THE RELATIONSHIP BETWEEN GAZE AND INFORMATION PICKUP DURING ACTION OBSERVATION: IMPLICATIONS FOR MOTOR SKILL (RE)LEARNING.

A Thesis Submitted for the Degree of Doctor of Philosophy

By

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January 2018

Abstract

The aim of the present thesis was to investigate the relationship between individuals' allocation of overt visual attention during action observation and their consequent pickup of information. Four interrelated studies were conducted to achieve this. In Study 1 we examined the effects of visual guidance – colour highlighting of relevant aspects of the action – on observational learning of the golf swing. The results showed that the visual guides facilitated novices' intake of information pertaining to the model's posture, which was reflected in faster learning. In the remaining studies, transcranial magnetic stimulation and eye tracking data were acquired concurrently to measure the interaction between gaze behaviour and motor resonance – a neurophysiological index of the motor system's engagement with a viewed action, and thus a correlate of information extraction. In Study 2, we directed observers' gaze to distinct locations of the display while they viewed thumb adduction/abduction movements. The results showed that, by directing gaze to a location that maximised the amount of thumb motion across the fovea, motor resonance was maximised relative to a free viewing condition. In Study 3 we examined the link between gaze and motor resonance during the observation of transitive actions. Participants viewed reach-to-grasp actions with natural gaze, or while looking at a target- or an effector- based visual guide. The results showed that the effector-based guide disrupted natural gaze behaviour, and this was associated with a reversal of the motor resonance response. In Study 4 we showed novice and skilled golfers videos of the golf swing and of a reach-grasp-lift action. The results revealed that, for both actions, the extent of motor resonance was related to the location of participants' fixations. The present work provides the first evidence of a relationship between gaze and motor resonance and highlights the importance of appropriate gaze behaviour for observational learning.

ACKNOWLEDGMENTS

There are a number of people that I would like to acknowledge, without whose help and support I would not have arrived at where I am today.

Dan, I am extremely grateful for the opportunity you have given me, for your support and your faith in me. Your endless enthusiasm, dedication and commitment have been invaluable, and they have made a big difference at times where I have felt a bit overwhelmed. I have thoroughly enjoyed learning from you and working with you, and our stimulating many-hours-long discussions and exchange of ideas. You have been an excellent, inspiring guide in this journey, and I could not have asked for a better supervisor. I hope that this thesis makes you as proud as it makes me, and I hope that I can continue to make you proud in the future.

Alex, although you joined my supervisory team after I had already started, you have been a keen supervisor, you have taught me a lot and you have been fun to work with. Thank you for your support, patience in training me, and for your bluntness – a quality much appreciated by an Italian!

Michael, you were the reason I became interested in research, and without your wise advice I would not be where I am now. For this, and for the continued support you have given me throughout my time at Brunel, I thank you.

Claudia, although I only had the pleasure of working with you for a short time, your friendliness, honesty and guidance have been invaluable. Thank you for giving me all your help and support during your time as my supervisor. I hope our paths will cross again in the future.

Mark, thank you for sharing your expertise, and for the support you gave me while you were part of my supervisory team.

Mum and dad, there are no words to say how grateful I am to you both. You have taught me to face the challenges of life with resilience and determination, to get back up after a defeat, and to work hard to achieve my goals and ambitions. Your unconditional love and support have been my strength and guide throughout the good times and the bad ones, and you have always been close by – despite the physical distance. I thank you for everything that you have always done for me. I love you dearly.

Marta, you have probably felt the pain of this last year almost as much as I have! Thank you for patiently listening to my endless complaining about software crashing, slow connections, and a million other things. You have always been there for me, always believed in me, and

always been my biggest supporter. I don't know what I would have done without our hours-long chats these past few years, without your advice and encouragement. You are my reference point, and I am lucky to have a sister like you. I love you.

Zia Lucia, my amazing auntie: I can never thank you enough for all the love and support you have given me through the years. None of this would have been possible without you. I love you.

To my lovely PhD friends at Brunel: I feel privileged to have met such a great bunch of people. Our socials, beer Fridays, dinner parties and girls' nights have been the rays of sunshine on many grey days. Jen and Adele, we have shared so much more than an office these past few years! With you both I have had the best laughs and the best cries, and I don't know what I would have done without your support. Anastasia, although you were one of the last ones to join the group it is as if I have known you forever. Your Mediterranean craziness was exactly what I needed, and it made me feel closer to home. Jamie, Toby, George, and Adam; Fabio, Colm, Marcelo, Patrick, Viktor, João: Sharing this journey with you has been great. Your company has been priceless, and I thank you for bringing the fun into the PhD life.

Francesco, your steady nerves and endless patience have helped me keep my calm on many occasions! Working with you was a real pleasure, and I hope we can continue to collaborate in the future.

Nicola, my second sister: thank you for having always been there for me. You are one of the best things that happened to me in the UK.

Giovanni, you have brightened up a rather dark period of my life. Your company and friendship have been invaluable.

To the people back home who have stayed close to me notwithstanding all the years and the distance: Alice, Auro, Recchie, I consider myself extremely lucky to have friends like you. Thank you for always being there.

To all the other friends who patiently took part, in one way or another, in my research projects (which includes you, Ilario), and to those who helped make the final write-up stage less lonely (which means you, Luca): I thank you.

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LIST OF ABBREVIATIONS

ADM: abductor digiti minimi

AO: action observation

AON: action-observation network

AOT: action observation treatment

APB: abductor pollicis brevis

CE: corticospinal excitability

ECR: extensor carpi radialis

EEG: electroencephalography

EMG: electromyography

FCR: flexor carpi radialis

FCU: flexor carpi ulnaris

FDI: first dorsal interosseous

FV: free viewing

fMRI: functional magnetic resonance imaging

IA: interest area

M1: primary motor cortex

MEP: motor evoked potential

MNS: mirror neuron system

PET: positron emission tomography

QE: quiet eye

RGL: reach-grasp-lift

TMS: transcranial magnetic stimulation

VG: visual guidance

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1 Chapter 1:

Introduction

1.1 Context of the Thesis

The use of action observation (AO) is extremely common in both sporting and non-sporting contexts. Coaches, teachers and instructors of motor and sport skills widely employ demonstrations as a complement to physical practice; this applies not only to the teaching of novel motor skills to children or sport novices, but also to the refinement of skilled performance and expertise. Furthermore, AO is increasingly being adopted as an adjunct to traditional physical therapy in the context of motor rehabilitation. AO-based approaches to motor skill learning/relearning represent a flexible, time- and cost- effective method to convey information to learners, which can be easily implemented in a variety of settings and domains. It is important to find ways of maximising the effectiveness of demonstrations, so as to facilitate the extent of learning via observation. One approach that could be employed to facilitate skill acquisition involves directing learners' attention to relevant information during AO. This form of perceptual training has been used in an attempt to improve athletes' anticipation and decision-making skill, occasionally with promising results. However, researchers have yet to test the effectiveness of attentional guidance for facilitating observational learning of motor skills.

Appropriate allocation of visual attention is crucial for successful observational learning. In order to develop effective attentional guidance protocols for motor learning and rehabilitation, it is necessary to uncover the ways in which eye movement behaviour affects information extraction. To this aim, researchers have started to investigate how the observer's allocation of attention during action observation modulates the extent of engagement of their motor system with the observed action. Despite this, the relationship between gaze and information pickup is still not well understood and needs to be explored further.

1.2 Structure of the Thesis

This Introduction is followed by a critical review of the literature relevant to the present work (Chapter 2). The review covers topics such as observational learning of motor skills, eye movements and attention, and the mirror neuron system. The aim of this section is to provide the reader with the necessary knowledge to appraise the concepts investigated in each of the four study chapters.

Chapters 3 to 6 represent the four studies of the present programme of research. Since these studies are presented as standalone papers (see Appendix A), each chapter has its own introduction, which includes a review of the relevant literature specific to the study. Some repetition of core material is therefore inevitable.

Finally, Chapter 7 consists of a general discussion that summarises and brings together the main results of the four studies. The implications of the research findings are discussed, and future directions for research and practice are presented.

2 Chapter 2:

Literature Review

2.1 Learning by Observing

Observational learning, also known as *modelling*, is the process of observing the actions of another person and subsequently adapting one's own actions accordingly (A. M. Williams, Davids, & Williams, 1999). Unlike imitation, observational learning is characterized by enduring changes in an individual's actions (Causer, McCormick, & Holmes, 2013). In the context of motor skill acquisition, approaches involving action observation (AO) offer a number of practical advantages. Observational practice can be undertaken independently, without supervision by coaches and instructors and it thus constitutes a cost- and time- effective complement to traditional instructional and physical practice. At the same time, thanks to technological advantages, specific aspects of the demonstrations can be manipulated in many ways so as to vary the type or amount of information conveyed to the learner. It is not surprising, then, that demonstrations represent a very pervasive instructional method employed for the teaching of novel motor skills (Hodges & Ste-Marie, 2013; A. M. Williams & Hodges, 2005).

Action observation-based methods have successfully been used to improve the acquisition and retention of novel sport skills (Ashford, Bennett, & Davids, 2006; Ashford, Davids, & Bennett, 2007; Ste-Marie et al., 2012; Weeks & Anderson, 2000). For instance, observation of a skilled model has been shown to aid novices' acquisition of the long jump (Panteli, Tsolakis, Efthimiou, & Smirniotou, 2013), acquisition and retention of the basketball jump shot (Wulf, Raupach, & Pfeiffer, 2005), learning of ballet dance sequences (Gray, Neisser, Shapiro, & Kouns, 1991), and novice footballers' movement patterns and coordination when learning to kick a ball towards a target (Horn, Williams, & Scott, 2002). Sakadjan, Panchuk and Pearce (2014) showed that, by integrating standard coaching sessions with observation of a skilled model, they could elicit faster improvements in novices' powerlifting technique than those achieved from coaching sessions alone. Similarly, combined action observation (AO) and physical practice of a badminton serve led novices to acquire a better movement form than did physical practice of the skill in the absence of observation (Wrisberg & Pein, 2002).

Observational learning is also widely used in domains other than sport. AO has been shown to aid balance (Shea, Wulf, & Whitacre, 1999) and to benefit learning of movement tempo and timing tasks (Rohbanfard & Proteau, 2011; Vogt & Thomaschke, 2007; Vogt, 1995). In the context of medical training, there is evidence that demonstrations can facilitate the acquisition of technical skills required to perform surgery and anaesthesia (Harris et al., 2017; LeBel, Haverstock, Cristancho, van Eimeren, & Buckingham, 2017; Welsher, Grierson,

& Grierson, 2017; Wulf, Shea, & Lewthwaite, 2010). Finally, AO is increasingly being used as an adjunct to traditional physical rehabilitation of motor function following motor impairment. Observation-based approaches aimed at improving motor re-learning, such as Action Observation Treatment, or AOT (Ertelt et al., 2007), involve the repeated observation of daily actions followed by their imitation. Studies have shown that AOT can help improve upper limb motor function in children with cerebral palsy (Buccino et al., 2012; Sgandurra et al., 2013) and motor recovery in postsurgical orthopaedic patients (Bellelli, Buccino, Bernardini, Padovani, & Trabucchi, 2010). AOT has also been found to be effective for improving motor function and control, autonomy in daily activities and quality of life in Parkinson's disease patients (Buccino et al., 2011; Pelosin et al., 2010). For example, Pelosin, Bove, Ruggeri, Avanzino and Abbruzzese (2013) reported that a single session of observation of repetitive finger movements resulted in reduced bradykinesia when patients performed the same movements. These improvements are reflected in increased activation of motor cortical areas, which suggests that the beneficial effects of AOT are due to the repeated activation of the same motor cortical representations that are involved in action production (Ertelt et al., 2007). AO-based approaches to motor rehabilitation thus represent a promising addition to traditional physical therapy. Since these approaches represent a form of covert motor training, which does not require actual execution of the movements, they are especially suited for aiding recovery in patients with impaired motor abilities (Buccino, 2014).

Action observation (AO) has been shown to benefit learning by improving the observer's cognitive representations of a movement (Ste-Marie et al., 2012). AO requires fewer cognitive resources than does performance of the same actions, which suggests that observational practice may be particularly effective for the learning of complex motor skills (Cordovani & Cordovani, 2016). Demonstrations provide learners with information about the relative motion patterns required to achieve a specific action; this information is then used by the learner to reproduce the modelled movements (Ashford et al., 2006). The combination of AO and physical practice leads to greater performance benefits than does physical practice alone (Shea, Wright, Wulf, & Whitacre, 2000), particularly with regard to coordination and movement form (Ashford et al., 2006; Horn et al., 2002; McCullagh, Weiss, & Ross, 1989). Al-Abood, Davids and Bennett (2001) trained participants on an underarm dart throwing task using physical practice only, or physical practice combined with either verbal instruction or AO. Following training, although overall movement outcomes did not differ between the three groups, the group who had engaged in observational learning displayed a movement form that more closely resembled the movements of the model compared to the groups who had not viewed the demonstration. Improvements in movement coordination patterns following combined physical practice and observation persisted even when motion information was reduced to the movement kinematics by the introduction of a point-light display (Al-Abood, Davids, Bennett, Ashford, & Marin, 2001). Observation of a model also leads to learning even in the absence of physical practice (Blandin, Lhuisset, & Proteau, 1999; Mattar & Gribble, 2005), and there is evidence to suggest that the extent of learning by observation is comparable to that achieved by action (Boutin, Fries, Panzer, Shea, & Blandin, 2010; Heyes & Foster, 2002). Bird and colleagues (Bird, Osman, Saggerson, & Heyes, 2005) trained participants on a computer-based serial reaction time task which required them to learn and respond to a complex sequence of targets appearing in one of four locations on the screen. Training involved either 1) performance of the task, 2) observation of the sequence of stimuli, or 3) observation of a model performing the sequence. Results revealed that both observation conditions resulted in learning of the sequence, and the extent of learning was comparable to that achieved via physical performance. Importantly, Bird et al. reported that, whereas stimulus observation promoted explicit learning of the task, action observation resulted in implicit learning. Implicitly learned motor skills are known to be more resistant to anxiety, and they tend to be performed better in transfer tests than skills which have been acquired through explicit learning mechanisms (Lam, Maxwell, & Masters, 2009a; and 2009b). Therefore, in some cases, observational learning may be preferable to action-based learning (but see Shea et al., 2000).

There is some evidence to suggest that observational practice may be inferior to physical practice in promoting learning. For instance, Blandin, Proteau and Alain (1994) trained participants to perform a sequential timing task using a training schedule involving either physical practice or a combination of observation and physical practice. Their results showed that physical practice resulted in more effective long-term learning than did the combined protocol. Similar results were reported by Wright, Li and Coady (1997). Furthermore, Ghorbani and Bund (2016) investigated the effects of video-based demonstrations and physical practice on novices' acquisition of the baseball pitch and found that the addition of observation to physical practice did not result in any learning benefit. According to Blandin et al., observational practice alone is not as effective as physical practice because it lacks the sensory feedback associated with movement execution, which helps improve muscle control. However, the majority of the available evidence supports the notion that action observation can effectively aid learning of skills of varying complexity (Cordovani & Cordovani, 2016). As illustrated above, learning advantages resulting from AO have been reported even in the absence of physical practice (Blandin et al., 1999; Mattar & Gribble, 2005), and the combination of action observation and physical practice has often been shown to lead to superior learning and retention compared to either type of practice alone (Al-Abood et al., 2001; Shea et al., 2000).

A process related to AO is that of imagery. Research shows that motor imagery (MI), which refers to the covert simulation of an action, recruits similar processes to those involved in both action perception and action production (McCormick, Causer, & Holmes, 2012). Motor imagery, like AO, has been shown to enhance learning and performance; mental simulation of a task has in some cases been found to be as effective as physical practice (Debarnot et al., 2011; Helene & Xavier, 2006). However, other researchers have reported contrasting findings, showing that performance improvements following physical practice are greater than those achieved through mental simulation alone (Gentili & Papaxanthis, 2015; Jackson, Lafleur, Malouin, Richards, & Doyon, 2003). A main difference between the covert states of AO and MI is that, whereas the former is driven by the presence of a perceptual stimulus, the latter relies entirely on the individual’s ability to recruit the motor representations that correspond to a specific action and generate a mental image of themselves performing the task (Buccino, 2014; Gatti et al., 2013; Robin et al., 2007). In fact, AO has been shown to be more effective than MI for novel motor skill learning, at least with regard to the early stages of the learning process (Gatti et al., 2013; Gonzalez-Rosa et al., 2015).

2.1.1 Observational learning theories

A number of theories have been proposed in an attempt to explain the mechanisms that enable individuals to learn novel actions through exposure to an appropriate model[1]. Early accounts of observational learning were shaped by Bandura’s influential work on social cognitive learning processes (Bandura, 1971; Bandura, 1986; Carroll & Bandura, 1987). Such approaches emphasized the key roles that cognition and social interactions play in the development and acquisition of novel behaviours. Carroll and Bandura commented that “Virtually all learning phenomena resulting from direct experience can occur vicariously by observing the behavior of others and its consequences” (1987, p. 397). In his social learning

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[1] A thorough description of the available theoretical models on observational learning is beyond the scope of the present work. Extensive overviews of observational learning theories have been provided elsewhere (e.g., Hodges & Ste-Marie, 2013; Hodges & Williams, 2007; Horn & Williams, 2004; A. M. Williams et al., 1999).

theory, Bandura (1971; 1977) noted that, in order for learning to occur via observation, the learner should develop *symbolic representations* of an activity, rather than basic stimulus-responses associations. He proposed four underlying functions that collectively determine the effectiveness of this phenomenon; notably, that the learner should pay attention to relevant information, retention of the information should occur, the desired behaviour should be accurately reproduced, and there should be adequate motivation to do so. The attention subprocess is key, and it is closely related to the retention function. The information that is attended to during the initial skill acquisition phase is used to gradually form a *symbolic code*, or a mental representation, of the observed action; this mental representation is then retained and used for later reproduction of the action (Bandura, 1986). The notions advanced by Bandura, and in particular his idea that "people cannot learn much by observation unless they attend to, and accurately perceive, the relevant aspects of the modeled activities" (1986, p. 51), were very influential in shaping subsequent conceptualisations of observational learning. Ecological approaches to motor learning (e.g., Gibson, 1979; Newell, 1991), such as the visual perception perspective model developed by Scully and Newell (1985), advocated that successful learning is contingent upon the observer's ability to extract relevant information from the environment (e.g., a model) and then to modify his or her behaviour accordingly. In recent years, research on observational learning has focused on the underlying perceptual and attentional processes (e.g., Ghorbani & Bund, 2016; Hodges, Williams, Hayes, & Breslin, 2007; Hodges & Williams, 2007). It is now generally agreed that visual attention plays a pivotal role in learning through observation, as mere exposure to a model guarantees neither appropriate distribution of attention, nor pickup of task-relevant information.

Social-cognitive and ecological accounts of observational learning thus acknowledge the central importance of attention for observational learning. This notion has generated a considerable body of research aimed at investigating the effects of attentional cueing on observational learning. Researchers have shown that directing observers' attention to critical aspects of a modelled action can improve learning and retention of motor skills in both adults and children (McCullagh, Stiehl, & Weiss, 1990; McCullagh et al., 1989; Meaney, 1994). For instance, Janelle and colleagues (Janelle, Champenoy, Coombes, & Mousseau, 2003) found that the addition of visual and verbal cues to a video model facilitated the acquisition of a football accuracy pass in novice footballers. These findings provide convincing evidence in support of the central role of attention for learning. Attentional cues can be used to direct learners' visual attention towards key components of a modelled action. By enhancing the saliency of fundamental aspects of the action through the use of such cues, we may facilitate accurate perception of the action. This, in turn, can lead to superior encoding of the mental representation of the action, therefore also facilitating action rehearsal and reproduction.

Although demonstrations provide all the information necessary for action execution, their effectiveness is contingent upon the observer's ability to identify and process key elements of the modelled action. Therefore, the development of effective attentional guidance protocols has important implications for the domain of motor learning and motor control. Such protocols may allow us to not only raise the bar for expertise, helping young athletes to accelerate their skill acquisition, but also to facilitate learning of novel motor skills in complete novices or children, and relearning of previously acquired motor skills (e.g., in the case of motor rehabilitation). Further research is needed to elucidate the specific types of perceptual training that are effective in improving learning and performance in different contexts and domains. It is likely that training will need to be differentiated according to the context, so as to take into account the specific task requirements and characteristics. For instance, in fast-paced dynamic sports contexts, learners may benefit from visual cueing aimed at increasing the efficiency of their eye movement patterns, so as to help them focus on areas that allow them to extract and process more information in less time. In contrast, when the aim is to facilitate observational learning, it may be more useful to direct novices' attention in such a way as to aid pick up of global aspects of the action to be learned; for example, the relative position and movements of the model's limbs and body. More research is needed to validate these propositions.

In order to understand how visual attentional guidance may best be employed so as to facilitate observational learning, it is necessary to consider the various functions and characteristics of the human attentional system and the interactions and dissociations between overt and covert visual attention

2.2 Eye Movements and Attention

The human retina is divided into the *fovea*, which occupies the central 2 or 3° of visual angle, the parafovea, which extends up to 5° on either side of fixation, and the periphery, which extends beyond the parafovea (Johansson, Westling, Backstrom, & Flanagan, 2001; Rayner, White, Kambe, Miller, & Liversedge, 2003). The fovea contains a very high concentration of *cones*, photoreceptor cells specialised for vision under high ambient light conditions, which are densely represented in the visual cortex. The light signal from one cone receptor is encoded by several neurons; hence, foveal vision is characterised by high acuity and sensitivity to fine detail. In contrast, the periphery of the eye is characterised by the predominance of *rods*, photoreceptor cells that initiate vision under low light conditions.

Rods have a many-to-one correspondence with the neurons responsible for encoding the light signals, and so peripheral vision does not allow resolution of fine spatial detail (Wandell, 1995). Thus, visual acuity decreases with increasing eccentricity from the fovea; acuity for motion perception, in contrast, falls off more slowly (Anstis, 2012). In fact, the peripheral retina is highly sensitive to moving stimuli (Edwards & Nishida, 2004) and enables accurate discrimination of their velocity (Mckee & Nakayama, 1984).

Visual perception of complex scenes relies on a combination of *saccades* – rapid eye movements that vary in their amplitude and velocity – and *fixations*, during which the eye position is maintained in a specific location. Saccades can reach velocities in excess of 500° per second, and fixations typically last 200-300 ms, although the precise duration hinges on a number of factors (Stevens et al., 2010). During saccadic eye movements, there is suppression of visual input to reduce perception of the resulting blur and ensure continuous processing (Haber & Hershenson, 1980), a phenomenon known as *saccadic masking*. In contrast, fixations are regarded as indices of information processing; typically, the location and the duration of fixations are regarded as reflecting attentional allocation and cognitive processing (Rayner, 1998; Schüler, 2017; Treue, 2003).

There is evidence that spatial attention and point-of-gaze can dissociate. In fact, attentional shifts can occur covertly; that is, in the absence of accompanying eye movements (Posner, 1980; Ryu, Kim, Abernethy, & Mann, 2013). Spatial attention can be deployed volitionally, in a top-down fashion – *endogenous* attention – or it can be attracted by exogenous stimuli (Carrasco, 2011; Parkhurst, Law, & Niebur, 2002). Dissociations between attention and gaze have been found during exogenous and endogenous control of attention (Hunt & Kingstone, 2003a; Hunt & Kingstone, 2003b). Furthermore, an important difference between overt and covert attention is that the latter can be deployed to multiple locations simultaneously, whereas point-of-gaze, and thus overt attention, can only be directed to a single location at a given time (Carrasco, 2011). Covert attention thus allows monitoring of the environment in the peripheral visual field, and it contributes to directing eye movements (Carrasco, 2011). Consistent with this, theoretical accounts of attentional control emphasise the flexible nature of visual attention. For instance, according to the *zoom lens* theory of attention (Eriksen & St. James, 1986), the breath of the attentional focus can be varied in size depending on the requirements of the task – a notion which is supported by neurophysiological evidence (Müller, Bartelt, Donner, Villringer, & Brandt, 2003). At the same time, it has been shown that individuals can fail to perceive information that they are directly fixating, a phenomenon known as *inattentional blindness*, which shows that eye movements do not always reflect attentional orienting (Drew, Võ, & Wolfe, 2013); a related phenomenon is *change blindness*, in which obvious changes to a visual scene are not detected (Simons & Rensink, 2005). Nevertheless, eye movements are normally accompanied by shifts in visual attention, whereby the two are often closely coupled. For example, the sudden onset of a stimulus in the periphery has been shown to automatically attract both gaze (Theeuwes, Kramer, Hahn, & Irwin, 1998) and covert attention (Yantis & Jonides, 1984). In multimedia learning tasks, when learners are shown pictures that contain conflicting information from that reported in the text, they fixate for longer on the pictures (Schüler, 2017), which supports the notion that fixations reflect attention and cognitive processing (Irwin, 2012).

Different eye movement patterns emerge in different tasks and contexts, which further illustrates how gaze reflects observers' intentions and cognitive processes. In his seminal study on eye movements, Yarbus (1967) was the first to show that observers look at a scene in very different ways, according to the task requirements. Yarbus asked his participants to observe a painting, and instructed them to provide judgements about the scene, to remember different aspects of it, or to watch it freely. Results showed clear task-related differences in the scanpaths employed; these findings have since been replicated (e.g., Tatler, Wade, Kwan, Findlay, & Velichkovsky, 2010). Although analysis of scanpaths may not be sufficient to classify the task in which an observer is engaged (Greene, Liu, & Wolfe, 2012), there now is convincing evidence that gaze behaviour is modulated by the instructions provided to the participant, and thus the goal of the observation task, as well as by the type of task (Foerster, Carbone, Koesling, & Schneider, 2011; Hermens, Flin, & Ahmed, 2013).

2.2.1 Gaze behaviour as an index of learning and expertise

The development of head-mounted eye trackers has allowed researchers to examine people's gaze behaviour in natural and dynamic contexts. Studies have shown that, during performance of well-learned actions such as making tea or preparing a sandwich, fixations are always directed on or close to the objects being manipulated, whereas task-irrelevant areas are hardly ever fixated (Hayhoe, 2000; Land, Mennie, & Rusted, 1999). The eyes typically precede the hands, and they shift to the next target before manipulation is complete, or even before hand-target contact (Land, 2009). Fixations serve a number of functions; namely, locating objects, directing hand movements towards them, and supervising completion of the action (Land & Tatler, 2001; Land, 2006). Despite these commonalities, gaze behaviour is modulated by the specific task requirements and characteristics (Hayhoe & Ballard, 2005; Land, 2006). For example, when driving, our gaze is typically directed on or close to the tangent point on the inside of an upcoming bend, so as to extract information about the curvature of the road ahead (Land & Lee, 1994; Land & Tatler, 2001). In contrast, for interceptive sports, performers employ proactive saccades to direct their gaze to the anticipated bounce point of the ball (Hayhoe, McKinney, Chajka, & Pelz, 2012); a short latency of this predictive saccade is associated with good performance (Land & McLeod, 2000). Furthermore, studies have shown that during observation of transitive actions, observers typically employ predictive gaze strategies which resemble those adopted during action execution (Flanagan & Johansson, 2003; Flanagan, Rotman, Reichelt, & Johansson, 2013; Gredebäck & Falck-Ytter, 2015). Thus, effective gaze behaviours play a key role for both perception and performance of visually-guided actions.

Proactive gaze reflects the ability to predict the actions of others, which develops early in life; its emergence is related to infants' motor competencies, in that it develops at the same time as the ability to perform an action (Ambrosini et al., 2013). Observation of actions that do not belong to one's motor repertoire is reflected in reactive, rather than proactive, gaze (Gredebäck & Falck-Ytter, 2015). Effective AO also seems to depend on whether the observer is in a position to perform the action. For example, Ambrosini and colleagues (Ambrosini, Sinigaglia, & Costantini, 2012) found that proactivity of gaze was severely impaired when the observer's hands were tied behind their backs.

When engaged in face recognition tasks, individuals typically direct their initial fixations to an area between the eyes and the tip of the nose, as they have learned that, by fixating on this central region, they extract the maximum amount of information pertaining to the gender, identity and emotional state of the individual (Peterson & Eckstein, 2012). Eye movement strategies are thus the result of extensive experience with the environment, whereby observers learn what information should be selected for further processing (Hayhoe & Ballard, 2005). This notion is consistent with the Information Reduction Hypothesis (Haider & Frensch, 1996; 1999), according to which, skilled performance on a task is reflected in the ability to selectively focus on and process only those sources of information that are relevant to the task while inhibiting processing of irrelevant information. It has been shown that gaze strategies acquired through extensive experience with a task can also be modified through experience. Peterson and Eckstein (2014) presented participants with a face recognition task comprising edited face stimuli for which the mouth was the only distinguishing feature. Through practice on the task, participants gradually shifted their initial fixations away from the central area between the eyes and the nose and towards the mouth, a shift that was reflected in improved performance.

