06	0.47
		RGL	0.22	0.05	0.15	0.07	0.46
	Expert	Baseline	0.23	0.09	0.26	0.06	0.84
		Golf	0.30	0.07	0.21	0.08	0.78
		RGL	0.28	0.06	0.17	0.07	0.62
	Overall	Baseline	0.20	0.04	0.18	0.05	0.84
		Golf	0.28	0.04	0.17	0.06	0.78
		RGL	0.25	0.04	0.15	0.07	0.62
FCU	Novice	Baseline	0.20	0.03	0.10	0.06	0.42
		Golf	0.30	0.04	0.12	0.11	0.49
		RGL	0.24	0.02	0.06	0.12	0.29
	Expert	Baseline	0.29	0.06	0.18	0.11	0.68
		Golf	0.35	0.07	0.20	0.16	0.81
		RGL	0.32	0.06	0.18	0.10	0.61
	Overall	Baseline	0.24	0.03	0.15	0.06	0.68
		Golf	0.32	0.04	0.15	0.11	0.81
		RGL	0.27	0.03	0.13	0.10	0.61
ECR	Novice	Baseline	0.17	0.03	0.09	0.04	0.29
		Golf	0.27	0.05	0.16	0.06	0.63
		RGL	0.20	0.03	0.09	0.09	0.36
	Expert	Baseline	0.22	0.05	0.13	0.06	0.45
		Golf	0.27	0.05	0.14	0.07	0.48
		RGL	0.26	0.06	0.16	0.04	0.54
	Overall	Baseline	0.19	0.03	0.11	0.04	0.45
		Golf	0.27	0.03	0.15	0.06	0.63
		RGL	0.23	0.03	0.13	0.04	0.54

Table A2
Normalised MEP Amplitudes (%) Recorded During Observation of Golf – Descriptive Statistics.

Muscle	Group	Stimulation Time	<i>M</i>	<i>SEM</i>	<i>SD</i>	<i>Min</i>	<i>Max</i>
FCR	Novice	Backswing	56.66	27.72	87.66	-40.24	254.77
		Forward swing	68.28	35.64	112.71	-13.93	355.39
		Acceleration	54.89	22.75	71.94	-31.46	193.69
	Expert	Follow-through	71.54	23.42	74.06	-22.42	179.06
		Backswing	81.89	37.66	106.51	-14.32	302.87
		Forward swing	61.89	20.90	59.11	-17.21	142.54
	Overall	Acceleration	87.82	37.80	106.93	-8.73	270.54
		Follow-through	45.83	24.77	70.05	-39.67	155.41
		Backswing	64.06	24.93	78.85	-47.23	240.15
FCU	Novice	Forward swing	62.49	20.42	64.56	-13.46	203.37
		Acceleration	83.34	23.46	74.18	-24.95	215.59
		Follow-through	66.58	18.95	59.91	-41.04	153.65
	Expert	Backswing	21.74	9.22	26.07	-15.10	50.81
		Forward swing	35.81	11.88	33.59	-14.86	92.36
		Acceleration	45.25	18.36	51.93	-15.75	140.73
	Overall	Follow-through	19.25	11.76	33.26	-22.34	76.59
		Backswing	34.05	14.33	45.33	-11.57	116.11
		Forward swing	68.95	18.43	58.29	10.94	197.32
ECR	Novice	Acceleration	76.65	29.56	93.47	-3.05	305.95
		Follow-through	50.54	23.06	72.92	-30.51	197.77
		Backswing	26.71	10.88	30.78	-3.49	84.75
	Expert	Forward swing	36.29	10.49	29.67	-10.96	77.83
		Acceleration	31.71	17.68	50.01	-12.07	130.11
		Follow-through	32.88	22.50	63.65	-24.52	164.51

Note. Amplitudes are expressed as percentage of change from the baseline condition.

Table A3
Normalised MEP Amplitudes (%) Recorded During Observation of the RGL Action – Descriptive Statistics.

Muscle	Group	<i>M</i>	<i>SEM</i>	<i>SD</i>	<i>Min</i>	<i>Max</i>
FCR	Novice	57.23	29.02	91.76	-42.24	231.58
	Expert	61.35	26.31	74.40	-27.73	156.92
FCU	Novice	39.09	15.13	47.85	-36.63	100.58
	Expert	20.89	19.83	56.08	-35.26	131.60
ECR	Novice	31.78	13.72	43.40	-21.39	119.39
	Expert	17.15	10.60	29.97	-30.68	77.32

Note. Amplitudes are expressed as a percentage of change from the baseline condition.

Table A4
Fixation Duration (ms) and Saccade Amplitude (° of Visual Angle) Recorded in the two Conditions – Descriptive Statistics.

Metric	Condition	Group	<i>M</i>	<i>SEM</i>	<i>SD</i>	<i>Min</i>	<i>Max</i>
Fixation duration	RGL	Novice	508.42	58.45	184.85	180.28	810.91
		Expert	359.85	55.13	155.93	170.44	595.34
		Overall	442.39	43.38	184.04	170.44	810.91
	Golf	Novice	345.09	28.97	91.60	176.06	526.45
		Expert	323.39	15.44	43.68	264.89	397.60
		Overall	335.44	17.24	73.15	176.06	526.45
Saccade amplitude	RGL	Novice	3.00	0.23	0.71	2.09	4.03
		Expert	2.69	0.27	0.75	1.54	3.71
		Overall	2.86	0.17	0.73	1.54	4.03
	Golf	Novice	2.85	0.27	0.87	1.31	4.32
		Expert	2.62	0.27	0.75	1.45	3.81
		Overall	2.75	0.19	0.80	1.31	4.32

Table A5
Fixation Duration (ms) and Saccade Amplitude (° of Visual Angle) during the Two Phases of the Golf Video – Descriptive Statistics.

Metric	Phase	Group	<i>M</i>	<i>SEM</i>	<i>SD</i>	<i>Min</i>	<i>Max</i>
Fixation duration	Static	Novice	297.93	20.51	64.87	164.99	378.92
		Expert	281.41	11.10	31.41	242.34	324.04
		Overall	290.59	12.26	52.01	164.99	378.92
	Dynamic	Novice	352.11	32.75	103.56	186.23	589.01
		Expert	340.23	19.35	54.73	262.46	423.52
		Overall	346.83	19.65	83.35	186.23	589.01
Saccade amplitude	Static	Novice	2.89	0.31	1.00	1.30	4.95
		Expert	2.79	0.37	1.04	1.43	4.55
		Overall	2.85	0.23	0.99	1.30	4.95
	Dynamic	Novice	2.74	0.24	0.77	1.29	4.24
		Expert	2.36	0.17	0.49	1.61	3.22
		Overall	2.57	0.16	0.67	1.29	4.24

Table A6
Dwell Time on the IAs for the RGL video – Descriptive Statistics.

IA	Group	<i>M</i>	<i>SEM</i>	<i>SD</i>	<i>Min</i>	<i>Max</i>
Bottle	Novice	58.36	6.40	20.25	29.48	87.97
	Expert	65.22	6.20	17.52	36.06	86.91
	Overall	61.41	4.45	18.86	29.48	87.97
Hand	Novice	21.22	3.83	12.10	8.72	46.77
	Expert	18.38	3.79	10.71	7.54	42.83
	Overall	19.96	2.65	11.26	7.54	46.77
Forearm	Novice	10.95	3.83	12.10	0.26	38.09
	Expert	10.06	2.69	7.62	0.32	19.86
	Overall	10.55	2.38	10.08	0.26	38.09

Note. Dwell times are expressed as a percentage of the total dwell time.

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