Efficient gaze behaviour appears to be a necessary condition for the achievement of expert performance in rapid visually-directed tasks (e.g., Hayhoe et al., 2012; Land & McLeod, 2000). Skill-related differences in gaze have been reported for many tasks, including driving (Crundall & Underwood, 1998; Land & Tatler, 2001), orienteering (Pesce, Cereatti, Casella, Baldari, & Capranica, 2007), air traffic control (Van Meeuwen et al., 2014), surgery (Hermens et al., 2013) and medical diagnosis (Balslev et al., 2012). Studies have shown that expert performers extract task-relevant information more quickly than novices, and they display more efficient gaze patterns, typically consisting of fewer fixations of longer duration on more targeted areas of the display (Mann, Williams, Ward, & Janelle, 2007). This has been reported in a wide range of sports, including football (Krzepota, Stepinski, & Zwierko, 2016; Savelsbergh, Williams, Kamp, & Ward, 2002), volleyball (Piras, Lobietti, & Squatrito, 2010), judo (Piras, Pierantozzi, & Squatrito, 2014) and karate (Milazzo, Farrow, Ruffault, & Fournier, 2016). However, in some cases, such as during 11-vs-11 football defensive play scenarios, skilled performers employ more fixations of shorter duration, when compared to novices (Roca, Ford, McRobert, & Williams, 2013; A. M. Williams & Davids, 1998). Similar results have also been found in expert dance observers (Stevens et al., 2010). These findings indicate that, through experience with a task, individuals develop the ability to efficiently adapt their gaze patterns to the specific task constraints (A. M. Williams, Davids, Burwitz, & Williams, 1994; A. M. Williams & Davids, 1998; A. M. Williams, 2000). Skilled performance is thus typically reflected in more efficient and flexible gaze, and the specific eye movement strategies adopted depend on the context. For instance, offensive football players exhibit a less exhaustive search of the display compared to defensive players, which reflects the specific requirements of their role and associated constraints (Helsen & Pauwels, 1993). Memmert, Simons and Grimme (2009) investigated the attentional abilities of expert handball players, experts from individual sports, and novices, and reported no differences in general visual attention. Therefore, gaze strategies are largely domain-specific, and the associated perceptual advantage does not transfer to other tasks (van Leeuwen, de Groot, Happee, & de Winter, 2017).

In aiming tasks, accurate performance is associated with a final target-directed fixation of long duration immediately preceding movement initiation, a phenomenon known as *quiet eye* (QE: Vickers, 1996). The QE typically lasts a minimum of 100 ms, during which gaze remains fixated on a specific location or object, within 1-3 degrees of visual angle (Vickers, 2016). Studies have shown that expert performers in interceptive and aiming sports such as basketball (Vickers, 1996), darts (Rienhoff et al., 2013), shooting (Causer, Bennett, Holmes, Janelle, & Williams, 2010), table tennis (Rodrigues, Vickers, & Williams, 2002), and football (Piras & Vickers, 2011) exhibit longer QE durations compared to novices (for a recent review, see Gonzalez et al., 2017). Furthermore, QE duration can distinguish successful from unsuccessful attempts (A. M. Williams, Singer, & Frehlich, 2002), and it can predict catching ability in children (Wilson, Miles, Vine, & Vickers, 2013). These findings provide considerable evidence for a perceptual advantage in expert performers, further supporting the notion that eye movements are an index of cognitive processing, attentional allocation and information extraction (Mann et al., 2007).

Perceptual ability is clearly related to successful performance in many fast-paced visually directed tasks. This has raised the possibility that we might accelerate the development of skilled performance by training novices to adopt expert-like gaze behaviours. Attempts to shorten the long road to expertise through perceptual training techniques have been made in multiple domains and have at times been successful in enhancing performance. Researchers have shown that perceptual training can effectively aid anticipation skills in badminton players (Hagemann, Strauss, & Canal-Bruland, 2006) and footballers (Savelsbergh, Van Gastel, & Van Kampen, 2010). Attentional guidance based on experts' gaze has also been shown to facilitate novice marine biologists' identification of fish locomotion pattern (Jarodzka, van Gog, Dorr, Scheiter, & Gerjets, 2013). In medical training, perceptual training involving visual guidance has been found to improve performance in a laparoscopy task (Chetwood et al., 2012) and diagnostic performance in novice radiographers (Litchfield, Ball, Donovan, Manning, & Crawford, 2010). However, although visual attentional strategies can be modified through perceptual training, this does not necessarily translate to performance improvements. For example, Panchuk, Farrow and Meyer (2014) reported that QE training effectively increased the duration of participants' final fixation on the target, but no corresponding improvements in golf putting performance emerged. Similarly, perceptual training was effective in modifying novice footballers' gaze behaviour during a football anticipation task, but this did not correspond to improved anticipation performance (Bishop, Kuhn, & Maton, 2014).

These discrepancies suggest that perceptual training programmes present a number of issues that may prevent their effectiveness. Firstly, training based on the eye movements of one expert, or on an average of several experts' gaze patterns, may not be ideal, as evidence suggests that experts' gaze patterns are more heterogeneous than those of novices (Robinski & Stein, 2013). This raises the question of what patterns should be selected to guide learner's gaze, or of what represents an ideal gaze strategy to teach novices. This is further complicated by the presence of individual differences in gaze, as eye movement patterns are inherently idiosyncratic (e.g., Greene et al., 2012). In visually-guided tasks requiring fast interaction with external stimuli, a specific type of gaze behaviour may allow information extraction in one trial, but it may not be sufficient for effective information pickup in the next trial; for example, due to movement variability. Therefore, it is possible that, by showing novices a variety of gaze exemplars, we may yield more benefits for performance (Dicks, Button, Davids, Chow, & Kamp, 2017). This would be consistent with findings from the observational learning literature – namely, that learners benefit more from viewing a combination of expert and novice models compared to either model type alone (Andrieux & Proteau, 2014). Individual preferences are also a key factor to be addressed, as there is evidence that instructing participants to adopt a visual search strategy different from their preferred one can actually impair their performance (J. G. Williams, 1987).

Perceptual training that is based on cueing of relevant areas presents two additional problems. First, many authors failed to record participants' gaze during training, and so it cannot be determined whether learners actually attended to the cued areas. In addition, even when cues are effective in guiding the allocation of overt visual attention, merely attending to relevant aspects of an action does not guarantee information pickup and processing (Beanland & Pammer, 2010; Litchfield et al., 2010). Novices may not know how to interpret attended information so as to appropriately respond to it, because they have not accrued the necessary knowledge to do so. As argued by Schuler (2017), "attending to relevant information is a necessary, but not a sufficient prerequisite for learning" (p. 219). It is also possible that, within the context of motor expertise, skilled performers' fixations may not be directed to the most information-rich regions of the display, but rather to areas which facilitate the processing of information in peripheral and parafoveal areas (e.g., Hagemann et al., 2006; Schorer, Rienhoff, Fischer, & Baker, 2013). Covert attentional shifts may be beneficial not only because they can prevent the loss of information inherent in saccadic eye movement, but also because they allow us to shift our attention more quickly than overt attentional shifts (A. M. Williams & Davids, 1998). Furthermore, peripheral vision is highly specialised for motion perception (Edwards & Nishida, 2004). Thus, skilled performers may be better at 'anchoring' their vision on a region that allows them to distribute their attention according to the requirements of the task.

The degree to which peripheral information is processed during fixation has not been thoroughly explored in sport; however, there are some exceptions. For instance, Rienhoff, Baker, Fischer, Strauss and Schorer (2012) tested the degree of central versus peripheral processing during QE in dart throwing, and found that occluding central parts of the display did not affect performance. In a later study, Schorer et al. (2013) analysed the relative contributions of foveal and peripheral vision to the anticipation of opponents' attacking position in volleyball, and found that, for experts, the sum of both fields of vision was superior to either source in isolation. Finally, in chess, superior performance is attributed to the use of not only foveal, but also peripheral, vision (Reingold, Charness, Pomplun & Stampe, 2001). This suggests that, even in relatively static contexts, peripheral vision may play a greater role than is commonly thought. In fact, whereas it is true that overt attention can facilitate visual processing by increasing acuity, covert attention – and thus peripheral vision – may suffice in situations where visual acuity is not needed (Beanland & Pammer, 2010).

2.3 The Mirror Neuron System

During the early 1990s, while investigating the neural correlates of action execution in the macaque monkey, di Pellegrino and colleagues discovered a class of neurons, in area F5 (ventral premotor cortex), which fired both when the monkey executed a range of actions and when it observed the same actions performed by either the experimenter or another monkey (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). These neurons were later termed *mirror neurons* (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996), and there now is direct evidence that they are also present in the human brain (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). Mirror neurons resonate with an observed action, whereby their response is also known as *resonance behaviour* (Rizzolatti, Fadiga, Fogassi, & Gallese, 1999), or *motor resonance* (e.g., Rizzolatti & Craighero, 2004; Watkins, Strafella, & Paus, 2003). Since their discovery, mirror neurons have stimulated a lot of research interest. Using a range of techniques and methodologies, researchers have considerably furthered our understanding of these cells and the various functions that they subserve.

The electrophysiological correlates of the mirror response have been explored using EEG and cellular recordings. Such investigations have shown that, in humans, AO is reflected in desynchronization of alpha (8-13 Hz) frequency range brain oscillations – i.e., the *mu rhythm* – recorded from central, frontal and parietal sites (Avanzini et al., 2012; Cochin, Barthelemy, Roux, & Martineau, 1999). EEG studies have shown that AO-induced desynchronization is present from infancy (Marshall, Young, & Meltzoff, 2011), and have helped to clarify the specific properties of mirror neurons, which determine the way in which they respond to AO. This, in turn, has helped to elucidate the specific mechanisms underlying the mirror response and their functions. Using intracellular recordings in monkeys, Gallese and colleagues (Gallese et al., 1996) were able to identify two main types of mirror neurons: *strictly congruent* neurons only fire when the observed and executed action are identical, both in terms of the goal and of the way in which this goal is achieved (e.g., grasping using a precision grip), whereas the majority of *broadly congruent* mirror neurons also discharge when the observed and executed action differ in terms of the effector used to achieve the goal. Caggiano and colleagues (2011) recorded the activity of macaques' F5 mirror neurons as they observed movies of grasping actions viewed from different perspectives. The majority of tested neurons were found to be sensitive to specific points of view; the remaining neurons (26%), in contrast, showed similar activity regardless of visual perspective. These findings were interpreted as evidence that different types of mirror cells subserve different functions. Broadly congruent and view-independent mirror neurons are involved in the coding of action goals, irrespective of the visual or motor details of the observed actions. In contrast, view-dependent and strictly congruent mirror neurons may be responsible for coding more specific and higher order aspects of a motor act, such as movement direction or invariant configurations between the effectors of a movement (Gallese et al., 1996), or the specific relationships between the pictorial aspects and the goal of the action (Caggiano et al., 2011). Studies on humans (Mukamel et al., 2010) and non-human primates (Kraskov, Dancause, Quallo, Shepherd, & Lemon, 2009) have also identified a class of mirror-like cells that exhibit opposite responses to those of typical mirror neurons: they discharge during action execution, but show complete suppression of activity during observation of the same actions. These *suppression* mirror neurons may be involved in inhibiting unwanted overt production of movements during AO, and in distinguishing between others' actions and those of the self (Kraskov et al., 2009; Mukamel et al., 2010).

Using brain imaging methods such as functional magnetic resonance imaging (fMRI) or positron emission tomography (PET), researchers have identified a parieto-frontal mirror neuron system, or MNS, in humans (for reviews on the MNS, see Fabbri-Destro & Rizzolatti, 2008; Rizzolatti & Sinigaglia, 2010; and Rizzolatti & Sinigaglia, 2016). Passive observation of actions leads to increased activity in a number of ventral premotor and inferior frontal cortical areas, including the left inferior frontal gyrus (in particular Brodmann's area 45, the human homologue of area F5), the rostral part of the inferior parietal lobule, and the superior temporal sulcus (Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Iacoboni, 2005; Rizzolatti et al., 1996; Rizzolatti, Fogassi, & Gallese, 2001). As well as contributing to our understanding of the areas comprising the human MNS, or *action-observation network* (AON, e.g., Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009), imaging studies have also revealed that the specific functional role of this network seems to depend on its anatomical location (e.g., see Fabbri-Destro & Rizzolatti, 2008; and Rizzolatti & Sinigaglia, 2016). Finally, the neurophysiological correlates of motor resonance have been studied using transcranial magnetic stimulation (TMS) in conjunction with electromyography (EMG) recordings. This technique involves delivering TMS pulses to primary motor cortex (M1) and recording the TMS-evoked responses from the contralateral muscles. The amplitude of these responses – the motor evoked potentials (MEPs) – reflects the degree of corticospinal excitability (CE), which is taken as a neurophysiological index of motor resonance (see, e.g., Hallett, 2007, for an introduction on TMS methods). TMS studies have helped elucidate the characteristics of the motor resonance response and have furthered our understanding of the various functions that it may fulfil.

Motor resonance has been shown to be finely tuned to the observed action. For instance, excitability changes during AO are typically restricted to the muscles involved in the action, and they are time-locked to the onset and kinematic components of the action (Borroni & Baldissera, 2008; Gangitano, Mottaghy, & Pascual-Leone, 2001; Gangitano, Mottaghy, & Pascual-Leone, 2004; Montagna, Cerri, Borroni, & Baldissera, 2005). Thus, the pattern of corticospinal facilitation recorded from the muscles involved in an observed action closely resembles the pattern of muscle activation during action execution. Alaerts and colleagues (Alaerts et al., 2010) 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. In addition, weight-induced modulations of MEP amplitudes are present even when the target object is hidden from view (Valchev et al., 2015). These results indicate that motor resonance is sensitive to subtle aspects of an observed action such as the degree of muscular force required to perform that action.

There is evidence that motor resonance is also involved in the encoding of action goals (Braukmann et al., 2017). For instance, facilitation of M1 excitability and of the short-latency connections linking key areas of the MNS with M1 is elicited by observation of transitive actions performed with a hand posture congruent with the goal of the action. However, no such modulations occur when the actor’s hand posture is incongruent with the action goal (Koch et al., 2010). In a related manner, observation of actions performed with unusual effectors induces corticospinal facilitation also in the muscles which are typically used to perform the action. Senna, Bolognini and Maravita (2014) showed that amplitudes recorded from the hand muscles were facilitated by observation of a grasping action performed with a foot; similarly, observation of a hand pressing a foot pedal elicited facilitation in the foot muscles. These findings suggest that action coding may involve two different processes: a somatotopic coding which strictly reflects the kinematic profile of the observed action, and a higher-order coding of the action goal based on the observer's motor experience (Senna et al., 2014).

Motor resonance is modulated by the observer's experience and familiarity with an action. EEG studies have shown that, in infants, the amount of mu desynchronization depends on the infant's motor competencies (Cannon et al., 2016). For instance, mu desynchronization was found in 14-16 month-old infants during viewing of crawling but not of walking, and the strength of this response was strongly related to the infant's own crawling experience (van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008). Hence, the MNS seems to selectively respond to actions that already belong to an observer's motor repertoire, whereby motor resonance could be regarded as an index of the observer's ability to perform an action. Further support for this notion comes from an earlier study by Buccino and colleagues (Buccino, Lui et al., 2004). In this experiment, participants observed mouth actions (i.e. speech reading, barking and lip-smacking) performed by humans, dogs and monkeys. Buccino and colleagues showed that observation of speech reading by a human and lip-smacking by a monkey elicited activation in areas part of the AON (including the IPL, the pars opercularis of the IFG and the ventral premotor cortex). In contrast, no motor resonance was found during observation of a dog barking – an action outside of the observers' motor repertoire.

Studies of the neurophysiological correlates of skilled performance suggest that expertise-related differences in MNS activity are largely domain-specific. For instance, observation of dance movements elicits stronger mu desynchronization in expert dancers than it does in dance novices, whereas no such differences emerge during viewing of everyday movements (Orgs, Dombrowski, Heil, & Jansen-Osmann, 2008). Similar findings have been reported in imaging studies (Cross, Hamilton, & Grafton, 2006; Pilgramm et al., 2010), which have shown that dance expertise is reflected in stronger activation in a number of areas of the AON. Expertise-dependent modulations of motor resonance are related to individuals' motor experience with an action, rather than to their visual familiarity with them (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006). Skill-related differences in motor resonance have been reported also in hockey players (Wimshurst, Sowden, & Wright, 2016), professional pianists

(Haslinger et al., 2005), expert ball jugglers (Tsukazaki, Uehara, Morishita, Ninomiya, & Funase, 2012), and expert badminton players (M. J. Wright, Bishop, Jackson, & Abernethy, 2011). Importantly, the stronger mirror response exhibited by experts is maintained even when the viewed action is reduced to its kinematic components – as in the case of point-light displays (M. J. Wright et al., 2011).

2.3.1 Mirror-based accounts of action understanding

The above findings suggest that a primary role of the MNS is that of understanding the actions and intentions of others. This is the core notion underlying a number of conceptualisations of the processes involved in action understanding. These accounts, such as the direct-matching theory of action understanding (Iacoboni et al., 1999; Rizzolatti & Sinigaglia, 2010), or the common coding principle (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Prinz, 1990), posit a close coupling between action perception and action production, which are regarded as sharing a common neural substrate[2]. The mirror mechanism, whereby AO recruits the same motor representations that are involved in action production, can be regarded as a form of visuo-motor matching process. This mechanism is responsible for mapping observed actions onto the observer's motor repertoire, and it therefore translates visual information into motor knowledge (Decety & Grèzes, 1999; Rizzolatti & Sinigaglia, 2010). Through the activity of the AON, individuals can recognise the actions and intentions of others, they can imitate these actions, and they can predict their goals. In support of these claims, observational learning has been shown to recruit a number

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[2] It has been suggested that motor imagery (MI), which refers to the mental simulation of a movement without overt movement production, also shares a common neural substrate with action observation (e.g., Grèzes & Decety, 2001; Jeannerod, 2001). Engaging in MI of an action has been shown to activate similar areas to those recruited by action perception and action production (Lacourse, Orr, Cramer, & Cohen, 2005). Like AO, MI modulates CE in a way that dynamically mimics the changes occurring during movement execution (Fadiga et al., 1999; Fourkas, Avenanti, Urgesi, & Aglioti, 2006), and it produces similar autonomic responses (Decety, 1996; Pfurtscheller & Neuper, 1997). The mental simulation of actions thus relies on the activation of the same motor representations which are involved in action perception and execution. Accordingly, motor imagery has been demonstrated to enhance learning and performance improvements, with some authors reporting that mental simulation of a task can be as effective as physical practice (Helene & Xavier, 2006). A thorough review of MI processes and their neurophysiological correlates is beyond the scope of the present work. For relevant papers and reviews on the topic the reader is referred to Holmes and Calmels (2008), Causer, McCormick and Holmes (2013), Gatti et al. (2013) and Di Rienzo et al (2016).

of areas that comprise the AON (Buccino, Vogt et al., 2004), and to lead to learning-related changes in the brain which resemble those resulting from physical practice (Stefan, Classen, Celnik, & Cohen, 2008). The visuomotor matching process can occur automatically, without the recruitment of higher-order cognitive processes (Barchiesi & Cattaneo, 2013; Uithol, van Rooij, Bekkering, & Haselager, 2011).

From a theoretical standpoint, the notion of motor representations of actions is consistent with social-cognitive accounts of observational learning. According to such accounts, effective learning via observation requires learners to attend to key features of an action; the cues that are attended to during the skill acquisition phase are then coded to form a mental representation of the movement that is retained for later reproduction of the action (e.g., Bandura, 1986; 2001). Research on observational learning has shown that directing learners' attention to key aspects of a modelled action can facilitate observational learning of motor skills (Janelle et al., 2003; McCullagh et al., 1990; McCullagh et al., 1989; Meaney, 1994). This finding can be explained by taking into consideration the activity of the MNS. By directing learner's attention to important aspects of an observed action, we can facilitate pickup of information pertaining to these features. Considering that the MNS is responsible for translating visual information into motor representations of actions, by facilitating information pickup we may also facilitate accurate mapping of the key features of the action into the observer's motor repertoire. There is evidence that the extent of activation of the motor representations corresponding to an observed action is related to the observer's ability to perform that action (Buccino et al., 2004; Calvo-Merino et al., 2005; Calvo-Merino et al., 2006; Cross et al., 2006). Therefore, a more complete and accurate motor representation would be expected to reflect the acquisition of a movement pattern that closely matches the characteristics of the observed action.

Mirror-based accounts of action understanding have received a number of criticisms. For example, the fact that individuals can understand actions that they cannot perform (Buccino et al., 2004) might suggest that the mirror response cannot be the mechanism at the core of action understanding, and that this function must rely on other inferential processes (Wood & Hauser, 2008). However, the ability to recognise actions that do not belong to the observer's motor repertoire can be explained by the activity of broadly congruent mirror neurons, which generalises to the goal of the action irrespective of the effector (Rizzolatti & Sinigaglia, 2010). Other authors have argued that AO-induced modulations in the activity of the motor system may represent a consequence, rather than a cause, of action observation, and that action understanding relies on systems other than the AON (e.g., Csibra, 2007;

Hickok, 2009). However, there is evidence of a mutual relationship between action perception and action production; for instance, perception of movements performed by a human actor impairs the simultaneous production of incongruous movements (Kilner, Paulignan, & Blakemore, 2003), and motor impairments are correlated with impairments in action recognition (Pazzaglia, Pizzamiglio, Pes, & Aglioti, 2008). In addition, direct evidence of the MNS involvement in action recognition processes comes from a recent study by Jacquet and Avenanti (2015), who showed that disruption of activity in inferior frontal cortex – a key component of the AON – reduced performance on a grip categorisation task. Finally, Hickok (2009) questioned the role of mirror neurons for imitative learning, arguing that monkeys have a very limited ability to learn by imitation despite the presence of mirror neurons in their brain. However, human beings' superior ability to learn by observation can be explained by the fact that the human MNS is more sophisticated than that of the monkey (Buccino et al., 2004); for example, it responds to the observation of intransitive movements as well as transitive actions (Maeda, Kleiner-Fisman, & Pascual-Leone, 2002; Patuzzo, Fiaschi, & Manganotti, 2003), and it also encodes the temporal aspects of actions (Gangitano et al., 2001) – properties which the monkey MNS does not possess.

Therefore, despite the criticisms outlined above, there now is compelling evidence that the MNS plays a key role in action perception and understanding (e.g., see Avenanti, Candidi, & Urgesi, 2013, for a review). There is general agreement that AO represents an embodied process (Gredeback and Falck-Ytter, 2015), whereby mirror-based action understanding can be thought of as *understanding from the inside* (Rizzolatti & Sinigaglia, 2010; and 2016). A number of findings suggest that the MNS may also be involved in other higher-order cognitive processes which are not directly related to motor production, such as language comprehension, emotion recognition and empathy. For example, listening to action-related sentences or sounds activates parts of the visuomotor circuits subserving action execution and observation (Aziz-Zadeh, Iacoboni, Zaidel, Wilson, & Mazziotta, 2004; Tettamanti et al., 2005). This is consistent with the discovery of a class of *audiovisual mirror neurons* in area F5 of the monkey brain, which discharge not only during action perception and performance, but also in response to action-related sounds (Kohler et al., 2002). As argued by Kohler et al., since these cells are located in the monkey homologue of Broca's area, they may be related to the origins of language, as they code abstract contents such as action sounds, and – like human language – they can access this content. Accordingly, perturbation of the speech motor area during speech perception has been shown to impair speech recognition (Meister, Wilson, Deblieck, Wu, & Iacoboni, 2007). Finally, the involvement of the MNS in imitation, emotion recognition and empathy is supported by studies of individuals with autistic spectrum disorder, which is characterised by impairments in imitation and social-communicative interaction (Lord, Cook, Leventhal, & Amaral, 2000). These individuals exhibit reduced motor facilitation during the observation of actions (Théoret et al., 2005) or emotional facial expressions, and the severity of the disorder is negatively correlated with activity in MNS areas (Dapretto et al., 2006).

2.3.2 Motor resonance, gaze and attention

As stated above, attentional allocation and abilities play a fundamental role for the effective extraction and processing of visual information. Therefore, an important issue that needs to be addressed is whether visual attentional processes may also modulate the mirror response during action observation, consistent with the existence of gaze-dependent mirror neurons in monkeys (Maranesi et al., 2013). Behavioural evidence suggests that spatial attention may indeed be fundamental for visuomotor matching processes. For instance, the action priming effects which result from AO are eliminated if visual attention is directed away from the effector of the action (e.g., Bach, Peatfield, & Tipper, 2007). Despite the existing wealth of research on motor resonance, however, the role that attention plays in the covert activation of the motor system has not been thoroughly explored to date. Studies that have explored the relationship between attentional processes and motor resonance have at times yielded contrasting results. For instance, Leonetti and colleagues (Leonetti et al., 2015) reported that presenting actions in the peripheral visual field resulted in a degradation of the motor resonance response, in that AO-induced facilitation lost its muscle-specificity. This suggests that point-of-gaze, and thus overt visual attention, may be necessary for accurate mapping of a viewed action into one’s own motor repertoire.

However, other studies suggest that directing gaze to the action may not be sufficient to elicit activation of the same motor representations involved in the action. Chong and colleagues (Chong, Williams, Cunnington, & Mattingley, 2008; Chong, Cunnington, Williams, & Mattingley, 2009) showed participants videos and static images of reaching and grasping actions. At the same time, participants performed an attentionally demanding task which required them to attend to a frame located in the middle of the screen and to judge the relative sizes of gaps that appeared to the sides of this central frame. Chong and colleagues reported that, by detracting participants’ covert attention away from the action, activation in MNS regions was reduced, despite the fact that the target stimulus for the attentional manipulation task spatially overlapped the action. Similar results were later reported by Betti, Castiello, Guerra and Sartori (2017). In addition, motor resonance is reduced during viewing of actions that are not relevant to the observation task (Chong et al., 2009; Puglisi et al., 2017). These findings thus suggest that the allocation of covert attention may also play a key role in determining motor resonance during AO.

These studies represent some initial attempts to elucidate how overt and covert visual attention modulate the neural correlates of AO. However, problematically, the TMS studies on AO that have been conducted to date have failed to include simultaneous recordings of participants' eye movements and MEPs, whereby the specific contributions of gaze to motor resonance remain to be determined. Preliminary evidence, however, suggests that the way in which we observe an action may indeed affect the extent of covert motor activation (Donaldson, Gurvich, Fielding, & Enticott, 2015; Leonetti et al., 2015), Therefore, the relationship between motor resonance, gaze and attention warrants further investigation.

2.4 Rationale for the Present Work

The concepts reviewed in this chapter highlight the importance of action observation for the learning of novel skills and the re-learning of previously acquired motor skills. Demonstrations represent one of the most commonly used methods for the teaching of novel motor skills, and observation-based approaches are also being used as an adjunct to traditional motor rehabilitation following motor impairment. Despite this, such approaches often present a number of issues that may prevent effective learning by observation. For instance, observational learning tasks can impose high attentional demands on the learners, who are required to attend to and process relevant aspects of the action, in order to then reproduce the observed behaviour. In addition, the issue of whether learners actually look at task-relevant areas has largely been neglected. The evidence presented above suggests that point-of-gaze and attentional allocation may determine the extent to which the observer's motor system is recruited during action observation – but this proposition needs to be tested further.

The present body of work was designed to investigate the relationship between overt visual attention – as indexed by point-of-gaze – and information pickup during action observation. Specifically, a first aim was to determine whether, by directing learners' attention to relevant aspects of an observed complex action, we could facilitate processing of task-relevant information and improve observational learning (Study 1). Having established that visual attentional guidance can indeed accelerate observational learning of a novel motor skill, the aim of the remaining studies (Studies 2, 3 and 4) was to explore the neurophysiological mechanisms underlying this effect. To this end, we employed a novel technique involving the combination of TMS and eye tracking, which allowed us to determine, on one hand, where learners direct their attention during AO, and on the other hand, whether and how gaze behaviour modulates the motor system's engagement with an observed action.

Investigating the relationship between gaze and mirror activity is key for determining what types of gaze behaviour are more likely to lead to effective pickup and processing of relevant information. This, in turn, will have implications for AO-based protocols in sports and beyond.

2.5 TMS Methods

In Studies 2, 3 and 4, the experimental protocol employed involved the combination of eye tracking and single-pulse transcranial magnetic stimulation (TMS). TMS is a non-invasive brain stimulation technique which is based on the principle of electromagnetic induction. The TMS stimulator produces an electrical current, which passes through a coil of wire; this generates a magnetic field which typically lasts about 100 μs. An electric field is induced perpendicular to the magnetic field, which briefly activates the brain region below the coil. When the TMS pulse is delivered over the primary motor cortex (M1) – as was the case in the present programme of research – it produces a brief focal response in the muscle corresponding to the targeted area. This response is known as the motor-evoked potential, or MEP. By using EMG recordings to measure the amplitude of the TMS-induced MEPs, it is possible to gauge the level of excitability of the corresponding area of M1 at a specific point in time. For this reason, TMS is widely used to investigate changes in corticospinal excitability elicited by the observation of others' actions.

Compared to other neurophysiological and neuroimaging methods that are commonly employed for investigating neural activity, TMS presents a number of advantages. For instance, EEG allows us to measure neuronal activity directly, and has excellent temporal resolution, but its spatial resolution is poor and there is a high degree of noise, which can make the interpretation of the results difficult. In contrast, functional neuroimaging methods such as fMRI and PET have very high spatial localisation but poor temporal resolution. TMS represents a valid alternative to the above techniques: although its spatial resolution is not as high as that of fMRI, its temporal resolution is good and, provided that the processing and the analysis of the EMG signal are performed in a rigorous manner, the interpretation of the results is relatively straightforward. In addition, the costs involved in conducting TMS research are considerably lower than those imposed by other techniques, whereby TMS can be regarded as a useful complement to other neuroimaging and neurophysiological methods.

There are a number of issues that need to be taken into consideration when conducting TMS studies. In first place, the type of TMS coil used determines the focality and the depth of the resulting electrical field, and thus the specific physiological effects resulting from the stimulation (Deng, Lisanby, & Peterchev, 2013; Klomjai, Katz, & Lackmy-Vallée, 2015). Figure-of-8 coils are formed by a pair of adjacent circular loops, with current flowing in opposite directions. Such coils produce a focal electrical field, which is maximal at the point of intersection between the two loops. Therefore, these coils enable us to investigate corticospinal activity of fine-grained cortical representations of, for example, hand muscles. In contrast, circular coils induce a non-focal ring-shaped electrical field that aligns with the coil perimeter, potentially stimulating a large number of brain regions below the coil. Circular coils are thus more suited to stimulation of larger motor areas, such as those controlling the upper limbs (Klomjai et al., 2015).

It should be noted that, when the TMS pulse is delivered, the coil emits a clicking noise which is clearly audible to the participant. This represents an additional caveat for TMS studies: if the TMS pulses are delivered at regular intervals, then the clicking noise associated with them may cue participants to the onset of the stimulation. This, in turn, may cause participants to tense their muscles in preparation for the stimulation, which would affect the amplitude of the resulting MEPs. When designing TMS protocols, researchers should take steps to avoid cueing the participant to the onset of the TMS pulses and therefore reduce the degree of anticipation of each stimulation. In the present programme of research, this was done by using pseudo-random time intervals for the delivery of the pulses, thus minimising the likelihood that the noises would act as auditory cues.

2.5.1 Innovating TMS research: the use of simultaneous eye tracking

A main contribution of the present work to the existing body of knowledge can be found in the experimental protocol employed in Studies 2, 3 and 4. In these studies, we combined the use of TMS with that of eye tracking, recording participants' eye movements while they completed the TMS protocol. Although both of these techniques are widely used within research, they had never been employed simultaneously previous to the present programme of research. This is surprising, especially considering recent findings which suggest that visual attention may play a key role in the covert simulation of others' actions (e.g., Bach et al., 2007; Leonetti et al., 2015). The technical problems involved with combining eye tracking and TMS may in part explain why this approach had never to date been adopted within research. For instance, if the camera of the eye tracker is too close to the TMS coil, the magnetic pulse may result in damage to the eye tracker. However, this problem can be circumvented by employing a remote eye tracking system – as was the case in the present studies – or a head-mounted system in which the camera is sufficiently removed from the TMS coil so as not to be damaged by the magnetic pulses.

The combination of eye tracking and TMS provides us with unique advantages that extend beyond those that can be achieved with the use of each method alone. Firstly, the delivery of the TMS pulses can be triggered via the eye tracking software. This allows us to accurately synchronise each pulse with the presentation of visual stimuli, and therefore with the onset of specific phases of the actions displayed. In addition, by simultaneously recording gaze and MEPs, it is possible to map the location and the characteristics of the participant's eye movements onto the amplitude of the MEPs recorded at specific points in time.

2.6 References

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3 Chapter 3:

Study 1. Looking to learn: The effects of visual guidance on observational learning of the golf swing

DOI: 10.1371/journal.pone.0155442

3.1 Abstract

Skilled performers exhibit more efficient gaze patterns than less-skilled counterparts do and they look more frequently at task-relevant regions than at superfluous ones. We examine whether we may guide novices' gaze towards relevant regions during action observation in order to facilitate their learning of a complex motor skill. In a Pre-test-Post-test examination of changes in their execution of the full golf swing, 21 novices viewed one of three videos at intervention: i) a skilled golfer performing 10 swings (Free Viewing, FV); ii) the same video with transient colour cues superimposed to highlight key features of the setup (Visual Guidance; VG); iii) or a *History of Golf* video (Control). Participants in the visual guidance group spent significantly more time looking at cued areas than did the other two groups, a phenomenon that persisted after the cues had been removed. Moreover, the visual guidance group improved their swing execution at Post-test and on a Retention test one week later. Our results suggest that visual guidance to cued areas during observational learning of complex motor skills may accelerate acquisition of the skill.

3.2 Introduction

Action observation (AO) represents one of the primary ways through which individuals acquire novel skills (Carroll & Bandura, 1987). Research has shown that observing the actions of others can effectively lead to long-term changes in the observer's behaviour. For instance, observation of an actor responding to a sequence of stimuli has been found to result in immediate, short-term learning of the observed sequence (Horvath, Gray, Schilberg, Vidrin, & Pascual-Leone, 2015) and the volume of learning accrued through action observation can be comparable to that achieved through physical practice alone (Boutin, Fries, Panzer, Shea, & Blandin, 2010). Demonstrations are widely used in the context of motor skill acquisition (Williams & Hodges, 2005). Researchers have demonstrated the effectiveness of AO for the learning of complex motor skills including ballet (Gray, Neisser, Shapiro, & Kouns, 1991), volleyball (Weeks & Anderson, 2000), football (Horn, Williams, & Scott, 2002), cricket bowling (Breslin, Hodges, & Williams, 2009) and long jumping (Panteli, Tsolakis, Efthimiou, & Smirniotou, 2013). Moreover, action observation has proven to be a useful complement to traditional stroke rehabilitation protocols (Ertelt et al., 2007).

Although AO appears to facilitate learning in a variety of contexts, its effectiveness may depend on the observer's ability to attend to the most informative aspects of the action (e.g. Boucheix & Lowe, 2010). It has been shown that, when confronted with complex sport-specific displays, experts attend to more task-relevant regions than novices do. Moreover, novices tend to be preoccupied with elements that are more visually salient than relevant (e.g. Roca, Ford, McRobert, & Williams, 2011). In observational learning contexts, such ineffective gaze behaviour may prevent or inhibit the acquisition of relevant information. Therefore, by directing the learner's visual attention to task-relevant regions, observational learning of motor skills may be improved (Causer, McCormick, & Holmes, 2013). Accordingly, our aim was to determine whether exogenous guidance may be used to train gaze behaviour during a video modelling intervention, and whether this, in turn, would facilitate novices' observational learning of the golf swing.

Researchers have shown that elite performers tend to exhibit more effective gaze patterns than their novice counterparts (Gegenfurtner, Lehtinen, & Säljö, 2011). Specifically, when trying to anticipate an opponent's next action, someone who is perceptually skilled often requires fewer fixations of longer duration in order to extract task-relevant information – which indicates an underlying efficiency to their gaze behaviour (Mann, Williams, Ward, & Janelle, 2007; Williams & Davids, 1998). Moreover, when compared to less-skilled performers, experts are more adept at ignoring redundant/task-irrelevant stimuli (Balslev et al., 2012; Jarodzka, Scheiter, Gerjets, & van Gog, 2010). Such efficiencies are typically borne out of considerable practice (e.g. Gegenfurtner et al., 2011; Peterson & Eckstein, 2014). Skill-based differences in gaze behaviours have been demonstrated in contexts other than sport, including air traffic control (Van Meeuwen et al., 2014), driving (Chapman & Underwood, 1998; Crundall & Underwood, 1998), medical diagnosis (Balslev et al., 2012) and surgery (Hermens, Flin, & Ahmed, 2013; Vine, Masters, McGrath, Bright, & Wilson, 2012). Accordingly, there is general agreement in the literature that eye movements are an index of learning and skill acquisition, to the extent that skilled performers' gaze is often highly predictive of anticipated future events (Flanagan & Johansson, 2003; Hayhoe, McKinney, Chajka, & Pelz, 2012; Land, 2009).

One theoretical framework that may explain skill-related differences in gaze behaviour and visual search strategies is the Information Reduction Hypothesis (Haider & Frensch, 1996; Haider & Frensch, 1999). According to this theory, individuals learn through practice to select and process only those sources of information that are relevant to the task at hand, and to ignore or inhibit processing of information that is redundant. Haider and Frensch (1996) presented participants with a task in which they had to verify the correctness of letters and digits strings. A part of the strings was always redundant to the task, but participants were not informed of this fact. After extensive practice, participants learned to select task-relevant letters while ignoring redundant ones, and the learning effect increased with practice on the task. In a later study, Haider and Frensch (1999) recorded participants' eye movements while they performed the same task and found that redundant letters were fixated progressively less with increased training. Accordingly, they concluded that information reduction occurs at the perceptual, rather than conceptual, level of processing.

Such short-term gains in gaze efficiency have been demonstrated for face perception, even when this process requires individuals to modify their pre-existing gaze behaviour. For instance, gaze strategies for face recognition are learned through extensive experience; initial fixations are typically directed to a region between the eyes and the tip of the nose – an optimal fixation point for the task, as it maximises the pickup of information pertaining to the individual's identity, gender, and emotional state (Peterson & Eckstein, 2012). However, when Peterson and Eckstein (2014) presented participants with a face recognition task in which the mouth was the only feature that discriminated different trials, the optimal gaze strategy was to focus on the mouth region. With practice, the majority of participants gradually shifted their initial fixations to the mouth area, which in turn resulted in improvements in recognition performance and processing efficiency.

If, as suggested by the Information Reduction Hypothesis, skill development depends on progressively learning to distinguish and select relevant information, then the question arises as to whether we can accelerate development by directing attention to areas that are task-relevant. This possibility, plus the notion that, with practice on dynamic perceptual tasks, gaze behaviour becomes more predictive and/or selective (Hayhoe & Ballard, 2005), has led to a groundswell of training programmes aimed at accelerating skill acquisition using exogenous attentional guidance. Cueing attention to task-relevant areas can effectively improve perceptuo-motor performance. For example, Singer and colleagues (1994) trained beginner and intermediate tennis players' anticipatory abilities using either physical practice or verbal tips on how to visually identify and interpret key postural cues. Participants who received verbal cues improved their reaction time and decision accuracy, whereas a physical practice group did not; similar results were reported by Williams and colleagues (Williams, Ward, Smeeton, & Allen, 2004). Verbal instructions may also improve novice football goalkeepers' anticipation skill (Shafizadeh & Plat, 2012).

In sport, verbal cueing paradigms have typically comprised explicit verbal instruction and rules, designed to increase participants' knowledge and understanding of relevant aspects of the task (e.g. Shafizadeh & Plat, 2012; Singer et al., 1994). However, high levels of cognitive processing and explicit knowledge of a skill can hinder performance, leading to skill breakdown (e.g. Lam, Maxwell, & Masters, 2009b). In contrast, implicit methods promote learning without a concurrent accumulation of explicit knowledge, yielding greater automaticity during subsequent skill execution (Vine, Moore, Cooke, Ring, & Wilson, 2013; Ward et al., 2008) and more robustness when the individual must perform under pressure (Maxwell, Masters, & Eves, 2000; Rendell, Farrow, Masters, & Plummer, 2011). One method by which we may direct learners' attention to task-relevant regions of a video model without providing explicit information as to why those regions are relevant, is to use exogenous spatial cues. Such cues are highly effective at capturing visual attention in an automatic manner (Koelewijn, Bronkhorst, & Theeuwes, 2009).

There is some evidence to suggest that visual cues can effectively aid perception, and consequently learning, of biological motion. Jarodzka, van Gog, Dorr, Scheiter, and Gerjets (2013) asked participants to view dynamic and realistic videos of fish swimming. Two experimental groups were provided with visual guidance that was based on an expert marine biologist's scanpaths. Specifically, for one group the guidance took the form of a red dot, whereas for the other it was presented as a *spotlight* in which the areas fixated were clearly visible and irrelevant areas were blurred out. A control group viewed the videos without guidance. All videos included a spoken description of the locomotion patterns. Subsequently, participants were shown novel videos of different fish swimming according to the previously learned patterns; they were required to identify the different locomotion patterns by identifying the body part used for propulsion (e.g., tail fin) and the way in which this part moves (e.g., undulation). The two experimental groups exhibited more effective visual search patterns and were consequently able to classify the locomotion of novel stimuli more accurately than were control participants. It is conceivable that visual guidance during observational learning of human movement may be similarly effective – but, prior to the present study, this notion was not empirically tested.

One potential issue with exogenous visual guidance is that it has typically been based on the gaze behaviours of experts (Chetwood et al., 2012; Jarodzka et al., 2013). Since the gaze patterns of experts are more heterogeneous than those of novices, Jarodzka et al. (2010) suggested that, when teaching perceptual strategies to novices, it may be preferable to use the perceptual processes of one expert rather than an average of different experts. However, the nature of the information picked up while fixating is less apparent. Therefore, generic rather than specific forms of visual guidance, designed to increase the salience of task-relevant regions, may be more effective in accelerating novices' information pickup during observational learning.

Increasing the perceptual salience of key information may be beneficial because during observational learning, the various task-relevant features or stimuli are often widely distributed across the visual field. In such cases, consistent with previous research (Williams & Davids, 1998), we would expect expert performers, but not novices, to be able to pick up the relevant information probably through their superior ability to extract information through parafoveal and peripheral vision. Therefore, by cueing visual attention to relevant features (i.e., increasing their perceptual salience) we may prompt novices to broaden their attentional focus and thereby distribute attentional resources more effectively. The above suggestion is consistent with the *zoom lens* theory of attention proposed by Eriksen and St. James (1986), who showed that the breadth of people's attentional focus could be manipulated by precueing different locations within a visual display, at varying degrees of eccentricity (see also Castiello & Umiltà, 1990). The zoom lens model has since been corroborated using fMRI. In a paradigm similar to that used by Eriksen and St. James (1986), Muller, Bartelt, Donner, Villringer, and Brandt (2003) showed that the extent of activation in participants' retinotopic visual cortex increased as they expanded their focus of attention – although the *level* of neural activity in any given sub-region of visual cortex tended to decrease, which is consistent with previously observed reductions in processing efficiency as a function of this ‘zooming out’ (Castiello & Umiltà, 1990; Eriksen & St. James, 1986).

Although researchers have used visual cueing to enhance athletes’ perceptual abilities, the use of such techniques to accelerate observational learning of novel motor skills has largely been neglected. In the present study, we address this issue by investigating the effects of visual guidance on observational learning of the full golf swing. Traditional approaches aimed at developing perceptual skills have involved the direction of attention either via verbal instructions or by the use of an expert model’s scanpaths to guide the observer’s gaze. In contrast, we employed a more generic method of visual guidance, in which experimental participants saw translucent colour patches superimposed over regions of a model golfer’s body and the apparatus (i.e. ball and club), which individually and collectively convey important postural information and spatial relationships for correct setup of the swing. Such implicit methods can arguably be processed in a more automatic and unconscious manner (Ward et al., 2008), thereby reducing the interference of movement execution that occurs under explicit instruction (Hardy, Mullen, & Martin, 2001). Accordingly, since explicit knowledge of the task is not necessary for implicit learning to occur (Hodges & Franks, 2002), we presented visual guides in the absence of any explicit verbal instruction. We predicted that these cues would attract participants’ overt visual attention, thereby enhancing the pickup of important positional information, without imposing an additional cognitive load for the task. Demonstrations have typically benefited movement form and dynamics rather than movement outcomes (e.g., Kernodle, McKethan, & Rabinowitz, 2008). Therefore, we assessed improvements in participants’ swing kinematics, rather than on the outcome of their swing (i.e., whether the ball reached a specified target). We hypothesised that, as a result of increased attention to the cued task-relevant information during observation, participants who undertook visually guided observational learning would improve their swing kinematics relative to a group who received no such guidance (free viewing). Finally, implicit learning of complex motor tasks is widely considered to be superior to explicit learning, because explicit knowledge of the rules governing the motor pattern interferes with movement execution by competing for mental resources (Hardy et al., 2001; Lam, Maxwell, & Masters, 2009a). In contrast, implicitly learned skills are not easily accessible to conscious inspection, are difficult to verbalize and do not place high demands on working memory (Williams & Hodges, 2004); hence, they are more resistant to anxiety and pressure, and less likely to be forgotten (Koedijker, Oudejans, & Beek, 2007; Lam et al., 2009a). Since we did not explicitly instruct the visually guided participants to attend to the visual guides, we predicted that these participants would show performance improvements without a concurrent accumulation of additional explicit rules over-and-above those accrued in the free viewing condition (cf. Abernethy, Schorer, Jackson, & Hagemann, 2012).

3.3 Method

3.3.1 Participants

Twenty-one right-handed healthy adults (9 females and 12 males; *M* age= 25.86 yrs; *SEM* = .38 yrs), with normal or corrected-to-normal vision participated. Fifteen participants had no previous experience of performing a golf swing and were randomly allocated to one of three groups: (i) free viewing (FV); (ii) visually guided (VG); or (iii) a control condition. The remaining six participants had played golf once prior to taking part, and were evenly distributed across the three conditions.

The Brunel University London Ethics Committee approved the protocol and the consent procedure (Appendix B), and the study was conducted in accordance with the ethical standards of the Declaration of Helsinki. Participants gave their written informed consent prior to taking part. Copies of the participant information sheet, informed consent form and demographic information questionnaire can be found in Appendices C and D.

3.3.2 Stimuli and apparatus

Videos of the model (a 25-year-old skilled male golfer with a handicap of 4) were recorded using a Canon HD camcorder, model XF105 (Canon Inc., Tokyo, Japan) and edited using Ulead Video Studio 11 Plus (Ulead Systems Inc., Taipei, Taiwan). Videos displayed a whole-body view of the model from a third-person perspective, with the model facing the participant. Although a first-person perspective may result in faster skill acquisition and better retention (Ste-Marie et al., 2012), such a view would have resulted in considerable loss of pertinent kinematic information.

Participants' eye movements during observational learning were recorded using a portable eye tracking device (Mobile Eye XG, 30Hz, monocular, ASL, Bedford, Massachusetts). Golf swings were performed using a 6-iron club; motor performance (swing execution) was recorded using a 10-camera, 3-D motion capture software at a 150Hz sampling rate (Cortex v.3.6.1.1315, Motion Analysis, Santa Rosa, California). Fifteen reflective markers were placed on anatomical landmarks important for the correct execution of a golf swing (see Figure 3.1); one marker was placed on the club head.

Figure 3.1. Motion capture reflective markers placement.

3.3.3 Procedure

The procedure was verbally reiterated to each participant before they completed a demographics questionnaire. Calibration of the motion analysis system was performed before testing each participant. The participant was given two minutes to write down a set of verbal instructions that they would use if they were to explain the correct execution of a golf swing to a novice. This rule formation task (see Appendix E) was included in order to assess the extent to which participants had developed explicit knowledge of the correct swing execution due to the intervention. The reflective markers were fitted prior to the Pre-test, for which the verbal instructions were as follows: *Please perform 10 full golf swings; your aim is to hit the ball in the direction of the wall while sending it as far as possible.* Because the aim of this study was to determine the effect of a relatively brief intervention, we did not wish to contaminate our data with practice effects. Pilot testing suggested that 10 swings would afford some degree of inter-trial consistency of the swing, while keeping physical practice to a minimum. After completing these swings, participants sat in front of a computer screen. The eye tracking device was calibrated using a 9-point grid displayed on the screen. Following successful calibration of the system the participant viewed one of three videos.

The FV group viewed a video of the model performing ten full golf swings; each swing was separated by a 2 s grey screen. Prior to the video the following instructions appeared: *Please watch the following 10 video clips, in which a skilled golfer will be executing a golf swing. Your aim is to learn about his technique*. VG participants were shown the same video as the FV group, with the exception that they also saw translucent colour patches superimposed on key regions during the setup phase of the swing (e.g., see Figure 3.2). The instructions prior to the VG video were the same as those for the FV video, with the addition of the following sentence: *Some patches of colour will appear on screen in each clip*. Visual guidance was designed to cue participants' overt visual attention to the ball and anatomical regions the relative positions of which are fundamental for achieving the correct setup, as consistently emphasised by golf coaches, instruction manuals and websites (Lamanna, 2016; Redford & Tremayne, 1977). These included: alignment of the head, hands and ball; correct positioning of the ball relative to the feet; an appropriate stance width; and stillness of the head. The control group viewed a video of the history of golf, which contained no reference to the golf swing whatsoever.

After performing ten more full swings (Post-test), participants completed the rule formation task without looking back at their previous answers, in order to assess the extent of explicit rule formation Post-test. Participants' motor performance was tested again after seven days to assess their retention of the skill. For the Retention test, participants performed ten swings in the absence of any demonstration.

Figure 3.2. Sample image taken from the intervention video. Colour patches were superimposed on key features at the setup phase.

3.3.4 Data analysis

3.3.4.1 Gaze data.

Gaze data analyses were conducted using ASL Results Plus (ASL, Bedford, Massachusetts); control participants did not provide eye movement data. Participants' videos were parsed into swing trials and further divided into three phases, according to the amount of motion involved: (1) a static *setup* phase, in which the golfer 'addresses' the ball; (2) a *practice* phase comprising a truncated practice swing, in which the model made minor recalibrations of his positioning; and (3) a *full swing* phase, in which the club head reached speeds of approximately 100 mph. This was done in order to monitor changes in gaze behaviour following the appearance of motion information, as research has shown that motion information automatically attracts visual attention (Mital, Smith, Hill, & Henderson, 2011). Moving areas of interest corresponding to the cued areas were then defined for each file in order to derive eye movement data. Dwell times (in ms) were averaged across phases and divided by the total duration of the phase. The resulting dwell time percentages were imported into statistical analysis software (IBM SPSS Statistics v. 20; IBM, Armonk, NY).

3.3.4.2 Kinematic data.

Participants' kinematics were modelled using Cortex (v.3.6.1.1315, Motion Analysis, Santa Rosa, California). A marker set was created in order to label the markers. A linear interpolation function was used to eliminate gaps in the data. Data were smoothed using a 6 Hz low-pass, Butterworth, zero-phase filter. Processed point-light videos were then collated, and each swing was assigned an arbitrary and unique ID. Visual inspection revealed highest inter-trial variability (predictably) at Pre-test, and that this variability was minimal for the final two swings, for the vast majority of participants. Therefore, for the sake of consistency across sessions (i.e. Pre-test, Post-test and Retention) only data from the final two swings of each testing session were compared. Two PGA-qualified professional golf coaches independently rated each participant's swings at each time point. Specifically, they were asked to provide a numerical rating, on a scale of 1 (very poor) to 10 (excellent), for the participants' setup and swing execution. For the setup, coaches rated the participants' posture (i.e., positioning of head, shoulders and knees), plus the relative alignment of these important anatomical landmarks and the feet. For the swing execution, coaches provided a score for the backswing, the club head position relative to the ball at the point of impact, and the follow-through. These scores were summed to obtain a total *performance score* for each participant. The inter-rater reliability of the coaches' scores was assessed.

3.3.4.3 Rule formation data.

The rules formed by the participants were scored by an expert golfer (handicap of 4) and a professional golf coach, who discussed each rule in detail before arriving at a unanimously agreed score. Each rule was assigned a score from 0 to 3 according to the validity and correctness of the information it contained; invalid or incorrect rules were awarded zero points. The experts agreed that the model's technique represented the benchmark for the highest score, for each of the rules. The validity rating assessed the degree of specificity, correctness and technical detail of the rule. For example, when executing a golf swing, a golf coach will instruct the learner to maintain his or her feet shoulder-width apart. Therefore, inclusion of this rule was assigned the highest possible score of 3. Other rules that referred to the positioning of the feet, however, were only partly correct. For example, "Keep your feet hip-width apart" was assigned a score of 2, as the sentiment is correct, but the anatomical referent is not; "Keep your legs slightly apart" was assigned a score of 1, as it is broadly correct, but without any anatomical referent whatsoever; and "Keep your feet 30 cm apart" was scored as incorrect or invalid (0 points) because it includes misinformation –even to the extent that such instructions could be dangerous (i.e., promoting instability).

For each participant, rule scores were summed in order to derive two separate total scores for, respectively, the number and the validity of rules formed during the Pre- Post- and Retention tests. Swings scores and data from the rule formation task were imported into SPSS for analyses.

3.4 Results

3.4.1 Gaze data

Descriptive statistics are reported in Table 3.1. A Group (FV/VGL) by Phase (Setup/Practice/Full Swing) mixed ANOVA was conducted in order to assess the effects of visual guidance on the total time spent looking at highlighted areas. The interaction between Phase and Group was non-significant, $F(2,24) = .04$, $p = .96$, $\eta_p^2 = .003$. There was a significant main effect of Group, $F(1,12) = 9.47$, $p = .01$, $\eta_p^2 = .44$. Participants in the VG group spent more time looking at the areas highlighted by the visual guides than did FV participants (see Figure 3.3). A significant main effect of Phase was found, $F(2,24) = 6.49$, $p = .006$, $\eta_p^2 = .35$. The dwell time on highlighted areas decreased with the progressing phases of the swing, and thus with the increasing amount of motion information contained in the display. Post-hoc tests revealed that, overall, participants spent significantly more time looking at the highlighted areas during the Setup (static) phase of the swing ($M = 41.23$, $SEM = 3.2$) than during the Full swing (dynamic) phase ($M= 26.01$, $SEM= 3.82$; see Figure 3.4).

Table 3.1. *Dwell Time (%) on highlighted areas – Descriptive Statistics*

Group	Phase	*M*	*SEM*	*SD*	*Min*	*Max*
FV	Setup	34.88	3.74	9.91	21.16	46.15
	Practice swing	29.11	3.04	8.05	20.39	44.43
	Full swing	19.22	4.95	13.09	0.00	40.62
	Overall	27.74	2.49	6.60	19.62	40.18
VG	Setup	47.58	5.19	13.73	22.99	59.92
	Practice swing	40.35	3.59	9.50	29.59	59.05
	Full swing	32.81	5.82	15.39	8.59	50.00
	Overall	40.25	3.21	8.49	24.87	51.19

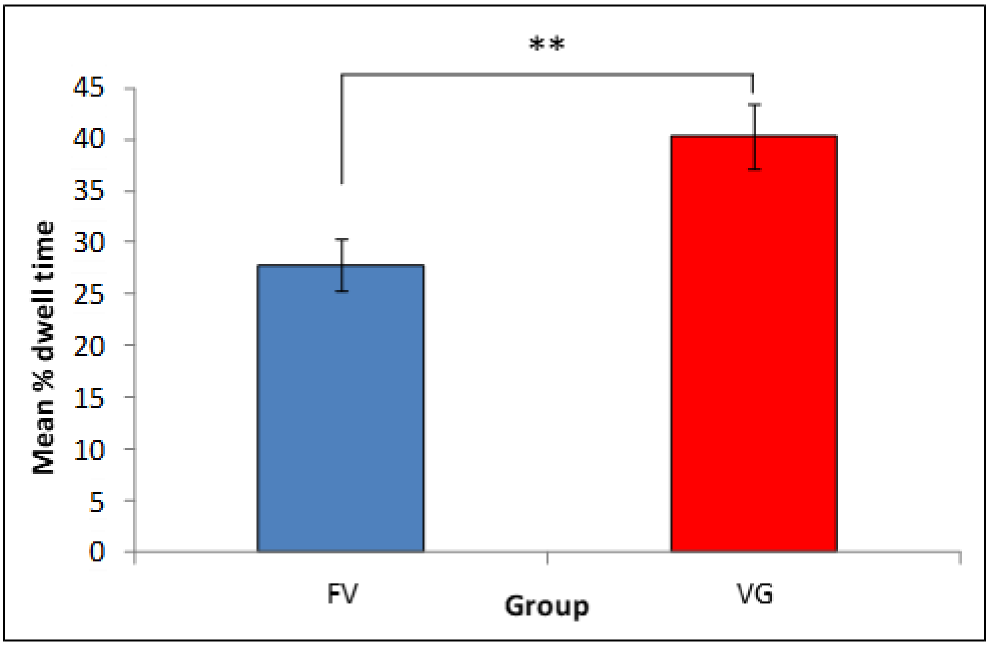

Figure 3.3. Mean percentage of dwell time on highlighted areas, by Group. Error bars represent standard error of the means; ** $p = .01$.

3.4.2 Swing execution

Descriptive statistics are reported in Table 3.2. A reliability analysis revealed a high consistency between the scores provided by the two coaches, *Cronbach's* $\alpha = .78$; discrepancies between the coaches' scores were found to be very minor and random. These scores were then averaged so as to obtain a single score for each participant's swing execution in the Pre-, Post-, and Retention tests; analyses were performed on these scores. For the swing scores at Retention, the variances between the three groups were unequal, $F(2,18) = 3.72$, $p = .045$. Moreover, the FV group's scores for Retention were not normally distributed, $D(7) = .31, p = .041$. In order to correct for the absence of normality, a square transformation was applied to all averaged swing scores.

A Group (FV/VG/Control) by Time (Pre-test/Post-test/Retention test) mixed ANOVA was conducted to assess the effects of the intervention on motor performance (see Figure 3.5). There was a significant main effect of Time, $F(2,36) = 5.70, p = .007, \eta_p^2 = .24$, and a significant Time x Group interaction, $F(4,36) = 2.78, p = .04, \eta_p^2 = .24$. The main effect of Group was not significant, $F(2,18) = 1.56, p = .24, \eta_p^2 = .29$. Contrasts revealed between-group differences in the changes from Pre-test to Post-test, $F(2,18) = 5.80, p = .01, \eta_p^2 = .39$. Pairwise comparisons with Bonferroni correction were then used to assess the differences between the three groups' motor performance scores across the Pre-test, Post-test and Retention phases. For the VG group, swing scores were significantly lower during the Pre-test than in the Post-test, $p =. 015$ and the Retention test, $p = .045$; scores achieved during the Post-test did not differ from those at Retention. For the FV group, performance scores during the Pre-test did not differ from those achieved during the Post-test. However, there was a significant difference between the scores in the Pre-test and those in the Retention test, $p = .034$. No significant differences were found between the Control group's Pre-test, Post-test and Retention test scores. Only VG participants significantly improved their motor performance from Pre- to Post-test. Moreover, this improvement persisted at Retention (i.e., 7 days after the first testing session), suggesting that the effects of the visual guides were relatively enduring.

Table 3.2. *Swing Execution Scores – Descriptive Statistics*

Group	Testing session	*M*	*SEM*	*SD*	*Min*	*Max*
FV	Pre	61.14	5.04	13.34	32.50	71.50
	Post	65.14	3.31	8.75	49.00	75.00
	Retention	71.14	2.12	5.62	61.00	77.00
VG	Pre	59.29	4.90	12.98	43.50	80.50
	Post	69.43	4.65	12.30	52.00	87.00
	Retention	68.86	3.19	8.45	56.50	82.00
Control	Pre	59.36	4.89	12.93	44.00	77.00
	Post	54.29	3.23	8.55	41.00	68.00
	Retention	61.14	4.49	11.89	46.50	76.00

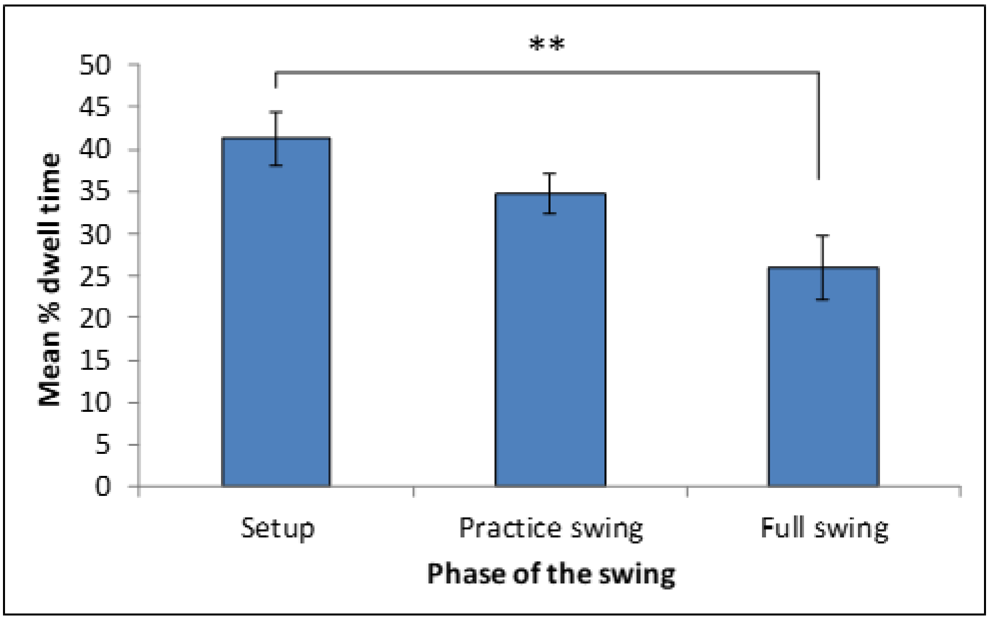

Figure 3.4. Mean percentage of dwell time on highlighted areas, by Phase. Error bars represent standard error of the means; ** $p = .006$.

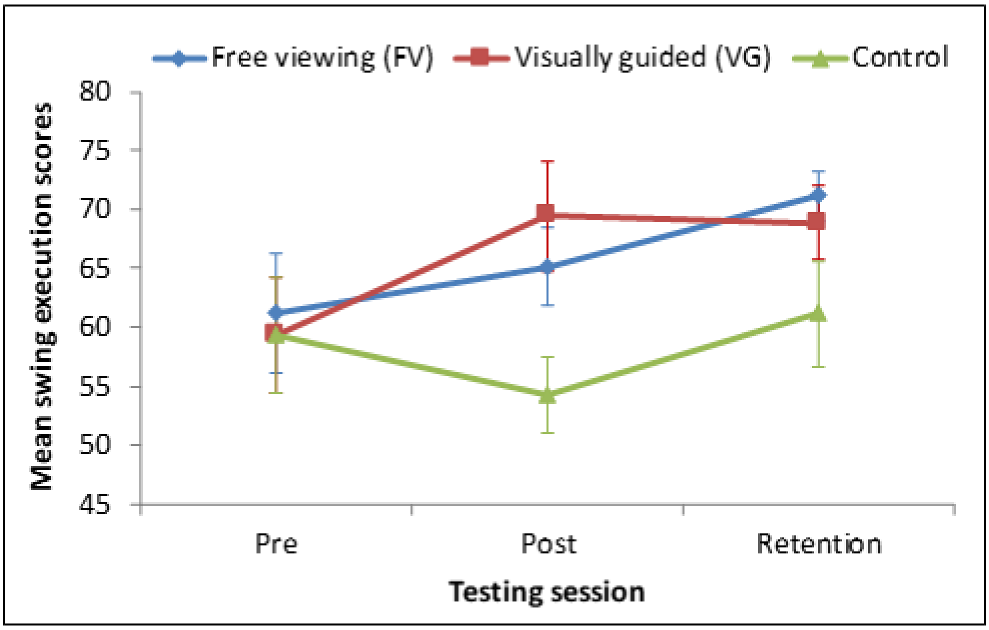

Figure 3.5. Mean swing execution scores. Error bars represent standard error of the means.

3.4.3 Rule formation task

Descriptive statistics are reported in Table 3.3. Two separate mixed ANOVAs were conducted in order to explore differences between the three groups' performances on the rule formation task before and after the intervention. There were no significant main effects or interactions for the quality of rules formed[1]. With regard to the number of rules formed, a Group (FV/VG/Control) x Time (Pre- and Post-test) mixed ANOVA revealed a significant main effect of Time, *F*(1,18) = 12.51, $p = .002$, $\eta_p^2 = .41$; participants formulated more rules after than before the intervention (see Figure 3.6)[2]. Some examples of the rules formed by the participants are provided in Table 3.4.

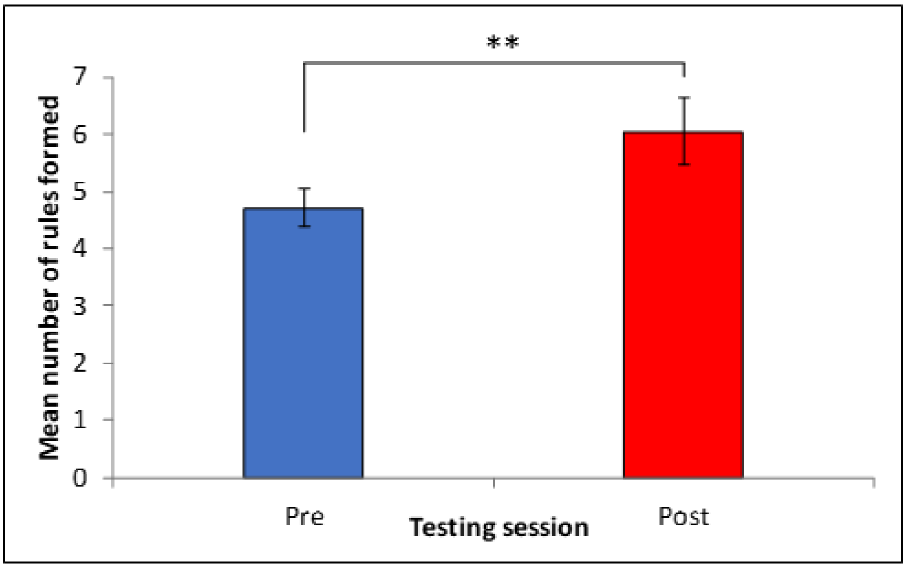

Figure 3.6. Mean number of rules formed before and after the intervention, collapsed across groups. Error bars represent standard error of the means; ** $p = .002$.

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[1] No significant main effects were found for Time, *F*(1,18) = .33, $p = .58$, $\eta_p^2 = .02$, or Group, *F*(2,18) = 2.74, $p = .09$, $\eta_p^2 = .23$. Similarly, the Group x Time interaction was not significant, *F*(2,18) = 1.19, $p = .33$, $\eta_p^2 = .12$.

[2] The main effect of Group was not significant, *F*(2,18) = .68, $p = .52$, $\eta_p^2 = .07$, nor was the Group x Time interaction, *F*(2,18) = 1.17, $p = .33$, $\eta_p^2 = .12$

Table 3.3. *Number and Quality of the Rules Formed Before and After the Intervention – Descriptive Statistics*

Variable	Group	Session	*Mean*	*SEM*	*SD*	*Min*	*Max*
Number of rules	FV	Pre	4.9	0.7	1.8	3	8
		Post	5.7	1.1	2.9	1	9
	VG	Pre	5.0	0.5	1.4	3	7
		Post	7.1	0.8	2.2	5	10
	Control	Pre	4.3	0.6	1.7	2	6
		Post	5.3	1.1	3.0	2	11
Quality of rules	FV	Pre	5.9	0.8	2.1	3	9
		Post	4.4	1.5	4.1	0	11
	VG	Pre	9.4	1.8	4.8	5	17
		Post	10.6	2.2	5.7	6	23
	Control	Pre	6.6	1.4	3.6	0	11
		Post	8.4	1.9	5.1	1	16

Table 3.4. *Examples of Rules Formed*

Rule formed	Validity
Bend your back slightly	3
Twist your foot when hitting the ball	0
Weight equally distributed on both feet	3
Rotate your hips through the motion	3
Keep your legs slightly apart	1
Follow through with the swing	3
Right arm should bend, left arm should always be straight	0
Align your feet	2
During the movement, the right leg should follow the direction of the club	0
Line up the club with the ball before the shot	3

Slightly lift your left foot to accompany the swing movement	0
Keep your eyes on the ball throughout	3
Look to the side as you hit the ball	0
When swinging, keep front leg still	0
Keep your feet in line with your shoulders	3
Focus on technique rather than power	3
Keep your head down until the ball has left the tee	3
Keep your head in line with the ball	3
Keep your head straight ahead and don’t look at the ball when it’s being hit	0
Watch your club as it follows through to where you’re hitting the ball.	0
Follow through when swinging the club	3
Keep your eyes on the ball	3
Look forwards as you hit the ball	0
When you swing the club, keep the lower arm straight	0
Bend the arm at the top of the club	1
Keep your feet slightly apart from each other	0
Keep your feet apart	1
Bend your knees slightly	3
Keep your legs straight	0
Pull the club back behind your left arm	1
Swing comes up past shoulder and continues round to opposite shoulder	2
Foot twists as you finish the strike	2
After striking the ball, turn your back foot to point in the direction of the ball	3
Feet twist after contact	0

3.5 Discussion

Our data show that, by guiding novices' attention to task-relevant aspects of a video model's performance, we accelerated their observational learning of a motor skill – in this case, the full golf swing. Consistent with previous findings (e.g., Boucheix & Lowe, 2010; de Koning, Tabbers, Rikers, & Paas, 2007; Jarodzka et al., 2013; Mayer, 2010) and our predictions, exogenous cues were successful in directing participants' overt visual attention to task-relevant regions of the modelled action in the absence of any explicit instructions to do so. Both experimental groups improved their performance significantly from Pre-test to Retention, whereas the control group evinced no such improvement. Thus, action observation per se promoted learning of the golf swing irrespective of the visual cues. However, only participants who received visual guidance improved their execution of the swing immediately post-intervention.

The above finding is consistent with social cognitive and ecological accounts of motor learning. Both these approaches emphasise the key role that attentional processes play during observational learning: unless the learner attends to and extracts the relevant information, mere exposure to a model does not guarantee learning (Bandura, 1971; Newell, 1991). Accordingly, when learning from complex visual displays, novices often fail to pick up task-relevant information because they focus their attention on features that are perceptually salient, regardless of their relevance to the task at hand (Boucheix & Lowe, 2010). As argued by Bandura, "People's perceptual sets, deriving from past experience and situational requirements, affect what features they extract from observations and how they interpret what they see and hear" (1977, p. 25). Our participants had negligible-to-no golfing experience, and so their attention was likely to be attracted by visually salient or socially relevant areas, such as the fast-moving club or the model's face, respectively. In order to avoid this, we superimposed translucent colour cues on key areas of the model's body and on the ball, the relative positions of which are typically highlighted by golf coaches and instructional manuals as fundamental to a correct setup (Lamanna, 2016; Redford & Tremayne, 1977). These guides were successful in directing golf novices' attention to these low-salience but highly relevant features, which resulted in participants spending more time looking at these individually and/or collectively informative regions, reflecting the strategies typically adopted by experts (Balslev et al., 2012; Gegenfurtner et al., 2011; Jarodzka et al., 2010).

Unlike the phenomenon of inattentional blindness, whereby fixations do not guarantee information pickup (Beanland & Pammer, 2010), there was a high degree of correlation between the extent to which key regions were fixated and motor performance. The VG participants' kinematics improved, suggesting that these participants *were* able to pick up relevant information pertaining to correct positioning and mechanics. Therefore, as argued by social cognitive and ecological motor learning theories (Bandura, 1971; Bandura, 1977; Newell, 1991), attentional processes do seem to play a central role in determining the extent of information pickup, and thus the effectiveness of action observation for skill acquisition. The performance improvements observed in the visually guided group immediately after the intervention suggest that the visual guides helped participants select and focus on the relevant information. As suggested by the Information Reduction Hypothesis (Haider & Frensch, 1996), expertise is reflected in an ability to select task-relevant information; hence, the technique employed here may act as a *shortcut* for developing expert-like gaze behaviours.

The free viewing group's improvements in performance are also noteworthy. Despite the lack of significant improvements immediately following the intervention, free viewing participants' performance scores at Retention were even higher than those of the visually guided participants, albeit not significantly so. This result is consistent with the notion that a third-person perspective, whereby the learner faces the model, can promote long-term learning and retention of motor skills (Ste-Marie et al., 2012). Thus, irrespective of the presence of visual guides, observational learning led to superior performance during a delayed Retention test, relative to controls. It is also possible that the very low number of demonstrations provided to participants was simply insufficient for the post-intervention effect on the visually guided participants' performance to manifest itself at Retention, relative to that of the free viewing group. In fact, both the frequency of demonstrations and the learner's control over this frequency have been proposed to be important for effective observational learning (Ste-Marie et al., 2012; Wulf, Raupach, & Pfeiffer, 2005). However, what should be emphasised is that the intervention employed here, despite being ephemeral in nature, was nevertheless effective in *accelerating* learning of the modelled skill. Therefore, such interventions may represent a way to promote efficiency of learning by reducing the number of observations needed to acquire novel motor skills.

Gaze data analyses showed that the time spent fixating on the highlighted areas decreased as the swing progressed – as the model's overall movement increased. This finding is not surprising for two reasons: first, researchers have shown that, during dynamic scene viewing, motion strongly attracts gaze (Mital et al., 2011); and second, the visual cues shown to the VG group were only present during the first few seconds of the setup phase and therefore disappeared prior to swing execution. Although both experimental groups attended to the highlighted regions to some degree, the VG group spent significantly more time looking at these areas even after the cues had disappeared. However, in the absence of any visual guides, and as the golfer started to move, it is likely that rapidly moving elements (e.g., the hands) automatically captured attention.

The rule formation task showed that, overall, participants tended to formulate more rules Post-test. This increase happened in the absence of any explicit instruction and was more pronounced in the VG group, suggesting that rule formation may actually have been *enhanced* by the presence of the cues. A viable explanation for this finding is that the visually guided participants, despite being unaware of the informativeness of the visual guides, may nevertheless have perceived them to be important, and consequently tried to make sense of them. However, a similar trend was observed in the control participants, despite the fact that their video contained no reference to the golf swing, and so may simply reflect the fact that, Post-test, participants were able to create rules because they had performed the swing several times. This result, coupled with the finding that the increase in the number of explicit rules formed yielded no corresponding increase in their validity, suggests that the increase in the number of rules did not result from the participants' increased explicit knowledge of the golf swing. In fact, as pointed out by Abernethy and colleagues (2012), one drawback of using questionnaires to assess explicit rule formation is that the number of rules formed is heavily contingent upon the nature of the instructions provided to the participant. It may be argued that, although participants did try to interpret what they had seen in the videos by assigning specific rules to different anatomical areas, they were unable to correctly process and interpret the visual information that they received. The results of the motor performance, however, suggest that since both the VG and the FV groups performed better in the Retention session, participants in these groups were able to extract meaningful information from the videos of the model via implicit learning mechanisms. This type of implicit learning may be preferable to explicit learning. As opposed to skills that have been learned implicitly, explicitly learned skills are disrupted under conditions involving anxiety and pressure, and do not lend themselves well to transfer tests (Rendell, Masters, Farrow, & Morris, 2011). In the case of golf, a suitable transfer test would be the use of a different club; notably one that engenders different kinematics from that used in the acquisition phase.

In conclusion, we were able to demonstrate that a brief intervention comprising exogenous orienting of overt visual attention to task-relevant regions of a video model successfully accelerated initial acquisition of the full golf swing. Our finding has important implications for the development of observational training programmes aimed at teaching novel motor skills to novices. Although traditional sport training programmes mainly focus on long-term retention and transfer of the skill (Broadbent, Causer, Williams, & Ford, 2015), the usefulness of cueing techniques should not be underestimated. Our results show that the application of simple visual guides during action observation of a complex motor skill was effective in guiding novices' attention to key areas, which in turn accelerated initial acquisition of the observed skill. The effectiveness of instructional techniques may be improved by the integration of such cueing methods into traditional training programmes. By aiding learners to identify and focus on important sources of information, we may enable them to achieve the correct movement form in less time than would be required in the absence of such attentional guidance.

Previous examinations of cueing techniques – most notably for improving anticipation skill in sport – have reported contrasting results, to the extent that a consensus on which is the most effective method has not yet been reached (Abernethy et al., 2012). Thus, future research focusing on the acquisition of motor skills through observational learning should directly compare cue types to ascertain their effectiveness for learning. Moreover, research is needed to determine whether simple visual guidance interventions such as the one employed in the present study may enhance observational learning in non-sporting contexts. The beneficial effects observed herein suggest that this intervention may be relevant not only for teaching and learning of sport-specific skills, but also for motor rehabilitation programmes (e.g., in stroke recovery). There is already evidence that action observation can improve motor function in patients suffering from motor deficits following stroke, and that these improvements are greater than those observed after traditional rehabilitation treatments that only employ physical practice (Ertelt et al., 2007). Therefore, the introduction of a visual guidance element may accelerate patients' reacquisition of previously-learnt skills. The simplicity and brevity of the intervention used herein suggest that it may be applied effectively in a wide variety of contexts – sporting and otherwise.

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4 Chapter 4:

Study 2. Motor resonance during action observation is gaze-contingent: A TMS study

DOI: 10.1016/j.neuropsychologia.2017.07.017

4.1 Abstract

When we observe others performing an action, visual input to our mirror neuron system is reflected in the facilitation of primary motor cortex (M1), a phenomenon known as *motor resonance*. However, it is unclear whether this motor resonance is contingent upon our point-of-gaze. In order to address this issue, we collected gaze data from participants as they viewed an intransitive action – thumb abduction/adduction – under four conditions: with natural gaze behaviour (free viewing) and with their gaze fixated on each of three predetermined loci at various distances from the prime mover. In a control condition, participants viewed little finger movements, also with a fixated gaze. Transcranial magnetic stimulation (TMS) was delivered to M1 and motor evoked potentials (MEPs) were recorded from the right abductor pollicis brevis (APB) and right abductor digiti minimi (ADM). Results showed that, relative to a free viewing condition, a fixated point-of-gaze which maximized transfoveal motion facilitated MEPs in APB. Moreover, during free viewing, saccade amplitudes and APB MEP amplitudes were negatively correlated. These findings indicate that motor resonance is contingent on the observer's gaze behaviour and that, for simple movements, action observation effects may be enhanced by employing a fixed point-of-gaze.

4.2 Introduction

Humans have an innate ability to recognize the actions of others and to imitate those actions. These behaviours have been associated with the *mirror neuron system* (MNS) in the brain, a network of frontal and parietal areas first identified in the non-human primate brain by di Pellegrino and colleagues (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). Di Pellegrino et al. found that mirror neurons in premotor areas discharged not only when a monkey performed an action, but also when it observed the same action being performed by an experimenter. Neuroimaging studies in humans have subsequently demonstrated that MNS activity ultimately extends to the premotor cortex and primary motor cortex (M1), which encode the specific motor programme used to produce the observed action (Buccino et al., 2001; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Grèzes, Armony, Rowe, & Passingham, 2003). As a result, mirror neuron activity is thought to play a pivotal role in the understanding and imitation of others' actions (Jeannerod, 2001; Rizzolatti, Fogassi, & Gallese, 2001).

The increase in corticospinal excitability (CE) during action observation is termed *motor resonance* (Rizzolatti & Craighero, 2004) and has been demonstrated via direct application of transcranial magnetic stimulation (TMS) to M1. Motor resonance is highly distinct, in that the activation is specific to the muscles used to perform the action (Alaerts, Heremans, Swinnen, & Wenderoth, 2009; Gangitano, Mottaghy, & Pascual-Leone, 2001; Valchev et al., 2015), is time-locked to the unfolding action sequence (Alaerts, de Beukelaar, Swinnen, & Wenderoth, 2012), and is sensitive to the specific kinematics of the action (Borroni, Gorini, Riva, Bouchard, & Cerri, 2011) – a specificity that is crucial for accurate motor learning through observation (Mattar & Gribble, 2005; Vogt & Thomaschke, 2007). Furthermore, merely observing a non-biological moving stimulus does not result in changes in CE (Lepage, Tremblay, & Théoret, 2010).

Facilitation of M1during action observation has been observed not only for transitive actions (e.g., Sartori, Bucchioni, & Castiello, 2012), but also for intransitive ones (Borroni et al., 2011; Burgess, Arnold, Fitzgibbon, Fitzgerald, & Enticott, 2013; Romani, Cesari, Urgesi, Facchini, & Aglioti, 2005). Moreover, action observation (AO) has been shown to elicit learning-related changes in the brain that mirror those derived from physical practice. For example, Stefan et al. (2005) applied single-pulse TMS and recorded the consequent motor-evoked potentials (MEPs) from two thumb muscles (flexor pollicis brevis and extensor pollicis brevis). The direction of thumb movements evoked by TMS, along two movement axes (flexion/extension and abduction/adduction), was recorded at baseline. When participants engaged in either physical practice or observation of movements performed in a direction *opposite* to baseline, subsequent TMS-evoked thumb movements occurred in the entrained direction. In a later study, Stefan, Classen, Celnik and Cohen (2008) asked participants to engage in a physical practice condition (thumb movements opposite to the direction of movements evoked by TMS pulses), and two conditions in which physical practice was combined with observation of synchronous movements that were either congruent or incongruent with the performed action. Both physical practice and the combination of physical practice with congruent movement observation enhanced motor memory formation and increased corticospinal excitability of the trained muscle. Moreover, the combined condition was more effective than practice alone.

Alaerts, Swinnen and Wenderoth (2010) devised three TMS experiments to examine the relationships of kinematics, hand contraction state and intrinsic object properties to M1 excitability. Participants viewed an actor’s hand picking up objects that varied in both actual and apparent weight; they also viewed the hand when it was not actually lifting the object, but either exerting an isometric force, or no force, thereby eliminating kinematic cues. Alaerts et al. observed that modulation of MEPs was congruent with the muscular force required, rather than with the observable properties of the objects that were being lifted. Thus, attention to both the kinematics of the observed action and the force requirements of that action may collectively determine the extent to which M1 is facilitated during action observation.

Researchers have found a strong link between eye movements and the mirror neuron system (MNS). Maranesi, Serventi, Bruni, Bimbi, Fogassi and Bonini (2013) used single- and multi-unit recording from F5 mirror neurons (ventral premotor cortex) in combination with gaze tracking to investigate the relationship between gaze behavior and mirror activity in macaque monkeys during both execution and observation of the same reaching-and-grasping action. Similar to previous findings in humans (e.g., Flanagan & Johansson, 2003), gaze behaviour tended to be predictive during action execution and during passive observation, in that gaze consistently moved toward the target object prior to the onset of the reaching movement. Maranesi et al also identified a class of mirror neurons as *gaze-dependent*; specifically, their discharge was greater when the monkey looked at the target than when it did not. Moreover, this discharge was not related to the time spent looking at the target, but it was related to the timing of the accompanying fixation. Prior to hand-target contact, the discharge was strongest for trials in which the gaze was proactive, as opposed to reactive, reflecting a tight coupling of effector and oculomotor control. However, the directionality of this relationship was ambiguous, as the issue of whether gaze was driving MNS activity, or vice versa, could not be established.

Subsequent published reports have helped to clarify this issue. Leonetti, Puglisi, Siugzdaite, Ferrari, Cerri, and Borroni (2015) partially replicated an earlier TMS study by Borroni et al. (2011), in which participants viewed video clips of an avatar picking up a ball from a table. In the original study, participants viewed either a natural action (a pronated hand reaching out for, then grasping, the ball), or an entirely unnatural one, in which a supinated hand performed the same task. The associated MEPs for two agonistic muscles – abductor digiti minimi (ADM) and opponens pollicis (OP) – were time-locked to the unfolding of the action sequence, insofar as they were larger during the hand opening and grasping phases, respectively. Conversely, for the impossible movement, only ADM activity was significant, during both phases. Borroni et al. (2011) suggested that, while participants could see that the motion of the little finger was unnatural, the activation witnessed was still specific to the muscle that would be active in order to move the digit – ADM. However, when Leonetti et al. (2015) presented the same stimuli so that participants viewed them in their near peripheral vision, the pattern of MEPs was discernibly different. The ADM and OP were both significantly activated throughout the opening, grasping and lifting phases in a highly similar pattern for both natural and impossible movements. The authors noted that the reduced visual acuity in peripheral vision led to a perceptual error; the participants perceived the impossible movements of the little finger as those of the thumb. These findings suggest that point-of-gaze appears to affect motor resonance, and therefore perceptual degradation in the periphery may be an impediment to effective observational learning. The presence of such a link between motor resonance and point-of-gaze may account for the findings of Study 1, which showed that directing observers' gaze during observational learning of a complex motor skill facilitated skill acquisition.

While the ability of the mirror neuron system to respond to subtle variations in kinematics and applied force is well-established, the contribution of human observers' point-of-gaze to motor resonance during action observation has not been directly tested. In the present study, we examined the effect of point-of-gaze manipulations on motor resonance as participants watched videos of continuous thumb adduction and abduction. We hypothesized that M1 motor resonance during observation of a simple thumb movement will be facilitated not only when point-of-gaze is relatively fixed, thereby reducing the loss of visual input associated with saccadic masking (Ross, Morrone, Goldberg, & Burr, 2001), but also when that fixation is located so as to focus overt visual attention directly on the location of biological motion. Participants observed the action under five different conditions: free viewing (i.e., normal viewing); with their gaze fixated on three different loci, each conferring different degrees of transfoveal motion; and a comparator condition in which they viewed little finger abduction and adduction with a fixed point-of-gaze, in order to assess the degree of muscle specificity of motor resonance. Single-pulse TMS was applied to M1 at a rate of 0.25 Hz and participants' eye movements were tracked throughout all conditions. This approach enabled us to determine the relationship between gaze behavior and motor resonance, as manifested in the amplitude of MEPs recorded from the effector muscles.

4.3 Methods

4.3.1 Participants

Eighteen participants (3 females and 15 males; *M* age= 28.33 years, *SEM* = 1.03) took part. All were right-handed as assessed using the revised Edinburgh Handedness Inventory (Oldfield, 1971), *M* = 79.41, *SEM* = 6.21, and had normal or corrected-to-normal vision. Participants were naïve to TMS; none of them had any contraindication to TMS or neurological, psychiatric or other medical problems (Rossi, Hallett, Rossini, Pascual-Leone, & The Safety of TMS Consensus Group, 2009; Wassermann, 1998). Participants gave their written informed consent prior to taking part and did not report any discomfort or adverse effects during the TMS protocol. The protocol was approved by the Brunel University London research ethics committee and was carried out in accordance with the ethical standards of the 2008 Declaration of Helsinki. Copies of the ethical approval letter, information sheet and informed consent form can be found in Appendices H and I.

4.3.2 Experimental stimuli and apparatus

All videos consisted of first-person perspective footage of a male actor's right hand, palm down on a desktop. This footage was used to extract a static image of the hand, which was used as a baseline reference condition, as well as to create five experimental video stimuli. These consisted of the actor performing continuous thumb or little finger abduction/adduction. The videos lasted for 1 minute, started and ended with a 6 s grey screen, and each abduction and adduction movement was synchronized to a metronome set at 1 Hz, such that a total of 48 full movements were performed in each video. In the free viewing condition (FV), participants viewed the image as they would normally. In the gaze-fixed conditions F1, F2 and F3, participants' visual attention was guided using a red fixation cross surrounded by a red circle, which subtended 2° of visual angle at the viewing distance of 60 cm and was superimposed over the image. The fixation circle was located along an imaginary line that bisected the angle between that of the thumb at full abduction and the stationary forefinger, at one of three degrees of eccentricity from the first metacarpophalangeal joint (see Figure 4.1). For condition F2P, in which the little finger moved instead of the thumb, the fixation cross was located over the proximal interphalangeal joint; this condition was included in order to assess the muscle specificity of the mirror response. The ability to accurately perceive and identify biological motion stimuli depends on whether the stimulus appears in the central or peripheral visual field, with performance deteriorating at increasing eccentricities from the fovea (Ikeda, Blake, & Watanabe, 2005). Thus, our gaze-fixed conditions were designed to vary the amount of biological motion detected by the fovea. More specifically, in conditions F1 and F3, the intended point of fixation was located below and above the moving thumb, respectively, whereby motion could only be detected extra-foveally. In contrast, in conditions F2 and F2P the participant’s gaze was directed onto a location that was constantly crossed by the moving thumb or little finger, respectively, thereby maximising the amount of biological motion detected by the fovea.

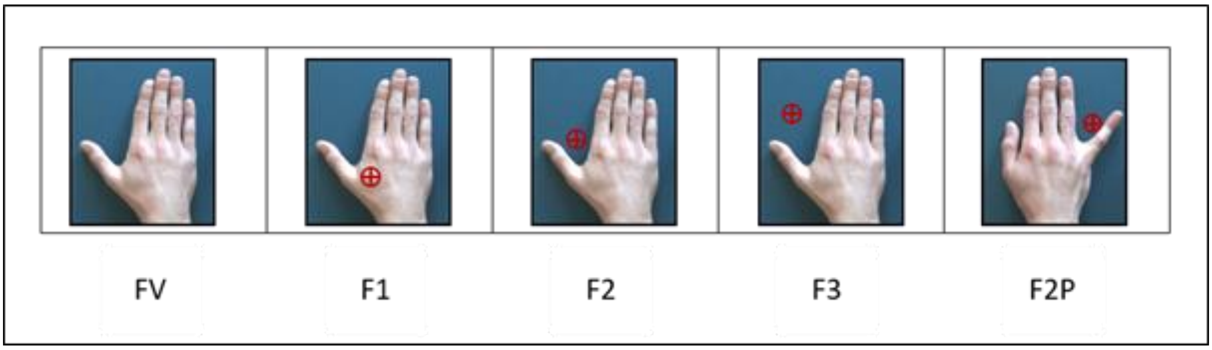

Figure 4.1. Screenshots from the five experimental videos corresponding to free viewing (FV) and gaze-fixed conditions. F1, F2 and F3 corresponded to gaze-fixed conditions when observing thumb abduction/adduction. F2P corresponded to the gaze-fixed condition during little finger abduction/adduction – the equivalent of F2 for thumb motion.

Videos were presented using Experiment Builder software (SR Research Ltd, Ontario, Canada), which also triggered the TMS pulses. The images were displayed on a 21-in. CRT monitor (100 Hz, screen resolution was set to 1024 x 768 pixels). Participants’ eye movements were recorded using an SR Research EyeLink 1000 eye tracker (SR Research Ltd, Osgoode, Canada) (monocular, right eye; 1000 Hz).

4.3.3 TMS

Self-adhesive surface electrodes (Ag-AgCl) measuring 1 cm in diameter were placed in a belly-tendon montage over the abductor pollicis brevis (APB) and abductor digiti minimi (ADM) muscles of the right hand to record motor-evoked potentials (MEPs) and a reference electrode was placed over the styloid process of the radius. Previous studies have shown that corticospinal facilitation during action observation can be specific to the muscles involved in the observed action (Alaerts et al., 2009; Valchev et al., 2015). Thus, since our stimuli consisted of thumb and little finger adduction and abduction movements, we selected the APB and the ADM because their main functions are to abduct (i.e. to move away from the hand) the thumb and the little finger, respectively (e.g., Palastanga, Field, & Soames, 2002). Electromyography (EMG) signals were recorded using Signal software (v. 6, Cambridge Electronic Design Limited, Cambridge, UK) and stored on a PC for offline analysis. EMG signals were band-pass filtered at 10-2000 Hz, digitized and displayed on a computer screen.

Transcranial magnetic stimulation was delivered using a Magstim 200 (Magstim Company Ltd., Whitland, UK) connected to a figure-of-eight coil (70 mm loop). The coil was positioned such that its centre was tangential to the scalp with the handle pointing at an angle of 45° relative to the mid-sagittal midline. In order to find the optimal scalp position (OSP) – the location on the scalp from which MEPs could be elicited in both the right ADM and the right APB – the coil was placed over the area of the left motor cortex corresponding to the 10-20 EEG position FC3 (American Clinical Neurophysiology Society, 2006) and was systematically moved, in both transverse and sagittal planes, in steps of approximately 1 cm. Thus, both muscles received TMS during all video conditions. Once the optimal stimulation site was determined, it was marked on the participant's scalp. The researcher continuously monitored the coil's position relative to this marker throughout the protocol.

Participants' resting motor threshold (rMT) was defined as the minimum level of stimulation required in order to elicit MEPs of at least 50 µV in magnitude, from at least 5 out of 10 consecutive TMS pulses (Rossini et al., 1994) in both targeted muscles. In order to elicit reliable MEPs during the experimental trials, stimulation intensity was set at 120% of the rMT. Stimulation intensities ranged from 40 to 66% of maximum stimulator output (M = 47.5, SD = 7.5). During each experimental condition, the first TMS pulse was delivered at the onset of the video so as to trigger the start of the trial; MEPs elicited by this first pulse were excluded from analyses. Subsequent pulses were delivered during abduction at a frequency of 0.25 Hz, when the thumb reached the mid-point between maximal adduction/abduction (see Figure 4.2). A total of 24 pulses were delivered in each experimental condition.

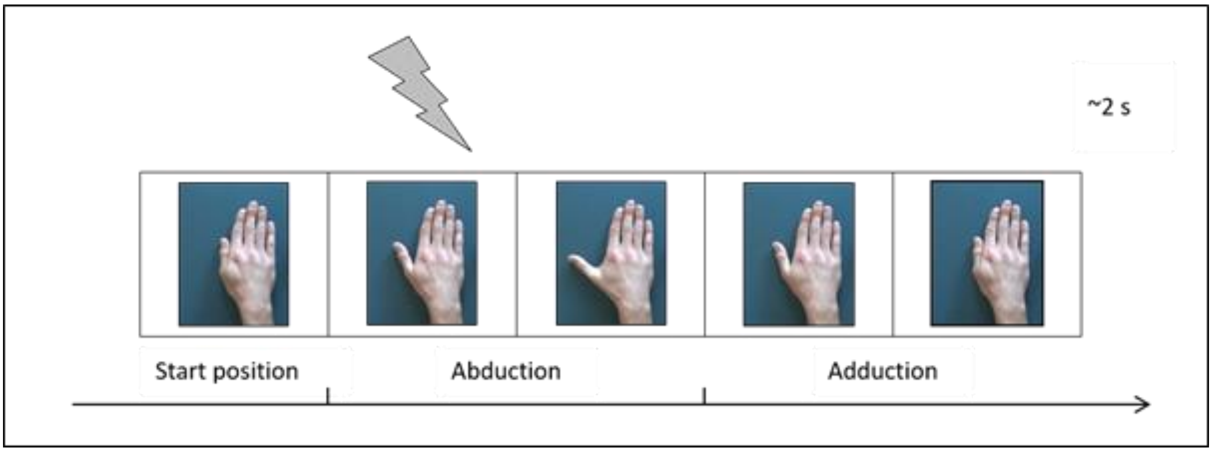

Figure 4.2. Example of a single trial procedure of thumb abduction/adduction (2 s in duration) in a FV condition. TMS pulses were delivered during the presentation of thumb abduction at a frequency of 0.25 Hz.

4.3.4 Experimental design, task and procedures

Participants sat in a padded adjustable chair facing the monitor screen, with their forearms lying pronated on a table in front of them, (cf. Alaerts et al., 2009) and their chin positioned on the chin rest mounted on the table's edge, to avoid head movements. Viewing distance was 60 cm from the monitor. The participants' hands were also pronated on the table, within the participant's field of view and located at approximately 53° of eccentricity from the centre of the fovea in the vertical plane. EMG activity was monitored continuously, and participants were reminded to relax their hand throughout the experiment.

The optimal stimulation site and rMT were determined prior to commencement of the experimental protocol by recording MEPs as per the procedures described above. The eye tracker was calibrated using a 9-point grid appearing on the PC monitor. Participants first watched a video of a static hand, which lasted approximately 2 minutes. This was done in order to assess the baseline level of CE; MEPs recorded during this baseline condition were then used to standardize the MEP amplitudes recorded during the experimental conditions. After the baseline condition, participants watched the video stimuli corresponding to the experimental conditions. These videos were organized into two blocks; each video was shown once in each block. Each video was preceded by an instruction screen. For the FV condition, the instructions were as follows: *In the following video, you will see a hand performing thumb movements. Please pay attention to the video throughout.* For the gaze-fixed conditions the instructions were the same as above, but with the addition of the following sentence: *Please maintain your gaze on the red fixation cross throughout the trial.*

The order in which the videos were presented within a block was randomized. There was a break of 10 minutes between blocks. Each testing session lasted 1.5 hours. The experimenter regularly monitored the participants' attentiveness and alertness throughout the protocol.

4.3.5 Data processing and analysis

Eye movement data were analysed using Eyelink Data Viewer (SR Research Ltd., Ontario, Canada). Saccades were defined as eye movements with velocities and accelerations exceeding 30°/s and $8{,}000°/s^2$ respectively; eye movements with velocities and accelerations below these parameters were defined as fixations.

Circular areas of interest (AOIs) corresponding to the required fixation area (see Figure 4.1) were created for each of the viewing conditions F1, F2, F3 and F2P. For the FV condition, a static AOI was superimposed over the entire hand, and a dynamic AOI was superimposed over the entire thumb. Preliminary analyses of the gaze data (average fixation duration and average saccade amplitude) identified one participant as a multivariate outlier; hence, this participant was removed from all subsequent analyses. In addition, the gaze data of two participants were discarded due to calibration error.

EMG data were analysed using the analysis features of the acquisition software (Signal v. 4.11, Cambridge Electronic Design Limited, Cambridge, UK). In order to screen the data for trials in which the background EMG exceeded an acceptable threshold, the root mean square of the background EMG during the 90 ms preceding the onset of the pulse was calculated. If this value was higher than 100 μV, the trial was excluded from the analysis. Post-experimental analyses revealed that none of the data met this criterion. Peak-to-peak amplitudes were measured for each MEP (mV) and then averaged across conditions. The averaged MEP amplitudes recorded in the various conditions during the first block of trials were compared to those recorded during the second block so as to determine whether there were any changes in MEP due to time. These analyses did not reveal any significant differences (all $p < .05$), indicating that there was no overall change in corticospinal excitability over time. Thus, MEP amplitudes were ultimately averaged across both blocks. Averaged amplitudes were normalized to the baseline reference condition (i.e., the static hand) and expressed as a percentage of that value as per the following equation: $X = (a - b) / b * 100$, where X is the normalized amplitude, a is the averaged amplitude recorded in a given condition, and b is the averaged amplitude recorded during the static condition.

Normality tests using Shapiro-Wilk were conducted on the normalized scores. Significant deviations from normality were found in several conditions, all $p < .05$;

consequently, analyses of MEP amplitudes were performed using non-parametric tests (Friedman's ANOVA). Post-hoc tests using Wilcoxon Signed Ranks Tests were then used for significant interactions. Normality tests also revealed significant deviations from normality for average fixation duration and average saccade amplitude, all $p < .05$; subsequent analyses were therefore performed using non-parametric tests.

4.4 Results

4.4.1 MEP amplitudes

Descriptive statistics for the raw and normalised MEP amplitudes are reported in Tables 4.1 and 4.2, respectively.

4.4.1.1 APB muscle.

A first Friedman ANOVA was conducted on the raw MEP amplitudes recorded across the static condition and the experimental conditions so as to determine whether observation of the moving fingers resulted in MEP facilitation from baseline. Results revealed significant differences, $\chi^2(5) = 13.98$, $p = .016$; however, post-hoc tests (Bonferroni-corrected threshold = .01) revealed that none of the contrasts between the static condition and each of the experimental conditions reached statistical significance[1].

Friedman ANOVA was then used to analyse the normalised MEP amplitudes recorded in the experimental conditions (Figure 4.3). Results revealed significant differences between the various conditions, $\chi^2(4) = 13.51$, $p = .009$. Post hoc tests were used to compare amplitudes in the free viewing (FV) condition to the amplitudes recorded in each of the thumb (F1, F2, F3) and little finger (F2P) gaze-fixed conditions. These tests revealed significant differences between FV and F2, $Z = -2.53$, $p = .011$ (Bonferroni-corrected threshold = .013). Specifically, APB MEP amplitudes recorded in condition F2 were significantly higher than those recorded during FV. Differences in MEPs recorded between F2P and FV only approached significance, $Z = -2.15$, $p = .031$; amplitudes recorded during FV were not significantly different from the amplitudes recorded in conditions F1 ($Z = -.21$, $p = .83$) and F3 ($Z = -1.07$, $p = .29$).

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[1] Amplitudes recorded during the static condition did not significantly differ from those recorded during FV ($Z = -.64$, $p = .52$), F1 ($Z = -.12$, $p = .91$), F2 ($Z = -1.3$, $p = .19$), F3 ($Z = -.12$, $p = .91$), and F2P ($Z = -1.73$, $p = .08$).

An additional Friedman's ANOVA was conducted to assess differences in the amplitudes recorded across all VG conditions. This analysis revealed no significant differences, $\chi^2(3) = 6.11$, $p = .107$.

Table 4.1. *Raw MEP Amplitudes (mV) – Descriptive Statistics*

Muscle	Condition	*M*	*Mdn*	*SEM*	*SD*	*Min*	*Max*
APB	Static	0.55	0.39	0.12	0.49	0.06	1.89
	F1	0.54	0.49	0.11	0.47	0.05	1.91
	F2	0.61	0.33	0.13	0.55	0.07	1.90
	F3	0.53	0.35	0.11	0.45	0.10	1.54
	FV	0.51	0.28	0.10	0.40	0.07	1.34
	F2P	0.60	0.43	0.12	0.49	0.08	1.78
ADM	Static	0.31	0.23	0.05	0.23	0.07	0.86
	F1	0.28	0.21	0.05	0.21	0.03	0.79
	F2	0.33	0.24	0.05	0.22	0.09	0.80
	F3	0.27	0.20	0.05	0.20	0.04	0.79
	FV	0.28	0.20	0.05	0.20	0.08	0.75
	F2P	0.37	0.20	0.07	0.29	0.04	0.94

Table 4.2. *Normalised MEP Amplitudes (%) – Descriptive Statistics*

Muscle	Condition	*M*	*Mdn*	*SEM*	*SD*	*Min*	*Max*
APB	F1	9.40	-2.29	12.41	51.19	-50.57	175.51
	F2	22.16	12.23	12.75	52.59	-43.52	166.95
	F3	14.63	1.30	12.07	49.77	-54.15	125.88
	FV	3.76	-5.18	7.95	32.79	-37.28	85.65
	F2P	15.91	9.43	6.00	24.73	-16.53	64.64
ADM	F1	-6.73	-11.37	7.07	29.16	-49.77	50.92
	F2	15.36	5.95	6.61	27.25	-17.38	89.10
	F3	-6.25	-2.34	4.67	19.26	-54.70	16.37
	FV	-1.70	-7.72	4.71	19.40	-29.70	45.31
	F2P	18.45	4.22	12.81	52.82	-40.64	186.69

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

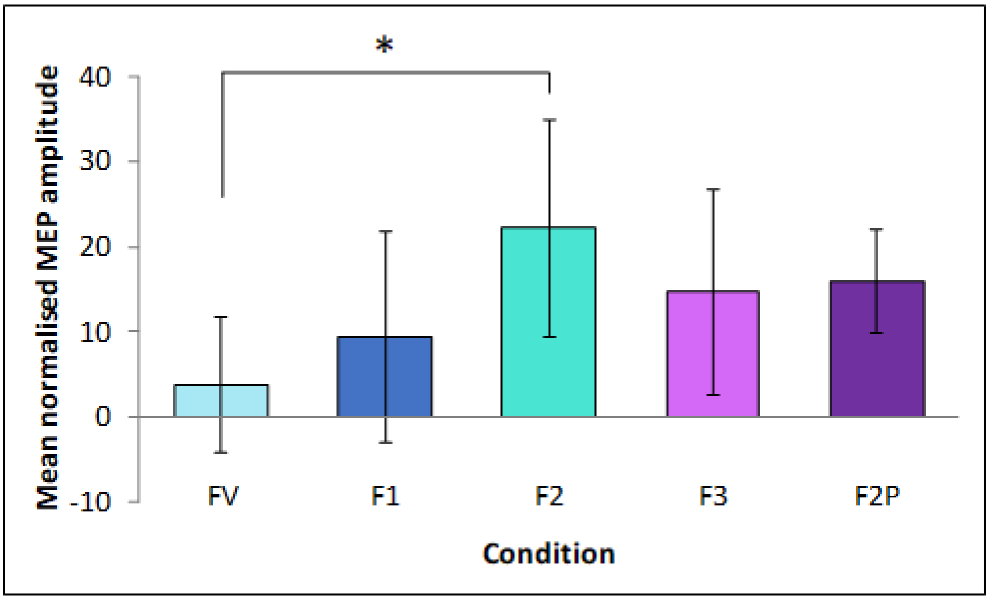

Figure 4.3. Mean MEP amplitudes recorded from APB, expressed as a percentage of the baseline condition. Error bars represent standard error of the means; * $p = .011$.

4.4.1.2 ADM muscle.

As for APB, Friedman ANOVA was conducted on the raw MEP amplitudes recorded across the static condition and the experimental conditions so as to determine whether observation of the moving fingers resulted in facilitation of ADM amplitudes from baseline. Results revealed significant differences, $\chi^2(5) = 18.24$, $p = .003$; however, post-hoc tests (Bonferroni-corrected threshold = .01) showed that none of the contrasts between the static condition and each of the experimental conditions reached statistical significance[2], all $p > .06$.

Friedman's ANOVA was then used to compare the normalised ADM MEP amplitudes recorded in the experimental conditions (Figure 4.4). The results revealed significant differences, $\chi^2(4) = 17.04$, $p = .002$. Post-hoc tests revealed that MEP amplitudes recorded during F2 were significantly greater than those recorded during FV, $Z = -3.39$, $p = .001$. ADM MEP amplitudes recorded during FV were not significantly different from the amplitudes recorded during F1 ($Z = -.88$, $p = .38$) and F3 ($Z = -.69$, $p = .49$). Finally, amplitudes recorded during F2P tended to be higher than those during FV, albeit this difference only approached significance, $Z = -1.87$, $p = .062$.

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[2] Amplitudes recorded during the static condition did not significantly differ from those recorded during FV ($Z = -1.82$, $p = .07$), F1 ($Z = -1.59$, $p = .11$), F2 ($Z = -1.63$, $p = .10$), F3 ($Z = -1.59$, $p = .11$), and F2P ($Z = -1.49$, $p = .14$).

A further ANOVA was conducted to compare the normalized amplitudes recorded during all VG conditions. This analysis revealed significant differences, $\chi^2 = 12.46$, $p = .006$. Contrasts (Bonferroni corrected threshold = .0083) revealed that amplitudes recorded during F2 were higher than amplitudes recorded during F3, $Z = -3.05$, $p = .003$. None of the other comparisons reached statistical significance[3]

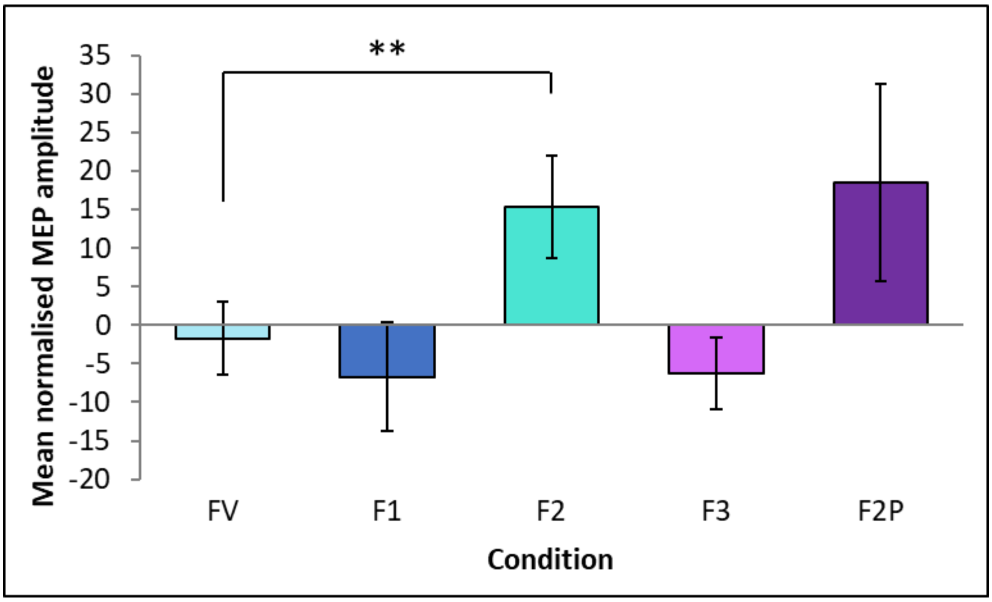

Figure 4.4. Mean MEP amplitudes recorded from ADM, expressed as a percentage of the baseline condition. Error bars represent standard error of the means; * $p = .001$.

4.4.2 Gaze data

Since in the gaze-fixed conditions participants maintained their eyes on the visual guide, we expected gaze metrics not to differ across the four conditions. In contrast, in the free viewing condition participants were free to explore the visual display; hence we expected gaze behaviour to be more varied. In particular, we expected to find saccades of greater amplitudes in the FV condition than in the gaze-fixed ones. Separate Friedman’s ANOVAs were used to compare the gaze metrics across all conditions accordingly. For all follow-up contrasts, the Bonferroni corrected threshold was set at .005. Descriptive statistics are reported in Table 4.3.

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[3] Amplitudes recorded during F1 did not differ from those recorded during F2 ($Z = -2.06$, $p = .04$), F3 ($Z = -.54$, $p = .59$) and F2P ($Z = -2.25$, $p = .025$). Amplitudes recorded during F2 did not differ from those recorded during F2P ($Z = -.17$, $p = .87$). Amplitudes recorded during F3 did not differ from those recorded during F2P ($Z = -1.4$, $p = .16$).

For fixation duration (Figure 4.5), the results showed significant differences between conditions, $\chi^2 = 36.85$, $p < .001$. Contrasts showed that fixation durations were significantly shorter in the FV condition compared to F1, F3, F2P (all $Z = -3.52$, $p < .001$) and F2, $Z = -3.46$, $p = .001$. In contrast, no differences were found between the various VG conditions[4].

For saccade amplitude (Figure 4.6), the ANOVA revealed significant differences, $\chi^2 = 24.85$, $p < .001$. Contrasts (Bonferroni corrected threshold = .005) revealed that amplitude was larger in the free viewing condition than during F1, $Z = -3.36$, $p = .001$; F2, $Z = -3.15$, $p = .002$; F3, $Z = -3.46$, $p = .001$; and F2P, $Z = -3.51$, $p < .001$. In contrast, saccade amplitudes did not differ between the various VG conditions[5].

Table 4.3. *Fixation Duration (ms) and Saccade Amplitude (° of Visual Angle) – Descriptive Statistics*

Metric	Condition	*M*	*Mdn*	*SEM*	*SD*	*Min*	*Max*
Fixation duration	F1	1454.48	1101.16	283.27	1133.09	547.81	5149.31
	F2	1444.40	982.41	318.10	1272.41	498.02	5526.35
	F3	1008.65	877.18	141.76	567.04	493.05	2751.08
	FV	613.06	568.25	71.07	284.28	284.54	1529.91
	F2P	1441.77	1173.78	326.55	1306.19	566.27	6108.81
Saccade amplitude	F1	1.16	1.06	0.12	0.49	0.57	2.22
	F2	1.13	0.94	0.15	0.58	0.48	2.33
	F3	1.11	0.96	0.13	0.51	0.59	2.39
	FV	2.04	2.04	0.12	0.49	1.27	3.15
	F2P	1.03	0.96	0.09	0.35	0.63	1.84

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[4] The duration of the fixations recorded in condition F1 did not differ from fixation durations in condition F2 ($Z = -.52$, $p = .61$), F3 ($Z = -2.43$, $p = .02$), and F2P ($Z = -.00$, $p = 1.0$) Similarly, fixation durations in condition F2 did not differ from those recorded in conditions F3 ($Z = -1.76$, $p = .08$) and F2P ($Z = -.47$, $p = .64$). Finally, fixation durations in condition F3 did not significantly differ from those in condition F2P ($Z = -2.64$, $p = .008$)

[5] The amplitude of the saccades recorded in condition F1 did not differ from the amplitude of the saccades recorded during conditions F2 ($Z = -.05$, $p = .96$), F3 ($Z = -.47$, $p = .64$) and F2P ($Z = -.65$, $p = .52$). Saccade amplitudes recorded in condition F2 did not differ from those recorded in conditions F3 ($Z = -.13$, $p = .90$) and F2P ($Z = -.47$, $p = .64$). Finally, saccade amplitude did not differ between conditions F3 and F2P ($Z = -.36$, $p = .72$).

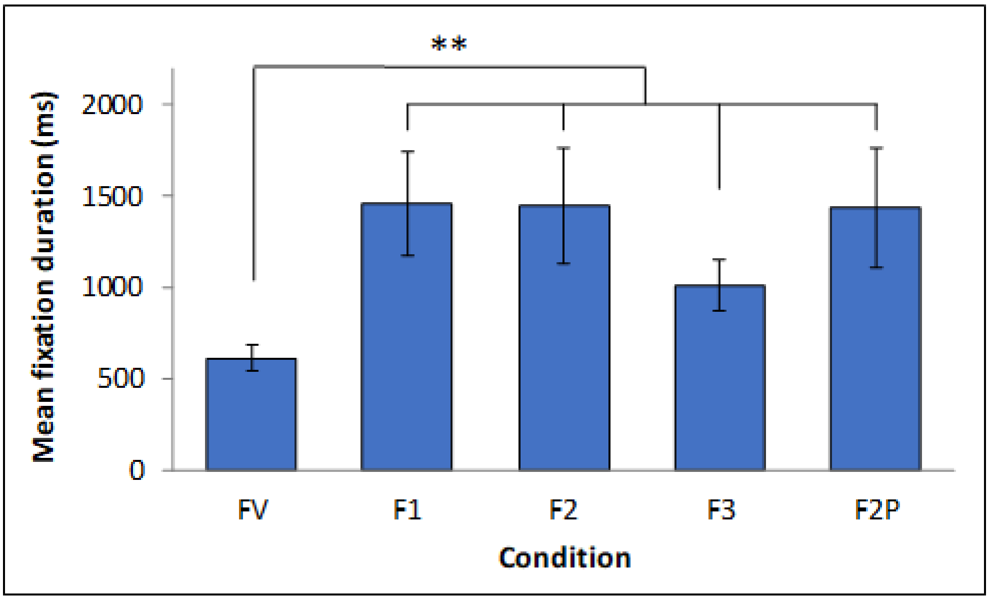

Figure 4.5. Mean fixation duration (in ms) across viewing conditions. Error bars represent standard error of the means; ** $p \leq .001$.

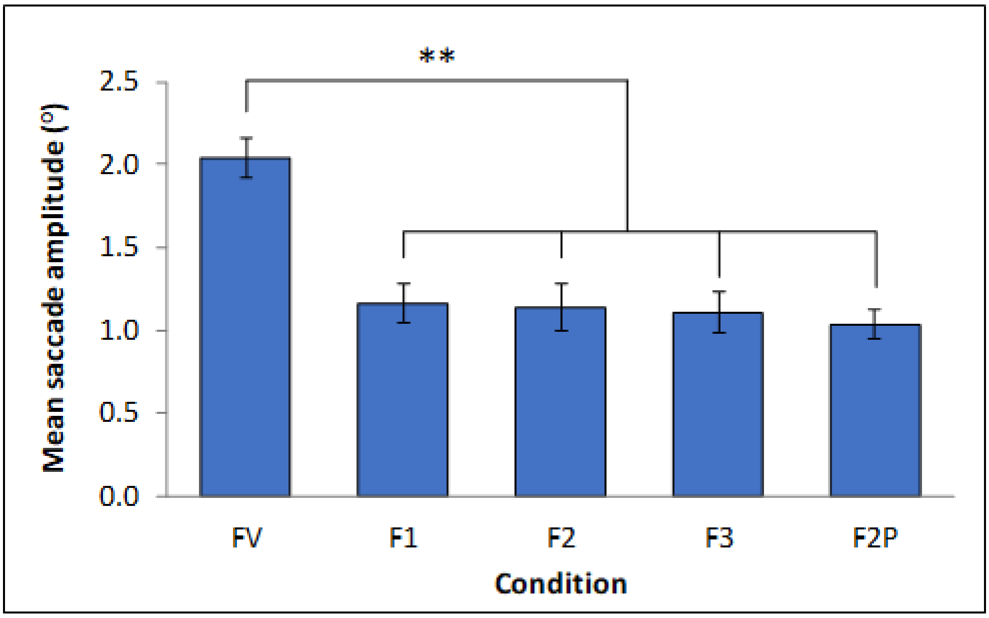

Figure 4.6. Mean saccade amplitudes across viewing conditions. Error bars represent standard error of the means; ** $p \leq .001$

With regard to dwell times, analyses of the gaze data revealed that, for each of the gaze-fixed conditions, participants predominantly maintained their gaze on the fixation points as instructed, as per our AOI analysis (Figure 4.7). Specifically, mean dwell time percentages for the specified loci ranged from 88.16% to 99.33% ($M = 95.71$, $SEM = .91$). In contrast, in the free viewing condition there were large interindividual differences in the percentage of dwell time spent exploring the two elements of the display – namely, the hand and the thumb.

Specifically, dwell time on the hand ranged from 5.8% to 91.6% (*M* = 39.69, *SEM* = 7.35), while dwell time on the thumb ranged from 3.4% to 88.3% (*M* = 51.6, *SEM* = 7.51).

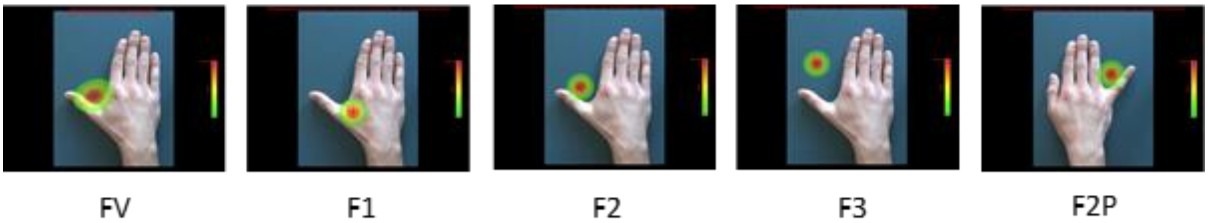

Figure 4.7. Heat maps depicting one participant's gaze data, for each condition. Green = shortest dwell time; red = longest dwell time (max duration = 45801 ms).

With regard to fixation duration and saccade amplitudes, separate Spearman's correlations were conducted in order to assess the relationships between these variables and MEP amplitudes, for both muscles, across all conditions. For APB, these analyses did not reveal any significant correlations[6]. For ADM, no significant correlations between MEP amplitudes and saccade amplitude or fixation duration were found for conditions F1, F2, F3 and FV[7]. In contrast, MEPs recorded during condition F2P were positively correlated to the average duration of the fixations made in that condition, $r_s = .51$, $p = .044$.

As reported above, in the FV condition there was great interindividual variability in the percentage of time that participants spent looking at the hand and thumb. Thus, the relationship between the MEP amplitudes recorded during free viewing, and the gaze behaviour adopted by participants in the same condition may have been modulated by the gaze behaviour adopted by the participant. The relationship between gaze behaviour and

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[6] Condition FV: amplitudes were not significantly related to fixation duration, $r_s = -.15$, $p = .59$, or saccade amplitude, $r_s = -.13$, $p = .63$. Condition F1: amplitudes were not significantly related to fixation duration, $r_s = .06$, $p = .84$, or saccade amplitude, $r_s = .32$, $p = .23$. Condition F2: amplitudes were not significantly related to fixation duration, $r_s = -.08$, $p = .78$, or saccade amplitude, $r_s = -.21$, $p = .45$. Condition F3: amplitudes were not significantly related to fixation duration, $r_s = -.31$, $p = .25$, or saccade amplitude, $r_s = .14$, $p = .62$. Condition F2P: amplitudes were not significantly related to fixation duration, $r_s = .08$, $p = .78$, or saccade amplitude, $r_s = -.05$, $p = .86$.

[7] Condition FV: amplitudes were not significantly related to fixation duration, $r_s = -.33$, $p = .21$, or saccade amplitude, $r_s = .08$, $p = .78$. Condition F1: amplitudes were not significantly related to fixation duration, $r_s = -.02$, $p = .96$, or saccade amplitude, $r_s = .04$, $p = .87$. Condition F2: amplitudes were not significantly related to fixation duration, $r_s = -.06$, $p = .82$, or saccade amplitude, $r_s = -.22$, $p = .42$. Condition F3: amplitudes were not significantly related to fixation duration, $r_s = -.43$, $p = .10$, or saccade amplitude, $r_s = -.11$, $p = .69$.

MEP amplitudes recorded from the APB and the ADM in the FV condition was consequently subjected to a second-order partial correlation in order to control for the differences in the percentage dwell time for hand and thumb. When controlling for dwell time on the hand and thumb, average saccade amplitude was negatively correlated with APB MEP amplitude, $r_p(11) = -.80, p < .001$, but no significant correlations were found between APB MEPs and fixation duration, $r_p = -.01, p = .49$. In contrast, ADM amplitudes were not significantly related to either saccade amplitude, $r_p = -.26, p = .19$, or fixation duration, $r_p = -.37, p = .10$.

4.5 Discussion

In the present study we investigated whether motor resonance in M1 during action observation is modulated by the observer's gaze behaviour. We compared MEP amplitudes from muscles of the thumb (APB) and little finger (ADM) when participants viewed video clips of thumb and little finger abduction/adduction under a number of conditions, in which the observer's gaze was fixed on one of three predetermined loci affording various degrees of transfoveal motion, or when they were able to view the videos as they would normally (i.e., free viewing). We predicted that, by directing participants' gaze to a location that maximized biological motion detection, we would observe greater facilitation of M1.

The results showed that, although observation of intransitive finger movements generally resulted in larger MEPs than observation of a static hand, this facilitation did not reach statistical significance. This is consistent with previous evidence showing that corticospinal facilitation is preferably elicited by observation of goal-directed actions (e.g., Enticott, Kennedy, Bradshaw, Rinehart, & Fitzgerald, 2010). Despite this, and in line with our predictions, our findings showed that MEP amplitudes were greater when participants maintained their gaze on a point that maximized foveal detection of biological motion (Condition F2) when compared with the free viewing condition. Our gaze data further supported our hypothesis that gaze behaviour would modulate motor resonance, in that MEP amplitudes were contingent on the observer's eye movements. Specifically, when participants were allowed to observe the action as they typically would (i.e., free viewing), MEP amplitudes were negatively correlated with the amplitudes of their saccadic eye movements. Additionally, when point-of-gaze was focused directly over the moving little finger, ADM facilitation increased with fixation duration. This finding, and the fact that the smallest MEP amplitudes were observed in the free viewing (FV) condition, are in line with our prediction that eye movements would inhibit information pickup and thereby reduce motor resonance. This supports our assertion that motor resonance during action observation in humans may be contingent on gaze behaviour; it is also consistent with previous research demonstrating gazedependency of premotor neurons (Maranesi et al., 2013) and degradation of motor resonance for peripherally-presented stimuli (Leonetti et al., 2015).

In natural contexts, gaze behaviour is comprised of fixations, in which the eye is maintained on a specific location and there is continuous perception of visual input, and saccades, eye movements of varying amplitude and velocity, during which there is a disruption of visual input. In healthy individuals, continuous perception and visual stability are achieved through a mechanism, known as *efference copy* or *corollary discharge*, which updates the retinal coordinates of visual stimuli across eye movements (e.g., Peterburs et al., 2013; Wurtz, 2008). Regardless, saccadic eye movements inevitably involve a suppression of visual input (Ross et al., 2001), particularly with regard to motion processing; in fact, displacement of a visual target goes undetected if it occurs during a saccade (Bridgeman, Hendry, & Stark, 1975; Shioiri & Cavanagh, 1989), and the perceptual threshold for detection increases with increasing saccade amplitude (Bansal, Jayet Bray, Peterson, & Joiner, 2015). Thus, since mirror neurons are thought to be responsible for transforming visual information into motor representations and motor knowledge, it could be inferred that during saccadic suppression, the resulting inhibition of visual input may reduce MNS activity.

Alternatively, it could be speculated that our reported relationship between saccades and MEPs was due to intracortical mechanisms of *surround* or *lateral* inhibition. In the latter, the activation of a specific set of neurons is associated with decreased activity in adjacent neurons, to aid in the selection of neural responses and to focus neural activity (Beck & Hallett, 2011). This mechanism has been found to operate in both motor (e.g., Mink, 1996; Poston, Kukke, Paine, Francis, & Hallett, 2012) and visual areas (Allman, Miezin, & McGuinness, 1985; Schwabe, Ichida, Shushruth, Mangapathy, & Angelucci, 2010). It could therefore be argued that the activity in cortical regions associated with control of eye movements (e.g., frontal eye fields) may have induced inhibition of adjacent premotor areas, for example, resulting in reduced MEP amplitude. However, intracortical inhibition has typically been demonstrated to occur within relatively focused regions of the brain, ones that are functionally and anatomically related.

Another finding of note is the similarity in facilitation that we observed in both APB and ADM muscles during condition F2 (see Figures 4.3 and 4.4). We expected MEPs recorded from ADM to be greatest in the condition in which gaze was fixated on the little finger (F2P), compared to when point-of-gaze was located over the moving thumb (F2). On the contrary, our results showed that MEP amplitudes recorded from both ADM and APB were largest during the F2 condition. It is possible that, rather than reflecting motor resonance activated by the perception of action, the observed modulations in MEP amplitudes may actually reflect a generic increase in CE as a result of observing a moving stimulus. However, motion perception per se does not result in CE increases (see, for instance, Lepage et al., 2010). In addition, although a number of researchers have reported muscle-specific increases in MEP amplitude as a result of action observation (e.g. Alaerts et al., 2009; Valchev et al., 2015), others have found either a non-specific facilitation, or no facilitation at all. Loporto and colleagues (Loporto, Holmes, Wright, & McAllister, 2013) showed participants videos of a static hand (baseline) or of the same hand performing either little finger or index finger adduction/abduction, and recorded MEPs from the FDI and the ADM. The authors found that MEP amplitudes showed facilitation from baseline only for the FDI during observation of index finger movements. In contrast, although ADM amplitudes recorded during observation of little finger movements were higher than those recorded during observation of index finger movements, they did not differ from baseline. Similar findings were reported by Ray, Dewey, Kooistra and Welsh (2013), who found no facilitation in flexor pollicis brevis during observation of thumb flexion/extension. Moreover, Kaneko, Yasojima and Kizuka (2007) reported both phase- and muscle-specific facilitation in the FDI during observation of index finger movements, but not in the ADM during observation of little finger movements. These findings are in line with our results for the ADM. Furthermore, Lepage, Tremblay and Théoret (2010) asked participants to observe index finger adduction and abduction, and found facilitation in both the ADM and the FDI. This potentially reflects a rapid, automatic response to action observation, resulting in a crude, non-specific mapping of the observed muscle. This suggestion is supported by our findings, which show that ADM amplitudes were facilitated during observation of thumb movements.

It should be noted that, in our videos, the movement of the thumb and that of the little finger differed in both velocity and amplitude. All of the actor's movements were synchronised with a metronome set at 1 Hz, whereby each adduction and each abduction movement took 1 second to complete. However, the angle between the thumb at full abduction and the stationary index finger subtended a larger amplitude than did the angle between the little finger at full abduction and the stationary ring finger. Thus, the thumb moved at a velocity of 6.7°/s, whereas the velocity of the little finger movement was 4.3°/s. These differences in movement characteristics may have further contributed to the generalised activation observed in the present study. Specifically, the cortical representation of the ADM may have been activated by observation of the faster, ampler – and inherently more natural – movement of the thumb, whereas observation of the slower and smaller movement of the little finger may not have been sufficient to elicit the same levels of activation. A recent published report assessed the neurophysiological effects associated with action observation suggesting that muscle specificity could be deduced for only 41% of the 85 studies reviewed (Naish, Houston-Price, Bremner, & Holmes, 2014). These findings suggest that the motor resonance effect may be muscle- and context-dependent to some degree, and that the muscle-specific aspect of MEP modulations during action observation may have been somewhat overemphasized. Future studies should assess which circumstances can elicit muscle-specific motor resonance by simultaneously recording MEPs from different muscles and using a variety of movements.

An alternative reason for the effects observed in the APB and the ADM may be found in the way in which we determined the optimal scalp position (OSP). Although the cortical representations of APB and ADM have been shown to overlap partially, the APB is located more laterally than the ADM (Pascual-Leone, Cohen, Brasil-Neto, & Hallett, 1994; Wilson, Thickbroom, & Mastaglia, 1993), and the optimal coil orientation for stimulating the two muscles is different (Bashir, Perez, Horvath, & Pascual-Leone, 2013). The *combined hotspot* used in our experiment involves finding a compromise location between the cortical representations of the muscles of interest, and it is commonly used in TMS studies which target more than one muscle (e.g., Leonard & Tremblay, 2007; Marangon, Bucchioni, Massacesi, & Castiello, 2013; Stinear & Byblow, 2003). Since in the present study the ADM was consistently less excitable than the FDI, we determined the OSP based on the amplitude of the responses observed in the ADM. Thus, it is possible that our OSP was inadvertently located more towards the centre of the cortical representation of the ADM, which may explain the observed similarity between the responses recorded from our two target muscles. Nonetheless, the combined hotspot method has been shown to yield responses that have a high inter-and intra-session reliability. Since these responses are based on stimulation parameters which take into account the responses of all the target muscles, this method may represent a more rigorous way of assessing the correct location for achieving consistent and reliable responses from all target muscles (Bastani & Jaberzadeh, 2012; see also Loporto et al., 2013).

Finally, it should be noted that normalized amplitudes recorded in the present study ranged from -54.15 to 175.51 for the APB and from 54.70 to 186.69 for the ADM. The observed similarity between the MEP modulations in both the ADM and the APB may be explained by this high interindividual variability. In an illustration of this phenomenon, Hétu, Gagné, Jackson and Mercier (2010) used TMS to investigate whether observing common everyday movements performed by proximal and distal upper-limb resulted in muscle-specific facilitation. Their participants watched videos of transitive hand and arm actions; TMS-evoked MEPs were recorded from the biceps and two hand muscles – opponens pollicis and FDI. Although their results showed a general muscle-specific effect of action observation, the authors reported high interindividual variability in the pattern of corticospinal facilitation. Whereas the majority of participants showed an increase in MEP amplitudes in the effector muscle, the magnitude of this effect varied greatly between individuals, to the extent that some participants exhibited no facilitation at all. Hétu et al. concluded that such variability reflected differences in observers' ability to precisely map the observed action onto their motor repertoire, which could explain our findings. Specifically, one-third of our participants ($n = 6$) exhibited ADM MEP amplitudes that were larger during observation of little finger movements than during observation of thumb movements, as expected. Hence, it is possible that our results simply reflect the fact that the majority of our participants lacked the ability to precisely map the observed action onto their motor system, thereby exhibiting a pattern of corticospinal facilitation that extended to the ADM muscle during observation of thumb movements.

The present study had some limitations. Although in some previous studies researchers have reported significant increases in CE as a result of observing intransitive actions (e.g., Burgess et al., 2013; Romani et al., 2005), such facilitation has typically been confined to the observation of goal-directed actions (e.g., Enticott et al., 2010). Therefore, it could be speculated that, had our participants observed a transitive action, we would have observed even greater facilitation. A second limitation is that participants were not instructed to observe the action with the intention to imitate; doing so elicits greater modulations in motor areas which are part of the putative human mirror neuron system (Buccino et al., 2004; Roosink & Zijdewind, 2010) than does passive observation of the same stimuli. However, our decision not to instruct participants to observe the action with this intention was due to the fact that the stimulus employed consisted of a very simple action, which was already present in the motor repertoire of our observers. Since simple adduction/abduction movements represent such a common, everyday action, it is possible that, by instructing participants to observe the action with the intention to imitate, we might have inadvertently prompted them to look for additional information, potentially compromising our point-of-gaze manipulations.

Our findings extend previous work by providing the first direct evidence of a link between gaze and motor resonance. Specifically, they suggest that, during observation of single-joint actions such as those used in the current study, maintenance of a relatively fixed point-of-gaze facilitates M1 to a greater extent than does natural viewing. Larger MEPs can be taken as an index of motor expertise, in that the amount of motor resonance during the observation of an action is greater for previously learned actions that are already present in the observer's motor repertoire (e.g., Jola, Abedian-Amiri, Kuppuswamy, Pollick, & Grosbras, 2012). Thus, our findings raise the possibility that the pickup of information, and therefore observational learning, may be facilitated by adopting specific gaze strategies (see also Hétu et al., 2010). This proposition is supported by the findings of Study 1; there, we demonstrated that visual attentional guidance aimed at directing observers' gaze to specific aspects of a modelled action accelerated observational learning of the action. This is consistent with previous research showing that attentional guidance can facilitate perception of biological motion (Jarodzka, van Gog, Dorr, Scheiter, & Gerjets, 2013; Vine, Masters, McGrath, Bright, & Wilson, 2012). The results of the present study suggest that the beneficial effects of visual guidance on information pickup may derive from the link between motor resonance and gaze behaviour. Specifically, learners may benefit from reducing eye movements, which can compromise the extraction of visual information, while at the same time maintaining their visual attention on loci that maximize motor resonance.

Practically, the notion of an optimal fixation point has implications for action observation in clinical and performance settings. For example, AO is increasingly being used as a means of motor and cognitive recovery from cerebral palsy, stroke and Parkinson's disease (Abbruzzese, Avanzino, Marchese, & Pelosin, 2015; Buccino, 2014; Ertelt et al., 2007). Research has consistently shown that action observation-based therapies improve motor function and increase activity in areas composing the observation-execution matching system; that is, the human correlate of the mirror neuron system (for a recent review, see Buccino, 2014). However, the effectiveness of protocols in which action observation is used to teach novel motor skills, or improve motor function, may depend on the learner's ability to maintain a suitable point-of-gaze. Consequently, by directing learners' gaze appropriately, we may maximize corticospinal facilitation and thereby accelerate motor skill acquisition/reacquisition.

To conclude, the present study contributes to the existing literature by providing evidence of a link between gaze and motor resonance, as indexed by MEP amplitudes. Motor resonance during action observation is thought to reflect the amount of learning and expertise with the observed action (Jola et al., 2012). Our results show that that the amount of motor resonance in the observer's motor cortex can be maximized by adopting specific gaze behaviours during action observation. This is a novel finding, and one which suggests that approaches based on directing learner’s gaze to increase motor resonance may allow us to effectively accelerate learning, or re-learning, of simple motor actions.

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5 Chapter 5:

Study 3. Exogenous guidance of the observer’s gaze modulates phase-specific motor resonance during observation of a transitive action sequence

5.1 Abstract

Action observation (AO) elicits changes in the observer’s brain activity which are comparable to those resulting from physical execution of the same actions. This effect, known as motor resonance, is attributed to the activity of the mirror neuron system, which is thought to underlie our ability to recognise and imitate the actions of others. Accordingly, AO is widely used as a tool for novel motor skill learning as well as for the re-learning of previously acquired motor skills. We recently showed that the observer’s point-of-gaze during the observation of thumb movements is related to motor resonance. However there currently is no evidence of a relationship between overt visual attention and corticospinal facilitation during the observation of more complex, object-directed actions. Accordingly, the aim of the present study was to determine whether, by directing observers’ gaze, we might modulate their corticospinal excitability during observational learning of a sequence of reaching and grasping actions. Single-pulse TMS was used to assess corticospinal facilitation during AO. Participants observed sequences of transitive upper-limb movements while maintaining their gaze on a target- or effector-based visual guide, or during free viewing. Overall levels of corticospinal excitability did not differ between conditions. However, directing the learner’s gaze to the effector muscle significantly altered their gaze behaviour, which in turn modulated the muscle-specific pattern of motor resonance. These findings provide the first evidence of a relationship between gaze behaviour and motor resonance during the observation of a transitive action. This suggests that, by directing observers’ eye movements appropriately, we may maximize the effects of AO – but in order to develop effective visual guidance-based interventions, the link between gaze and corticospinal excitability during AO needs to be investigated further.

5.2 Introduction

Action perception and action production are two closely related processes that lie at the core of our ability to interact effectively with our environment. Convincing evidence in support of the link between the observation and the execution of actions, which share a common neural substrate, comes from behavioural, neuroimaging and neurophysiological findings (for a recent review, see Rizzolatti & Sinigaglia, 2016). Behaviourally, action perception has been shown to directly affect action production. For instance, viewing another individual performing a movement impairs the simultaneous execution of an incongruent movement (Kilner, Paulignan, & Blakemore, 2003), and the speed of observed movement can automatically modulate the timing of the observer's subsequent movement execution – even when the movements are unrelated to the observed ones (Watanabe, 2008). In addition, eye tracking studies have reported a congruency between proactive gaze behaviour naturally adopted by individuals during action execution and the gaze patterns displayed whilst observing the same actions being performed (Causer, McCormick, & Holmes, 2013; Flanagan & Johansson, 2003), lending further support to the idea of a shared neural mechanism for action perception and action production.

Neuroimaging and neurophysiological studies have furthered our understanding of the close relationship between action observation (AO) and action execution by showing that AO of a task results in changes in neural activity similar to those resulting from physical practice of that same task (Rizzolatti & Sinigaglia, 2016). Using fMRI, researchers have provided evidence that observing an action elicits activation, in the observer's brain, of the same areas that are involved in motor preparation and action execution (Buccino et al., 2001; Iacoboni, 2005). TMS studies have shown that the correspondence between action and perception is reflected in selective increases in corticospinal excitability of primary motor cortex during action observation, and specifically in the areas corresponding to the muscles involved in the observed action (e.g., Borroni & Baldissera, 2008; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Gangitano, Mottaghy, & Pascual-Leone, 2001). This phenomenon, known as *motor resonance* (Decety & Jackson, 2004), is attributed to the activity of the mirror neuron system, or MNS, a network of premotor and parietal areas which is thought to play a key functional role in our ability to understand the actions, intentions and emotions of others, as well as for imitation (Fabbri-Destro & Rizzolatti, 2008). Through the activity of the MNS, human beings are able to map observed actions onto their own motor repertoire, translating sensory information into motor knowledge. Recently, direct evidence of a link between action perception and motor activation has come from studies which have shown that interfering with premotor regions of the MNS can reduce action recognition and alter AO-induced modulations in corticospinal facilitation (Avenanti, Annella, Candidi, Urgesi, & Aglioti, 2013; Jacquet & Avenanti, 2015; Koch et al., 2010).

The motor resonance effect is present from a very early stage (Lepage & Théoret, 2006; Marshall, Saby, & Meltzoff, 2013; Marshall, Young, & Meltzoff, 2011), and it can occur automatically (but see, for example, Betti, Castiello, Guerra, & Sartori, 2017). The AO-induced pattern of corticospinal facilitation has been shown to be time-locked to the unfolding phases of the action (de Beukelaar, Alaerts, Swinnen, & Wenderoth, 2016; Gangitano et al., 2001). For instance, the abductor digiti minimi (ADM) muscle, which is responsible for abducting the little finger, is very active during the execution of a whole-hand grasp but not during execution of a precision grip. In contrast, the first dorsal interosseous (FDI), a flexor of the index finger, is involved more in the performance of precision grips than in the execution of whole-hand grasps. Accordingly, the motor-evoked potentials (MEPs) recorded from the ADM are facilitated more during observation of a whole-hand grasp than during viewing of a precision grip, whereas the opposite pattern is found for the FDI (Bunday, Lemon, Kilner, Davare, & Orban, 2016).

There is evidence that motor resonance is related to motor competence and familiarity with an action. Calvo-Merino and colleagues (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005) investigated the effects of motor expertise on AO-induced changes in brain activity. Their results showed that expert dancers exhibited strong activation in MNS areas during observation of the dance style in which they had been trained, but this was not the case for a different, but motorically similar, dance style. In a later study, the same authors were able to establish that expertise-related modulations in motor resonance are specifically linked to the observer's *motor*, rather than *visual*, familiarity with an action (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006). Relatedly, EEG studies have shown that, in infants, desynchronization of the mu rhythm, which reflects MNS activity (Nyström, Ljunghammar, Rosander, & von Hofsten, 2011), is related to the child's specific motor experiences and competencies (Cannon et al., 2016; van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008). These studies suggest that, very early in life, our own action experiences are closely related to our perception of others' actions.

Performance improvements brought about by action observation are reflected in the emergence of learning-related changes in the brain that mirror those derived from physical practice (Cross, Hamilton, Cohen, & Grafton, 2017; Stefan, Classen, Celnik, & Cohen, 2008). Furthermore, changes in corticospinal excitability during AO are closely linked to subtle spatial and temporal dynamics of the observed movements. For example, studies have shown that observation of a model learning to reach in a novel dynamic environment (e.g., a clockwise force field) resulted in better performance when participants were subsequently tested within an identical field, compared to when they had observed a model performing similar movements in a random, unlearnable one (Mattar & Gribble, 2005; A. Williams & Gribble, 2012). Evidence suggests that not only is activation greater when participants observe an action with the intention to imitate it (Frey & Gerry, 2006), but also when the model is attempting to learn (McGregor, Vesia, Rinchon, Chen, & Gribble, 2017). In their investigation of motor resonance during AO of a finger-tapping task, Lagravinese and colleagues (Lagravinese, Bisio, Ruggeri, Bove, & Avanzino, 2017) found that repeated observation of finger-tapping performed at a frequency of 3 Hz – a faster cadence than would ordinarily occur – resulted in an increase in the frequency of participants' execution of finger tapping, and a concomitant change in motor resonance. Prior to the AO training, corticospinal excitability of the index finger muscle was highest during observation a more common frequency of finger tapping (i.e., 2 Hz). This effect was no longer present after a single session of AO, and after multiple sessions, corticospinal excitability was found to be highest during the observation of the 3 Hz tapping (Lagravinese et al., 2017). Collectively, these studies provide convincing evidence of the MNS' fundamental involvement in observational learning.

Considering the effectiveness of AO for learning, it is not surprising that observation-based methods represent one of the most pervasive approaches for the teaching of many skills (Andrieux & Proteau, 2016; Lago-Rodríguez, Cheeran, Koch, Hortobagy, & Fernandez-del-Olmo, 2014). Researchers have shown that demonstrations by a suitable model can reliably lead to learning of skills of varying complexity, including ballet (Gray, Neisser, Shapiro, & Kouns, 1991), football (Horn, Williams, & Scott, 2002) and long jumping (Panteli, Tsolakis, Efthimiou, & Smirniotou, 2013). Observational learning is also widely used in contexts other than sports, such as for the training of medical skill (Cordovani & Cordovani, 2016). In addition, AO-based approaches can effectively aid recovery of motor function following motor or neurological impairment (Ertelt et al., 2007; Pelosin et al., 2010), and they are thus increasingly being adopted as a complement to traditional rehabilitation approaches (Buccino, 2014). However, observation-based approaches to the (re)learning of motor skills can impose high attentional demands on the learners (Buccino, 2014), whereby the effectiveness of AO for learning may depend on the observer's ability to appropriately attend to relevant aspects of the action.

Gaze and attention play a crucial role for the pickup and processing of visual information. We previously demonstrated that attentional allocation and point-of-gaze can modulate both the behavioural effects of action observation (Study 1) and its neurophysiological correlates (Study 2). In addition, the priming effects typically resulting from action observation and automatic imitation – whereby perception of actions facilitates similar responses and interferes with dissimilar responses – are eliminated if attention is diverted away from an action (Bach, Peatfield, & Tipper, 2007). This occurs even when the stimulus towards which attention is directed spatially overlaps the displayed action (Chong, Cunnington, Williams, & Mattingley, 2009). Attentional allocation has also been shown to modulate motor resonance. For instance, the automatic AO-induced enhancements in MNS activity are reduced when participants are requested to simultaneously perform an attentionally demanding task at fixation (Chong, Williams, Cunnington, & Mattingley, 2008), which suggests that focusing overt attention – as indexed by point-of-gaze – over an action may not be sufficient to elicit motor resonance (Woodruff & Klein, 2013). Evidence in support of the above proposition comes from a recent study by Betti et al. (2017). In a set of experiments, the authors demonstrated that, during the observation of non-interactive, object-directed actions, gaze remained anchored on the actor's hand even upon the sudden appearance of a distractor stimulus (i.e., a red dot) in a location spatially removed from the hand, indicating that overt attention was maintained on the biologically-relevant stimulus. Despite this, the corresponding amount of motor resonance decreased, indicating that the sudden onset of the dot automatically attracted participants' covert attention. Based on these results, Betti et al. argued that mirror activity can dissociate from overt attention as indexed by point-of-gaze, but it is strongly associated with covert attention. However, this interpretation is somewhat compromised by the fact the authors recorded MEPs and gaze in two separate experiments rather than concurrently.

It should be noted that, although attention can be shifted covertly (Posner, 1980), saccadic eye movements are typically accompanied by concurrent shifts in attention (Shepherd, Findlay, & Hockey, 1986). Locus of attention and point-of-gaze are often closely coupled, especially in tasks requiring the processing of complex information; accordingly, fixations are widely regarded as an index of selective attention, information pickup and information processing (Irwin, 2012; Mann, Williams, Ward, & Janelle, 2007; Treue, 2003). The close coupling between gaze and attention suggests that, by focusing gaze on a given aspect of an observed action, the allocation of attention to that particular aspect – or to related features – may also be facilitated. In line with this, in Study 2 we provided evidence of a link between eye movements and motor resonance during the observation of a simple intransitive action. We investigated the effects of point-of-gaze manipulations on corticospinal excitability of abductor pollicis brevis (APB) and ADM during observation of thumb adduction/abduction movements. Focusing gaze over a point which maximised motion perception by the fovea was found to maximise the amount of motor resonance. Furthermore, when participants watched the videos with natural gaze behaviour, there was a negative correlation between MEP amplitude and saccade amplitude. These findings are in line with studies that have reported degradation of motor resonance when actions are presented in peripheral vision (Leonetti et al., 2015), and with the discovery of view-dependent mirror neurons (Maranesi et al., 2013). Directing observers' gaze – and thus their overt attention – during action observation so as to facilitate the allocation of covert attention may allow us to optimise information pickup and enhance the beneficial effects of AO on learning. Consistent with this possibility, in Study 1 we showed that visual guidance aimed at directing learners' attention to relevant areas of an observed action effectively accelerated observational learning of the golf swing, an effect which may be explained by the link between mirror activity and attentional allocation as indexed by locus of eye fixation, which we found in Study 2.

The aim of the present study was to extend our previous findings by investigating the link between motor resonance and gaze during the observation of transitive actions. In Study 2 we found that, during viewing of intransitive thumb movements, corticospinal excitability is maximised when gaze is fixated directly over the moving thumb. Here, we planned to determine how directing observers' gaze in different ways modulates corticospinal facilitation during viewing of a model performing a sequence of target-directed precision grips. Participants were allowed to watch the action sequences freely and under two visually guided conditions, in which a visual guide was used to direct point-of-gaze, and thus overt attention. Specifically, participants' gaze was directed towards either the target, or the moving effector. The amplitude of the MEPs recorded in each of the three conditions was compared so as to determine whether visual guidance can be used to maximise motor resonance during observation of goal-directed actions. Based on previous findings of EMG and TMS studies on the involvement of hand muscles in the performance and observation of reach-to-grasp actions, we expected to observe a phase-specific pattern of facilitation in both the APB and the FDI. The APB muscle acts to abduct the thumb; hence, we expected the representation of this muscle to be more strongly activated when participants observed the hand opening phase of the reach-to-grasp sequence of actions, compared to when they viewed the grasp phase of the action. In contrast, the FDI is a flexor of the index finger, which is highly involved in the execution of precision grips. We thus expected the FDI to behave in the opposite manner to the APB; that is, we predicted greater activation during viewing of the grasp phase compared to the hand opening phase. Finally, since the ADM is not one of the prime movers involved in the production of reach-to grasp movements, we expected ADM amplitudes to be similarly facilitated by observation of both phases.

Motor resonance is known to be positively related to motor competence and familiarity with an action (Calvo-Merino et al., 2005; Cannon et al., 2016; van Elk et al., 2008). Furthermore, recent studies have revealed the existence of a correlation between the amount of MNS activity during action observation and subsequent AO-induced changes in behaviour (e.g., Aridan & Mukamel, 2016; Frey & Gerry, 2006; Krüger et al., 2014). The link between mirror activity and gaze/attentional allocation needs to be further investigated to identify ways of facilitating covert activation of the motor representations that correspond to an observed action, thereby maximising the beneficial effects of action observation on behaviour.

5.3 Methods

5.3.1 Participants

After providing written informed consent, 21 participants (9 males, 12 females; *M* age = 24.43, *SD* = 4.71) took part in the study. Participants were right-handed, as assessed using the Edinburgh Handedness Inventory (Oldfield, 1971), *M* = 76.19, *SD* = 18.09. Participants had normal or corrected-to-normal vision; prior to taking part, they were screened to ensure that they did not have any neurological, psychiatric or other medical problems or any other contraindication to TMS (Rossi, Hallett, Rossini, Pascual-Leone, & The Safety of TMS Consensus Group, 2009; Wassermann, 1998). Participants provided written informed consent prior to taking part, and they did not report any adverse effects or discomfort during the TMS protocol. The study was conducted in accordance with the standards of the Declaration of Helsinki (2008), and it was approved by the Brunel University London research ethics committee. Copies of the ethical approval letter, participant information sheet and informed consent forms are reported in Appendices J and K.

5.3.2 Experimental stimuli

Six squash balls mounted on wooden stalks of different heights formed the targets for the action sequences. Videos were filmed using a Canon HD camcorder, model XF105 (Canon Inc., Tokyo, Japan) and they displayed first-person footage of an actor reaching for, and then grasping, each target in a pre-defined sequence using a precision grip (Figure 5.1). Male participants viewed videos of a male actor, whereas female participants observed a female actor. The actors' movements were synchronised with a metronome set at 0.66 Hz, so that a full movement cycle (i.e. reaching for the ball, grasping it, then drawing the hand back) took three seconds to complete. Each video trial was preceded by a 2 s grey-screen and lasted a total of 20 s. Red translucent circular patches were superimposed over the videos using Camtasia Studio (v.8, Techsmith, Michigan, US), to act as visual guides (see Figure 5.2).

Figure 5.1. Sequential screenshots displaying one reach-and-grasp action.

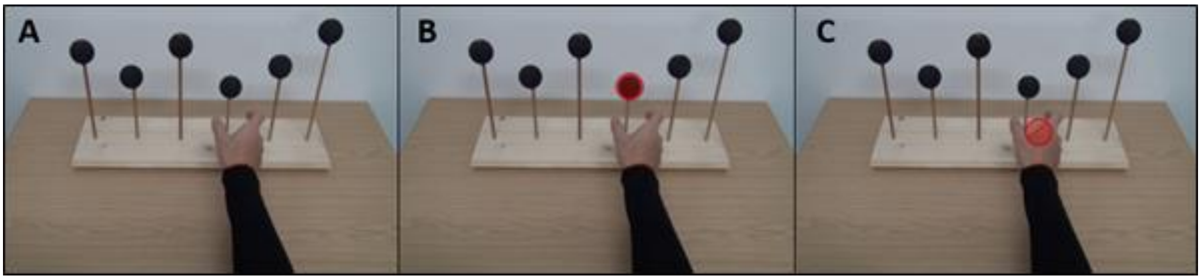

Figure 5.2. Screenshots taken from, respectively, the FV video (A), the VGM video (B) and the VGT video (C).

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

5.3.3 TMS

Pairs of self-adhesive surface electrodes (Ag-AgCl; 1 cm diameter) were placed in a belly-tendon montage over the APB, the FDI and the ADM of the right hand to record MEPs. A reference electrode was placed over the styloid process of the radius. EMG traces were acquired using Signal software (v.6, Cambridge Electronic Design Limited, Cambridge, UK); they 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 Rapid (Magstim Company Ltd., Whitland, UK) connected to a circular coil (130 mm outer diameter; 50 mm inner diameter). The coil was held tangentially to the scalp, with Side A visible so as to achieve optimal stimulation of the left hemisphere. Participants wore a tight-fitting swim cap. The distance between the inter-aural points and that between the nasion and the inion was measured; the intersection between the lines connecting these points, which corresponded to the vertex (Cz), was marked on the cap. In order to locate the optimal scalp position 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 along the sagittal and frontal planes in steps of 1 cm. Once the optimal scalp position had been located, it was marked on the cap 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 amplitudes of ≥ 50 µV from at least 5 out of 10 consecutive stimulations (Rossini et al., 1994), was determined. Stimulation intensities used in the experimental trials corresponded to 120% of the participant's rMT and ranged from 62 to 97% of the maximum stimulator output ($M = 79.1$, $SD = 9.7$).

5.3.4 Experimental design, task and procedures

Upon arrival at the lab, participants completed a demographics questionnaire. They then sat facing the monitor screen, their arms remained pronated on a table (height: 827 mm) in front of them. Participants' chin and forehead were positioned on a support affixed to the table. To facilitate relaxation of the target muscles, their right forearm was supported by a cushion so that the fingers of the right hand were suspended above the table. EMG was constantly monitored by the experimenter, and participants were reminded to keep their hands relaxed throughout the experimental protocol. Prior to commencing the protocol, the rMT and optimal scalp position were determined as described above, and fifteen MEPs were recorded while participants observed a static image of a hand resting on a table, so as to determine baseline levels of corticospinal excitability. A second baseline measurement was taken upon completion of the protocol, to assess whether there were any changes in baseline excitability that were unrelated to the experimental manipulations. The eye tracker was calibrated using a 13-point grid which appeared on the PC monitor facing the participant. Eye movements were recorded during all AO trials.

Previous studies have shown that MNS activity during action observation is modulated by the intentions of the observer; specifically, observing an action with the aim of learning it elicits stronger motor resonance than does passive observation or the intention to merely recognise the action (Muthukumaraswamy & Singh, 2008; Roosink & Zijdewind, 2010) Therefore, participants were instructed to attentively observe the videos so as to learn about the sequence. To promote high levels of attention and engagement with the task, upon completion of each block, participants were asked to report the observed sequence by pointing at each of the targets in the correct order.

Participants completed three conditions, the order of which was counterbalanced. Each condition consisted of six action observation trials (Figure 5.2). In the free viewing (FV) condition, participants observed the action as they would naturally. In the visual guidance conditions, participants were instructed to maintain their gaze on a translucent visual guide. In one of these conditions, the guide was superimposed over the FDI and it was present for the entire trial (visual guidance on the muscle; VGM). In the other condition, the guide was stationary, and it appeared over each of the targets, in sequence (visual guidance on the target; VGT), 33 ms before the onset of the actor's hand movement toward that target; it disappeared 33 ms after the actor's fingers had released the target. The visual guides measured 2.1 cm in diameter, which corresponded to 2° of visual angle at the viewing distance of 60 cm. A different movement sequence was viewed in each of the conditions.

During each AO trial, five pulses were delivered during observation of the ball pinches, and five additional pulses were delivered during the hand opening phase. This was done in order to assess whether any facilitation in corticospinal excitability due to action observation was muscle-specific and time-locked to the observed action. A total of 60 TMS pulses were delivered in each condition. Participants were given a 5-minute break after completing each block; each testing session lasted ~1.5 hours. Before beginning the protocol, and upon completion of each experimental block, participants completed the Stanford Sleepiness Scale (SSS, Hoddes, Zarcone, & Dement, 1972), so as to monitor changes in their alertness and fatigue. This is a 7-item questionnaire involving sentences describing different levels of alertness. These range from *Feeling active, vital, alert or wide awake* (1) to *No longer fighting sleep, sleep onset soon. Having dream-like thoughts* (7). Participants have to circle the statement that best represents the way they are feeling.

5.3.5 Data processing and analysis

5.3.5.1 Sequence recall.

Sequence recall was scored by allocating 1 point for each target recalled in the correct order in the sequence, whereby the maximum possible score was 6. The sum of the resulting scores was then transformed into a percentage.

5.3.5.2 *Gaze data.*

Data Viewer software (SR Research Ltd., Ontario, Canada) was used to analyse participants' eye movements during action observation. Interest areas (IAs) were superimposed over the different elements of the display. Specifically, a circular IA was superimposed over each target (target IA) from the onset of the video. Two dynamic IAs were superimposed over the actor's hand (hand IA) and over the trajectory of the hand movement (hand path IA). In addition, for the visually guided conditions, a circular IA was superimposed over the visual guides (VG IA). Dwell times for each of the IAs were averaged across trials and expressed as a percentage of the total dwell time. Other gaze metrics investigated included average fixation duration (in ms) and average saccade amplitude (in degrees of visual angle). Saccades were predefined as eye movements with velocities of more than 30°/s and accelerations above $8{,}000°/s^2$.

5.3.5.3 Motor-evoked potentials.

Analyses features of the data acquisition software (Signal v. 4.11, Cambridge Electronic Design Limited, Cambridge, UK) were used to analyse EMG data. A pre-stimulus interval of 90 ms was used to record background EMG; trials in which this value exceeded 100 μV were excluded from the analyses (1.93 % of all trials). Peak-to-peak amplitudes were measured for each MEP and averaged for each condition (raw amplitudes). Averaged amplitudes recorded during the first baseline period were compared to those recorded during the second baseline period; since tests revealed no significant differences between the two for all muscles of interest, the recorded amplitudes were averaged to obtain an overall baseline measure of corticospinal excitability. The averaged MEP amplitudes recorded in the various conditions were then normalised to the averaged baseline amplitudes and expressed as a percentage of change from baseline (normalised amplitudes).

For all analyses, significance levels were set at $p < .05$. Normality tests using Shapiro-Wilk revealed significant deviations from normality for a large number of variables; thus, MEP and gaze data were analysed using non-parametric tests. Bonferroni correction was used to correct for multiple post hoc tests.

5.4 Results

Preliminary analyses revealed that one participant was an outlier for the FDI amplitudes recorded in the VGM condition, and another participant was an outlier for the ADM amplitudes recorded in the FV condition. Three more participants were found to be univariate outliers for, respectively, fixation duration in condition VGM, total dwell time in condition FV, and dwell time on the hand and hand path in condition VGT. These data were thus discarded from the analyses.

5.4.1 Stanford Sleepiness Scale and sequence recall

Results revealed that alertness levels, as assessed using the SSS, did not differ across the four time-points (*M* = 2.40, *SEM* = 2.23). Sequence recall was high overall (*M* = 88.36, *SEM* = 4.34) and it did not differ between conditions.

5.4.2 Gaze data

Descriptive statistics are reported in Table 5.1. Separate Friedman ANOVAs were used to compare fixation durations and saccade amplitudes across the three conditions.

The ANOVA for fixation duration revealed significant differences between conditions, $\chi^2 = 9.3$, $p = .01$ (Figure 5.3A). Post hoc tests using Wilcoxon (Bonferroni corrected threshold = .017) revealed that fixation durations were shorter in the VGM condition, when gaze was kept on the FDI muscle, than they were in the VGT condition, in which the visual guide was placed over the targets, $Z = -2.46$, $p = .014$. Fixation durations in the VGM condition were also shorter than those in the FV condition, $Z = -2.43$, $p = .015$. Fixation durations did not differ between the FV and the VGT conditions, $Z = -.50$, $p = .61$.

The ANOVA for saccade amplitude revealed significant differences between conditions, $\chi^2 = 8.67$, $p = .013$ (Figure 5.3B). Post hoc tests using Wilcoxon (Bonferroni corrected threshold = .017) revealed that saccade amplitudes were smaller during FV than during the VGT condition, Z = -2.62, $p = .009$. Saccade amplitudes during FV also tended to be smaller than those during VGM, but this difference only approached significance, $Z = -2.31$, $p = .02$. No significant differences in saccade amplitudes were found between conditions VGT and VGM, $Z = -.16$, $p = .88$.

Table 5.1. *Fixation Duration (ms) and Saccade Amplitude (° of Visual Angle) – Descriptive Statistics*

Variable	Condition	*M*	*Mdn*	*SEM*	*SD*	*Min*	*Max*
Fixation duration	FV	388.95	375.06	31.02	142.14	231.65	772.45
	VGT	440.04	372.56	55.33	253.55	225.42	1201.47
	VGM	332.73	333.15	22.02	98.49	157.83	496.62
Saccade amplitude	FV	2.68	2.81	0.11	0.53	1.52	3.60
	VGT	3.00	2.93	0.14	0.64	2.10	4.52
	VGM	2.93	2.82	0.12	0.56	2.10	4.00

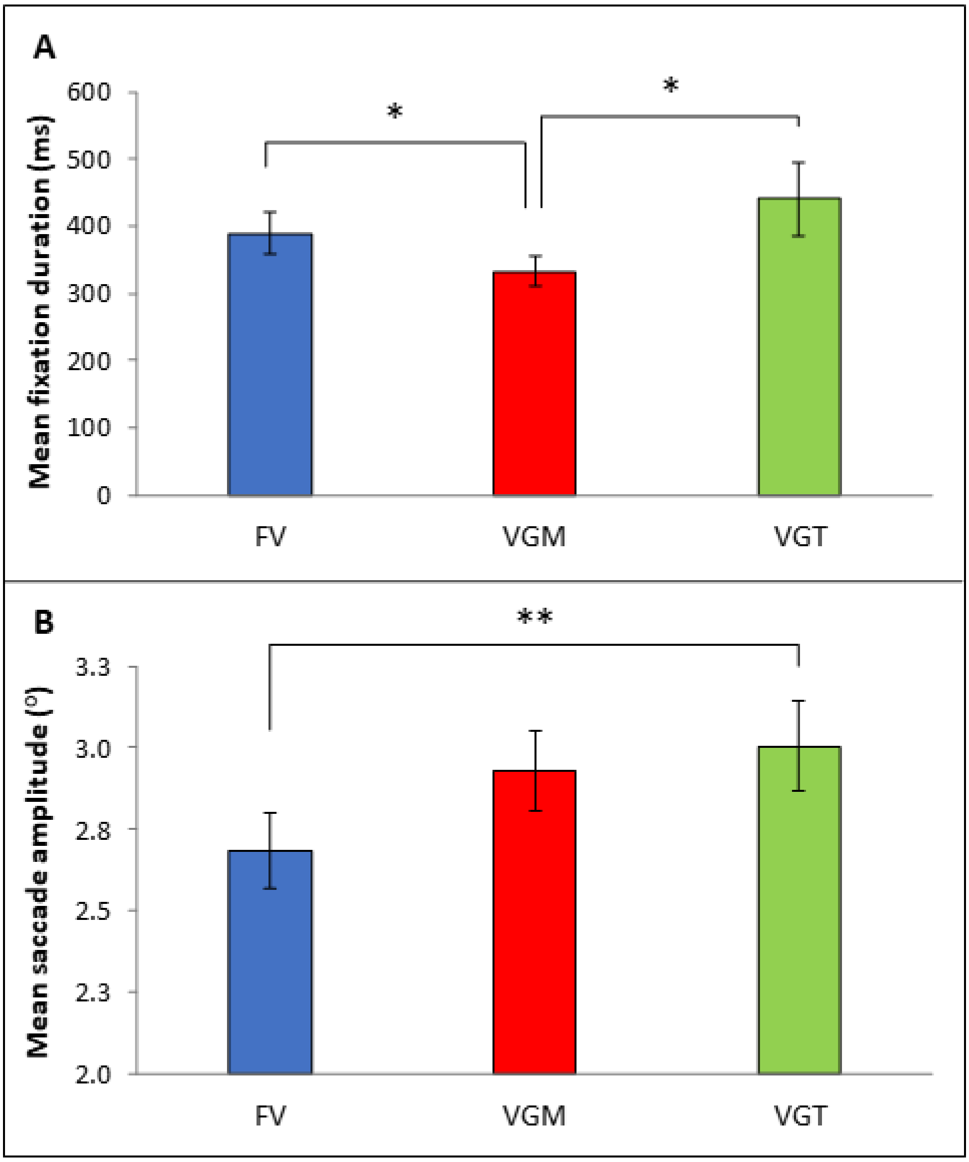

Figure 5.3. A: Mean fixation durations (in ms) for each of the three conditions, * $p \leq .015$. B: Mean saccade amplitude (in ° of visual angle) for each of the three conditions, ** $p = .009$. Error bars represent standard errors of the means.

5.4.3 Dwell times

Descriptive statistics are reported in Table 5.2. Separate Friedman ANOVAs were used to compare dwell times on the IAs across the various conditions. Results revealed significant between-condition differences in dwell times on each of the IAs (Figures 5.4 and 5.5).

For dwell time on the targets, results revealed significant differences between the conditions, $\chi^2 = 16.9$, $p < .001$. Dwell time on the targets was shorter when the visual guide was placed over the muscle compared to the FV condition, $Z = -3.88$, $p < .001$. Dwell time on the targets was also shorter during VGM than during VGT, $Z = -3.42$, $p = .001$. No significant difference was found between the VGT and the FV conditions $Z = -.26$, $p = .79$.

For dwell time on the hand, results revealed significant differences between the conditions, $\chi^2 = 15.47$, $p < .001$. Participants looked longer at the hand during condition VGM than during both free viewing, $Z = -3.47$, $p = .001$, and condition VGT, $Z = -3.66$, $p < .001$. No significant differences in dwell time on the hand were found between conditions FV and VGT, $Z = -.52$, $p = .60$.

For dwell time on the hand path, results revealed significant differences between the conditions, $\chi^2 = 8.03$, $p = .018$. Dwell time on the hand path was longer during VGM compared to VGT, $Z = -2.43$, $p = .015$. Dwell on the hand path also tended to be longer in condition VGM compared to condition FV, but this difference only approached significance, $Z = -2.35$, $p = .019$. No significant differences were found between conditions FV and VGT, $Z = -.28$, $p = .77$.

For dwell time on the visual guide, Wilcoxon test revealed that participants looked significantly longer at the guide when this was placed on the target compared to when it was placed on the FDI muscle, $Z = -3.67$, $p < .001$.

Table 5.2. *Dwell Time (%) on the IAs – Descriptive Statistics*

Condition	IA	*M*	*Mdn*	*SEM*	*SD*	*Min*	*Max*
FV	Targets	76.40	79.35	2.55	11.42	47.52	91.46
	Hand	8.33	6.00	1.68	7.53	1.66	28.90
	Hand path	1.56	0.87	0.42	1.90	0.00	6.92
VGT	Targets	73.75	78.62	4.49	20.58	21.08	94.82
	Hand	5.97	4.94	1.41	6.32	0.33	29.57
	Hand path	1.49	0.87	0.39	1.76	0.00	6.90
	VG	55.61	52.38	4.74	21.72	11.92	87.22
VGM	Targets	44.72	43.35	5.30	24.28	2.71	88.12
	Hand	20.72	19.08	2.68	12.28	3.88	55.13
	Hand path	2.81	3.07	0.38	1.73	0.45	6.04
	VG	23.90	24.87	3.90	17.89	0.44	55.39

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

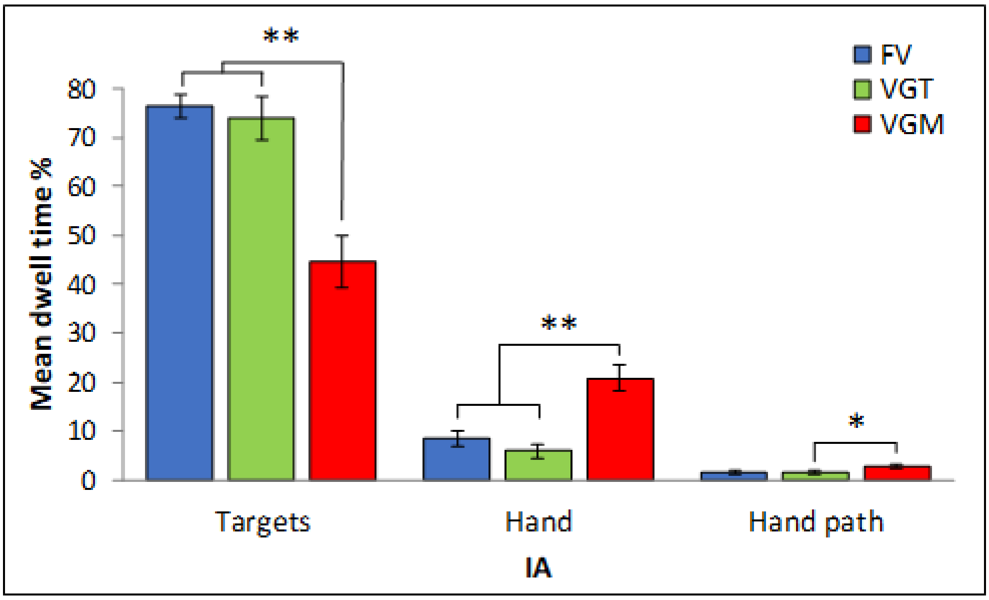

Figure 5.4. Mean dwell time (as a percentage of the total dwell time) on the various IAs in each of the three conditions. Error bars represent standard error of the means; * $p = .015$; ** $p \leq .001$.

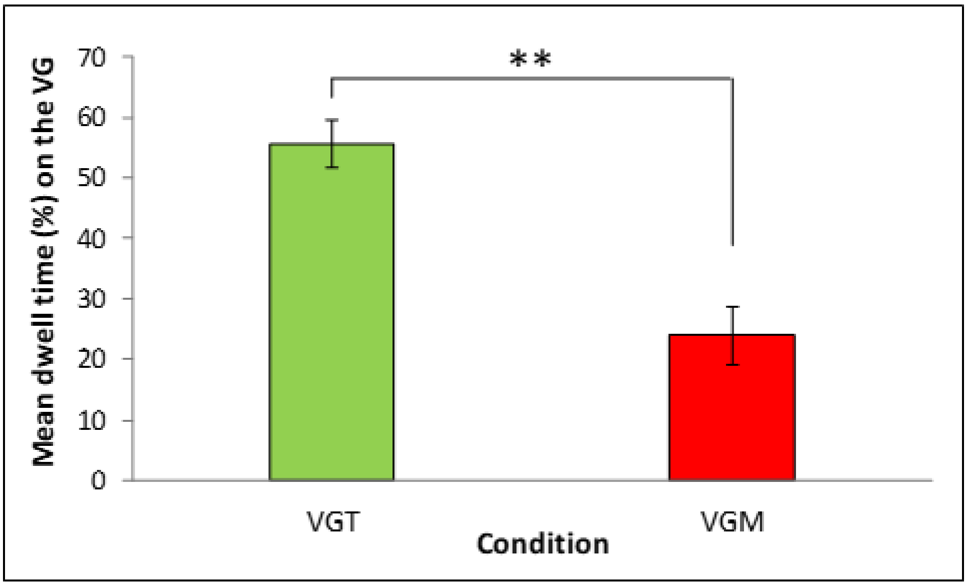

Figure 5.5. Mean dwell time (as a percentage of the total dwell time) on the visual guide in the two VG conditions. In condition VGT, the guide was placed on the targets; in condition VGM, the guide was placed on the FDI muscle. Error bars represent standard error of the means; ** $p < .001$.

5.4.4 MEPs

5.4.4.1 Raw amplitudes.

Descriptive statistics are reported in Table 5.3. In order to determine whether there was a facilitatory effect of task on corticospinal excitability, Friedman ANOVAs were used to compare the averaged raw amplitudes recorded during each of the three experimental conditions with those recorded during baseline. Results revealed that baseline amplitudes were significantly lower than those recorded in each of the experimental conditions, for all muscles (Figure 5.6). Specifically, for the APB, results revealed significant differences, $\chi2$ = 23.46, p < .001. Amplitudes recorded during baseline were significantly lower than those recorded in the other conditions, all p ≤ .001. For the FDI, results revealed significant differences, $\chi2$ = 23.00, p < .001. Amplitudes recorded during baseline were significantly lower than those recorded in the other conditions, all p ≤ .001. Similarly, for the ADM, results revealed significant differences, $\chi2$ = 18.14, p < .001. Amplitudes recorded during baseline were significantly lower than those recorded during each of the three experimental conditions, all p ≤ .001.

Table 5.3. *Raw MEP Amplitudes (mV) – Descriptive Statistics*

Muscle	Condition	*M*	*Mdn*	*SEM*	*SD*	*Min*	*Max*
APB	Baseline	1.17	0.67	0.24	1.09	0.07	4.30
	FV	1.69	1.31	0.30	1.36	0.15	6.21
	VGM	1.68	1.39	0.26	1.21	0.18	4.93
	VGT	1.80	1.58	0.32	1.47	0.20	6.71
FDI	Baseline	1.14	0.88	0.19	0.89	0.19	3.68
	FV	1.54	1.19	0.20	0.91	0.17	3.28
	VGM	1.71	1.37	0.24	1.11	0.52	4.11
	VGT	1.58	1.63	0.22	1.01	0.10	3.95
ADM	Baseline	0.53	0.46	0.09	0.40	0.07	1.61
	FV	0.76	0.67	0.12	0.54	0.14	2.21
	VGM	0.96	0.62	0.16	0.75	0.16	2.31
	VGT	1.00	0.92	0.18	0.83	0.22	3.40

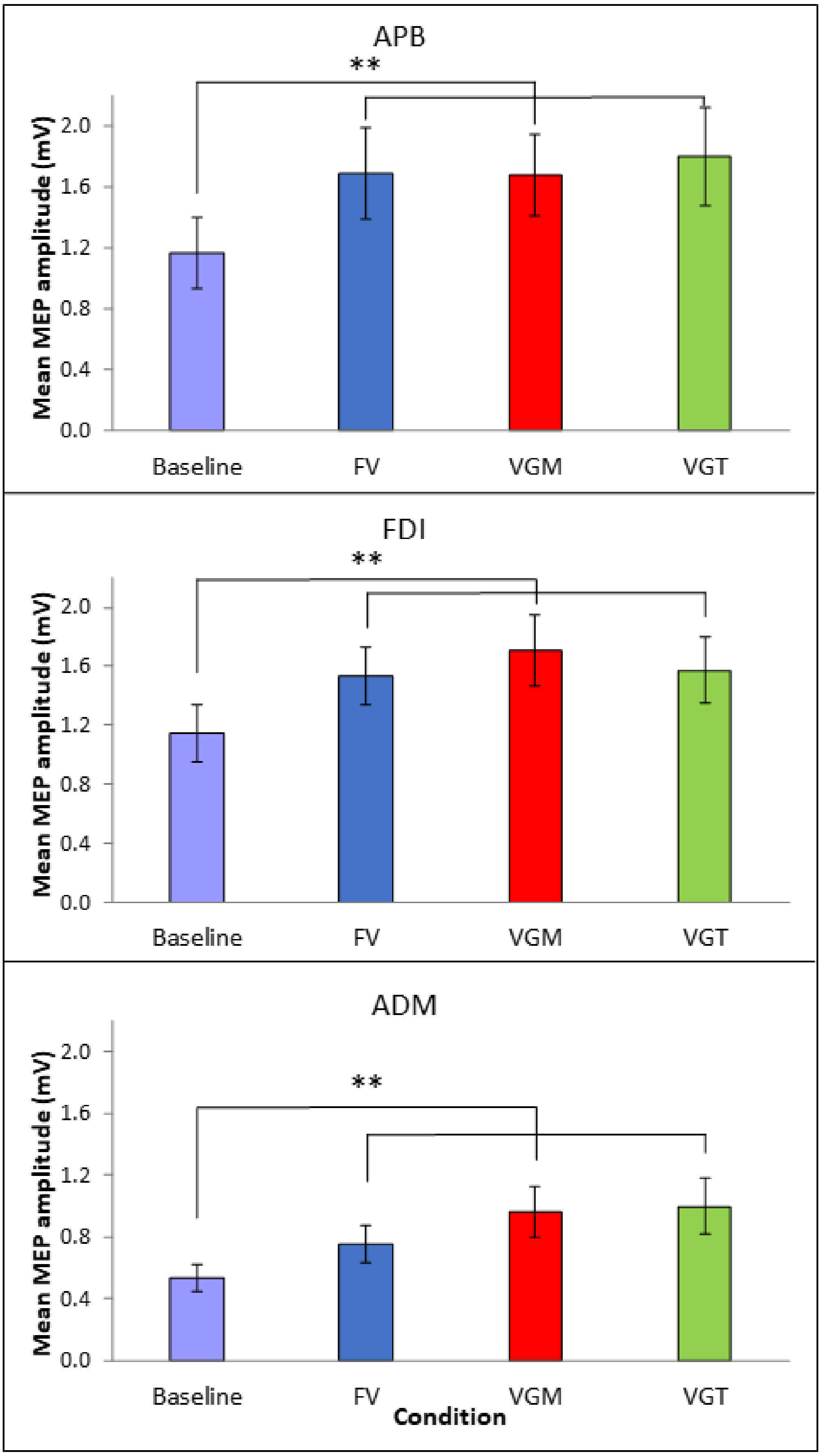

Figure 5.6. Mean raw MEP amplitudes (in mV) recorded from the three target muscles during baseline and in each condition. Error bars represent standard error of the means; ** $p \leq .001$.

5.4.4.2 Normalised amplitudes.

Descriptive statistics are reported in Table 5.4. Separate Friedman ANOVAs were used to compare MEP amplitudes recorded during the 3 conditions from, respectively, the APB, the FDI and the ADM. These revealed no significant differences between conditions for the APB, $\chi^2 = 1.14$, $p = .57$, the FDI, $\chi^2 = 2.80$, $p = .25$, or the ADM, $\chi^2 = 2.1$, $p = .35$.

Table 5.4. *Normalised MEP amplitudes (%) – Descriptive Statistics*

Muscle	Condition	*M*	*Mdn*	*SEM*	*SD*	*Min*	*Max*
APB	FV	72.00	65.56	13.68	62.69	-15.88	249.78
	VGM	78.69	66.92	16.19	74.17	-26.91	239.85
	VGT	78.42	62.85	16.20	74.22	-20.23	263.21
FDI	FV	51.85	47.59	11.78	53.97	-12.41	191.02
	VGM	62.76	52.97	12.88	57.62	-42.96	188.13
	VGT	51.71	37.08	12.38	56.74	-46.69	171.90
ADM	FV	44.43	37.18	11.63	52.01	-22.63	210.28
	VGM	93.34	60.73	21.59	98.92	-33.57	338.10
	VGT	110.34	75.29	26.01	119.20	-29.21	393.61

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

Separate Wilcoxon signed rank tests were conducted to determine whether normalised amplitudes recorded from each of the three muscles during each condition differed according to whether the actor's hand was grasping the target or whether it was in the hand-opening phase of the action. Descriptive statistics are reported in Table 5.5.

First, amplitudes recorded across the three conditions were averaged to obtain a total average amplitude value for MEPs recorded during the grasping phase and those recorded during hand opening. For the APB, results confirmed our hypotheses; amplitudes were larger during hand opening than during grasp, $Z = -1.79$, $p = .037$. The same was found for the ADM, $Z = -2.49$, $p = .007$. In contrast, no significant differences were found between the FDI amplitudes recorded during observation of the two phases of the action.

In order to determine whether the differences between amplitudes recorded during observation of the grasp and hand opening phase were affected by the gaze manipulation, separate Wilcoxon tests were conducted for each condition and for each muscle (Figure 5.7).

For the APB muscle, Wilcoxon tests revealed that in the FV condition, amplitudes recorded when observing the hand opening phase of the action were significantly higher than those recorded during observation of the grasp phase, *Z* = -1.72, *p* = .04. The same was found for the VGT condition, *Z* = -2.14, *p* = .017. In contrast, no significant differences were found in condition VGM, *Z* = -1.51, *p* = .13.

For the FDI muscle, no significant differences were found for amplitudes recorded in the two phases of conditions FV, *Z* = -1.13, *p* = .26, and VGT, *Z* = -.26, *p* = .79. In contrast, for condition VGM, amplitudes recorded during hand opening were significantly larger than those recorded during observation of grasping, *Z* = -1.68, *p* = .047.

For the ADM muscle, Wilcoxon test revealed significant differences in each of the three conditions. Specifically, amplitudes recorded during observation of the hand opening phase were larger than those during the grasping phase in all three conditions (FV *Z* = -2.58, *p* = .005; VGM *Z* = -1.72, *p* = .04; VGT *Z* = -1.93, *p* = .03).

5.4.5 Correlations between MEPs and gaze

In Study 2, we found a negative relationship between saccade amplitudes and MEP amplitudes; thus, Spearman's correlation was used to determine whether the amplitude of the saccades made by the participant during action observation was related to the normalised amplitude of the MEPs recorded in that condition. No significant correlations between MEP amplitude and saccade amplitude were found in conditions FV or VGT[1]. However, results revealed that, in condition VGM, the normalised amplitudes recorded from the APB and the FDI were negatively related to the amplitude of the saccades made in that condition, respectively, *r* = -.37, *p* = .05, and *r* = -.44, *p* = .026.

An additional Spearman's correlation was conducted to determine whether the normalised MEP amplitudes recorded from the target muscles in the three conditions were

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[1] **FV:** amplitudes recorded from APB were not significantly related to fixation duration, r_s = .18, *p* = .22, or saccade amplitude, r_s = -.12, *p* = .30. Amplitudes recorded from FDI were not significantly related to fixation duration, r_s = -.31, *p* = .08, or saccade amplitude, r_s = .003, *p* = .50. Amplitudes recorded from ADM were not significantly related to fixation duration, r_s = .08, *p* = .36, or saccade amplitude, r_s = .26, *p* = .13. **VGT:** amplitudes recorded from APB were not significantly related to fixation duration, r_s = .20, *p* = .19, or saccade amplitude, r_s = -.07, *p* = .38. Amplitudes recorded from FDI were not significantly related to fixation duration, r_s = -.27, *p* = .12, or saccade amplitude, r_s = -.20, *p* = .19. Amplitudes recorded from ADM were not significantly related to fixation duration, r_s = -.19, *p* = .20, or saccade amplitude, r_s = -.09, *p* = .34. **VGM:** amplitudes recorded from APB were not significantly related to fixation duration, r_s = -.23, *p* = .17. Amplitudes recorded from FDI were not significantly related to fixation duration, r_s = -.18, *p* = .22. Amplitudes recorded from ADM were not significantly related to fixation duration, r_s = .19, *p* = .21, or saccade amplitude, r_s = .21, *p* = .18.

related to the amount of time spent looking at the various IAs (dwell time). This analysis revealed that[2], in condition FV, normalised MEP amplitudes recorded from the APB and the FDI were both negatively correlated with dwell time on the hand path, respectively $r = -.48$, $p = .03$, and $r = -.60$, $p = .005$, whereas no significant correlations were found for the ADM. No significant correlations were found in condition VGM. In condition VGT, normalised MEP amplitudes recorded from the APB were positively correlated with dwell time on the targets, $r = .46$, $p = .04$.

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[2] **FV:** amplitudes recorded from APB were not significantly related to dwell time on the hand, $r_s = -.27$, $p = .25$, or targets, $r_s = .16$, $p = .50$. FDI MEP amplitudes were not significantly related to dwell time on the hand, $r_s = -.32$, $p = .17$, or targets, $r_s = .21$, $p = .37$. ADM MEP amplitudes were not related to dwell time on the hand, $r_s = -.13$, $p = .60$, hand path, $r_s = .10$, $p = .69$, or targets, $r_s = -.04$, $p = .86$. **VGT:** APB MEP amplitudes were not significantly related to dwell time on the hand, $r_s = -.22$, $p = .35$, or hand path, $r_s = -.30$, $p = .21$. FDI MEP amplitudes were not significantly related to dwell time on the hand, $r_s = -.19$, $p = .65$, hand path, $r_s = -.29$, $p = .22$, or targets, $r_s = .00$, $p = 1$. ADM MEP amplitudes were not related to dwell time on the hand, $r_s = -.14$, $p = .56$, hand path, $r_s = -.12$, $p = .62$, or targets, $r_s = -.04$, $p = .87$. **VGM:** APB MEP amplitudes were not significantly related to dwell time on the hand, $r_s = -.26$, $p = .25$, hand path, $r_s = -.27$, $p = .25$, or targets, $r_s = .15$, $p = .52$. FDI MEP amplitudes were not significantly related to dwell time on the hand, $r_s = -.21$, $p = .37$, hand path, $r_s = -.24$, $p = .31$, or targets, $r_s = .25$, $p = .30$. ADM MEP amplitudes were not related to dwell time on the hand, $r_s = -.03$, $p = .89$, hand path, $r_s = .18$, $p = .44$, or targets, $r_s = .03$, $p = .89$.

Table 5.5. *Normalised MEP Amplitudes (%) Recorded during Observation of Grasp vs Hand Opening – Descriptive Statistics.*

Muscle	Condition	Phase	*M*	*Mdn*	*SEM*	*SD*	*Min*	*Max*
APB	Overall	Grasp	66.74	73.87	10.33	47.33	0.62	141.52
		Open	85.52	61.67	16.16	74.06	-24.88	242.60
	FV	Grasp	62.87	59.68	11.46	52.52	-11.69	213.54
		Open	80.63	64.65	16.65	76.29	-31.41	283.57
	VGM	Grasp	68.69	55.96	14.70	67.35	-16.13	181.92
		Open	88.04	70.86	19.60	89.83	-40.38	301.52
	VGT	Grasp	68.65	71.49	12.82	58.76	-20.89	172.21
		Open	87.90	61.07	20.43	93.62	-19.55	355.46
FDI	Overall	Grasp	51.08	40.80	11.20	51.33	-38.18	207.92
		Open	56.29	34.31	12.69	58.14	-19.21	220.67
	FV	Grasp	48.68	43.06	13.26	60.75	-27.20	244.16
		Open	54.52	33.56	12.84	58.85	-8.59	221.31
	VGM	Grasp	58.90	53.32	12.67	56.68	-41.00	176.26
		Open	65.61	51.18	16.17	72.33	-45.31	243.01
	VGT	Grasp	50.28	47.05	12.16	55.72	-53.41	203.34
		Open	52.78	27.50	13.98	64.05	-39.93	223.44
ADM	Overall	Grasp	74.47	52.07	16.34	74.90	-14.29	318.05
		Open	99.97	88.35	21.85	100.13	-46.77	367.70
	FV	Grasp	30.62	20.29	7.83	35.03	-14.97	103.51
		Open	57.99	48.01	16.94	75.78	-38.71	324.51
	VGM	Grasp	80.43	44.08	21.18	97.05	-24.32	310.29
		Open	105.60	77.50	24.18	110.81	-52.65	365.82
	VGT	Grasp	98.66	68.39	24.26	111.16	-18.63	403.73
		Open	121.59	78.71	28.70	131.53	-48.95	403.95

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

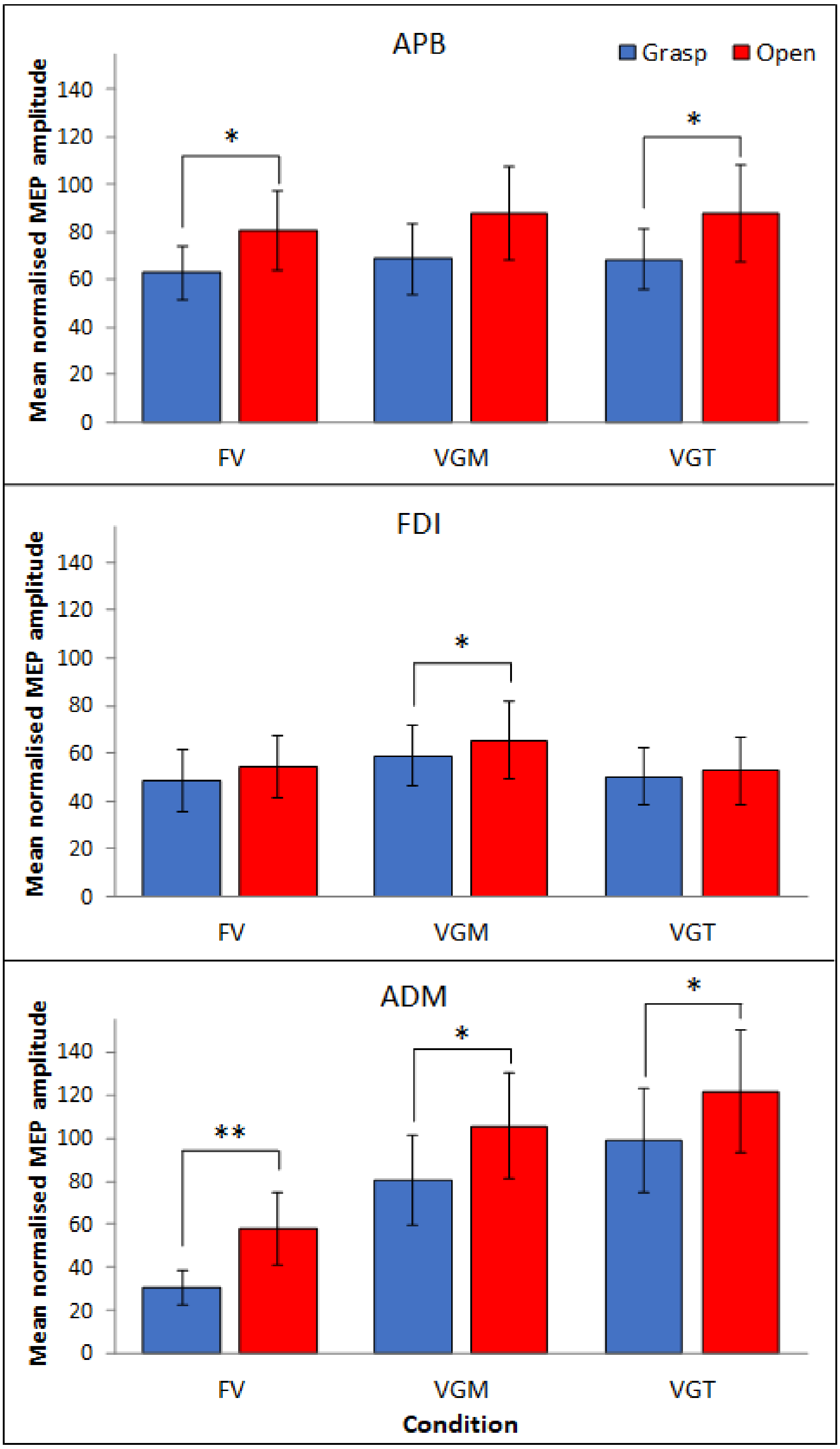

Figure 5.7. Mean normalised MEP amplitude (expressed as a percentage of the baseline condition) recorded from the three target muscles during observation of the two phases of the action. Error bars represent standard error of the means; * $p < .05$, ** $p = .005$.

5.5 Discussion

The aim of the present study was to investigate potential relationships between gaze and motor resonance during the observation of reach-to-grasp actions. Participants watched videos of an actor reaching for and grasping 6 targets in a sequence, with natural gaze behaviour or while maintaining their eyes on a target- or effector- based visual guide. No between-condition differences were found in overall levels of corticospinal excitability. However, findings revealed that, by directing gaze to the moving effector (i.e., the FDI), the characteristics and the location of eye movements were significantly altered, relative to free-viewing and target-directed gaze conditions. Furthermore, these changes in gaze behaviour were accompanied by a modulation of the phase-specific pattern of corticospinal excitability. The present results expand previous findings by showing that motor resonance during the observation of reach-to-grasp actions is related to how participants move their eyes, as well as where they direct their gaze.

Analysis of the gaze data revealed that a dynamic visual guide on the muscle was more effective at modifying natural gaze behaviour than a guide placed over the targets. In the VGT condition, a static visual guide appeared upon each target as the actor's hand left the table to reach towards it and it vanished when the fingers released the target, before reappearing over the next target. The sudden onset of the visual guide on the spatially removed targets required participants to perform large-amplitude eye movements so as to shift gaze to the highlighted location, resulting in larger saccade amplitudes compared to the free viewing condition. However, the amount of time that participants spent looking at the various IAs was comparable across FV and VGT. Thus, although placing the visual guide onto the targets resulted in larger saccadic amplitudes than the FV condition, it nevertheless allowed natural gaze behaviour to emerge. In both the free viewing and the VGT condition, the most fixated areas were the targets, whereas the actor's hand was viewed for a very small proportion of the overall dwell time. Research has shown that during performance and observation of object-directed actions, gaze is initially directed to the actor (Webb, Knott, & MacAskill, 2010). As soon as the target of the action can be inferred from the preshaping of the hand, gaze is directed to the forthcoming target in a proactive way (Ambrosini, Pezzulo, & Costantini, 2015), and it is maintained upon the target until the hand releases it, at which point it shifts towards the next target at around the time of hand-target contact (Flanagan & Johansson, 2003). Overt attention is thus largely maintained over the action targets; the actor's hands are hardly ever fixated, consistent with our findings.

In contrast, results revealed that directing participants' gaze onto the muscle significantly disrupted natural gaze behaviour, changing not only the low-level characteristics of participants' eye movements, but also the *location* of their gaze – i.e., the areas to which they directed their overt attention. In the VGM condition, the visual guide was placed on the FDI and it dynamically followed the muscle throughout the sequence of actions. Maintaining gaze on the moving guide thus required participants to track its motion using a combination of smooth pursuit eye movements, saccades and fixations. Accordingly, directing gaze onto the moving effector resulted in significantly shorter fixation durations, and tended to increase saccade amplitude – albeit not significantly so – compared to free viewing. Placing the visual guide on the muscle also changed dwell times on the various interest areas, reducing the amount of time that participants spent looking at the targets and increasing dwell on the hand and hand path compared to both the FV and the VGT conditions. Despite this, the most fixated areas in the VGM condition were still the targets, on which gaze was maintained for almost 45% of the time. This indicates that, although our participants did attempt to follow the VG, their attention was inherently drawn to the action targets, as per the natural gaze behaviour in the FV condition. Studies have shown that gaze behaviour is affected by the task goal and instructions (Flanagan & Johansson, 2003; Hayhoe & Ballard, 2005; A. M. Williams, Janelle, & Davids, 2004). In the present study, the participants' task was to observe the action with the intention of learning the observed sequences. Target-looking behaviour might have been encouraged by the inherent task-relevance of the targets; this may also explain why dwell time on the visual guide was lower in the VGM condition than during the VGT condition, in which the guide was already located over the action targets. Relatedly, higher dwell times on the hand path during VGM are likely due to the fact that, when switching from the targets to the visual guide, participants' gaze jumped ahead to the hand path. In addition, target-looking might have further been promoted by the fact that participants repeatedly observed the same actions; short-term experience with an action increases the predictive nature of gaze behaviour (Möller, Zimmer, & Aschersleben, 2015). Our gaze results thus show that the visual guides were effective in directing gaze, in that participants did maintain their eyes on them at least to some degree. However, it appears that the guide was somewhat harder to follow when it was dynamic (i.e., over the effector) than when it was comparatively static (i.e., over the targets). Accordingly, directing gaze to the FDI considerably disrupted the natural gaze behaviours otherwise adopted by the participant.

Results revealed that all the conditions were effective in eliciting motor resonance, as shown by the significantly larger amplitudes recorded during AO compared to those recorded during observation of a static hand. Observation of target-directed actions thus resulted in a covert activation of the associated motor representations, which is in line with the results of previous studies (e.g., Alaerts, Swinnen, & Wenderoth, 2010; Borroni & Baldissera, 2008; Enticott, Kennedy, Bradshaw, Rinehart, & Fitzgerald, 2010). Contrary to our predictions, however, we did not find any significant between-condition differences in the normalised amplitudes recorded from the three muscles, which suggests that our gaze manipulations were not effective in modulating overall levels of corticospinal excitability.

Previous studies have shown that, during the observation of reach-to-grasp actions, there is a facilitation of corticospinal excitability, in the hand muscles involved in the observed action, which is comparable to that observed during action execution. This facilitation has often been shown to be time-locked to the onset of the action, as well as phase-locked to its unfolding kinematics. For instance, during the execution of reach-to-grasp actions, the APB shows increased activity during reaching, and in particular during the hand opening phase, whereas FDI activation peaks during the grasp phase and it is minimal during reaching (Lemon, Johansson, & Westling, 1995). Similarly, during observation of a reaching and grasping action, FDI shows a suppression of activity during the hand opening phase – particularly at the beginning of the action – and a positive modulation during the finger closing phase (Borroni & Baldissera, 2008; Montagna, Cerri, Borroni, & Baldissera, 2005). Results revealed that, when considering the overall amplitudes regardless of condition, the expected phase-specific pattern of motor resonance was present in the APB: APB amplitudes were larger during observation of the hand opening phase compared to the grasp phase of the action. Contrary to our predictions, FDI amplitudes did not differ between observation of the two phases of the action, whereas ADM amplitudes showed the same pattern of phase-dependent modulation as those recorded from the APB.

Further analyses, however, revealed that the phase-specificity of the motor resonance response was modulated by our gaze manipulations. Specifically, we found that directing gaze to the moving effector (VGM condition) affected the pattern of motor resonance for both the APB and the FDI. During natural viewing, overt attention was predominantly maintained over the targets, and participants were able to map the observed action onto their motor repertoire – at least to some degree. The same was found for condition VGT, during which participants' gaze was similar to that adopted during free viewing. Accordingly, the APB showed phase-specific facilitation in conditions FV and VGT, but not in condition VGM: when gaze was directed to the FDI, although a trend towards phase-specific facilitation was still observable (see Figure 5.7), amplitudes recorded from the thumb during observation of the hand opening phase did not significantly differ from those recorded during observation of the grasp phase. This indicates that, by disrupting natural gaze, we can reduce phase-specific motor resonance in APB. The FDI, in contrast, tended to show larger amplitudes during observation of the hand opening phase than during observation of the grasp phase. This difference did not reach statistical significance during free viewing and when gaze was directed to the targets, but it became significant during VGM, when gaze was directed onto the FDI. Directing gaze to the FDI muscle thus resulted in a pattern of facilitation in the FDI that was opposite to the expected one. Since the FDI is a flexor of the index finger that acts as a prime mover during performance of precision grips, we expected to see greater facilitation during the grasp phase of the action compared to the hand opening phase. However, there is some evidence to show that, during action observation, the index finger flexors can display a pattern of facilitation opposite to that recorded during execution of the same actions. For instance, Gangitano, Mottaghy and Pascual-Leone (2001; 2004) found that, during viewing of reaching and grasping actions, FDI amplitudes were positively correlated with finger aperture (see also Baldissera, Cavallari, Craighero, & Fadiga, 2001). The pattern of FDI facilitation that we observed in condition VGM is thus consistent with these findings. Therefore, our results suggest that focusing point-of-gaze, and therefore overt visual attention, on the effector of an observed action may facilitate accurate mapping of the action onto the observer's motor repertoire.

The link between point-of-gaze and motor resonance was further confirmed by the results of our correlational analyses. These showed that, during free viewing, APB and FDI MEP amplitudes were negatively correlated with the amount of time that the participant spent looking at the hand path. The hand path IA did not contain any visual information about the effector, which may explain the negative relationship between resonance and dwell time on this area. Results also revealed that in the VGM condition, when natural gaze was disrupted by the introduction of the effector-based visual guide, a negative relationship emerged between saccade amplitude and the amplitude of the MEPs recorded from the APB and the FDI. This negative correlation between eye movement amplitude and corticospinal facilitation replicates the findings of Study 2, and is likely to have resulted from the inhibition of visual input that accompanies saccadic eye movements (e.g., Bansal, Jayet Bray, Peterson, & Joiner, 2015; Ross, Morrone, Goldberg, & Burr, 2001). Accordingly, in the present study, when gaze was directed to the moving effector, fixation durations decreased, and saccade amplitudes tended to increase compared to when the action was viewed with natural gaze. In addition, in the VGM condition, amplitudes recorded from the APB were positively correlated with dwell time on the targets. Participants tended to look at the targets even when the visual guide was located over the muscle, as per the natural gaze behaviour adopted during free viewing, and this was associated with increased APB amplitudes. Consistent with our previous findings, the present results suggest that participants' point-of-gaze and eye movement characteristics are important factors to consider when assessing AO-induced corticospinal facilitation.

Cavallo and colleagues (Cavallo, Bucchioni, Castiello, & Becchio, 2013) reported that, when viewing others' actions, motor plans corresponding to the action goal are initially loaded before movement onset; at movement onset, motor excitability is modulated according to situational constraints, and it reflects the pattern necessary to achieve the action goal. During movement observation, however, the type of movement and the effector are taken into account, and there is a transition towards phase-specific modulation (Cavallo et al., 2013). In line with this, the presence of contextual precues containing information about the type of grasp required to perform the observed action has been shown to evoke anticipatory modulations in M1 already during observation of the reaching phase of the action (de Beukelaar et al., 2016). These findings may help to explain why we did not always observe phase-specific facilitation in the present study. The targets were visible from the onset of the video, and so the participants could see that a precision grip was required, which possibly resulted in a pre-loading of the motor plan prior to movement onset. Once the hand started to move, natural gaze allowed our participants to observe the movement so as to modulate the motor plan for the thumb in a phase-specific and time-locked way, based on the relative kinematics of the hand and fingers. Accordingly, phase-specific facilitation was enhanced in APB during conditions FV and VGT. In contrast, when natural gaze behaviour was disrupted by instructing participants to maintain their eyes on a visual guide that followed the FDI throughout the movement, this modulation was significant only for the muscle on which the eyes were focused.

Our results showed that ADM amplitudes were facilitated from baseline, and that amplitudes recorded during observation of the hand opening phase were higher than those recorded during observation of the grasp phase. Since the ADM is not directly involved in the action, we did not expect to find any differences in the modulations of ADM amplitudes based on the kinematics of the action. However, there is evidence that AO-induced facilitation can occur also in muscles which are not directly involved in the observed action (Borroni & Baldissera, 2008). This appears to be the case in particular for the ADM muscle, the excitability of which can be facilitated by the observation of, for example, thumb (Study

2) or index finger movements (Lepage, Tremblay, & Théoret, 2010). One possible explanation for this seemingly anomalous finding is that some degree of abduction of the little finger always accompanies thumb abduction in everyday reach-to-grasp movements (Mason, Gomez, & Ebner, 2001), a phenomenon that is consequently mirrored in motor resonance.

In recent years, researchers have started to investigate how observers' point-of-gaze and attentional allocation modulate the AO-induced effects on corticospinal excitability – with mixed results. Some studies have found that allocation of overt attention to an action is not sufficient to elicit motor resonance (e.g., Chong et al., 2008; Chong et al., 2009; Woodruff & Klein, 2013). Recently, Betti and colleagues (2017) reported that diversion of participants' covert attention away from an observed action by introduction of a sudden-onset distractor stimulus, reduced motor resonance despite the fact that gaze was maintained over the effector of the action, suggesting a dissociation between point-of-gaze and corticospinal excitability during AO. However, consistent with our findings, there also is evidence in support of a link between gaze and motor resonance. When actions are presented in the peripheral visual field, AO-induced facilitation of MEP amplitudes loses its kinematic specificity and mirror responses consequently become less accurate (Leonetti et al., 2015). Furthermore, the findings of Study 2 showed that MEP amplitude during AO decreases with increasing saccade amplitude, and it is modulated by the locus of participants' fixations. The discrepancy between studies which have reported the existence of a relationship between gaze behaviour and corticospinal excitability during AO, and those reporting evidence against such a relationship, may be explained by the fact that point-of-gaze does not necessarily ensure information pickup. Studies have shown that fixation of gaze on a salient but task-irrelevant object does not guarantee that the object will be noticed (Drew, Võ, & Wolfe, 2013; Droll, Hayhoe, Triesch, & Sullivan, 2005). This represents one of the inherent problems of eye tracking studies, which is that eye movements do not allow us to directly infer cognitive processing: looking does not equal seeing (e.g., Kok & Jarodzka, 2017; A. M. Williams et al., 2004), and attention can be shifted covertly, in the absence of eye movements (Posner, 1980).

Despite this, however, eye movements are necessarily accompanied by shifts in attention, which shows that there often is a close coupling between gaze behaviour and attentional allocation (Rayner, 1998; Shepherd et al., 1986). Therefore, it can be argued that, rather than being related to point-of-gaze *per se*, the modulations in the phase-specific motor resonance we observed may have been due to attentional allocation. Focusing point-of-gaze on a specific location may help us distribute covert attention on and around the locus of eye fixation, thus leading to more efficient information pickup and processing. This proposition is supported by the findings of studies on multiple object tracking, which show that, when tracking the motion of multiple objects amongst an array of distractors, observers typically focus their gaze on a point close to the centre of mass of the set of moving targets (Fehd & Seiffert, 2010; Zelinsky & Neider, 2008). This strategy is beneficial to task performance because it enables observers to covertly distribute their attention around the targets, which are monitored and tracked through peripheral vision (Vater, Kredel, & Hossner, 2017). Directing observers' overt attention during AO in such a way as to facilitate the allocation and distribution of covert attention to the various aspects of the action may therefore facilitate information pickup (Study 1).

There are some limitations to the present study. A main limitation is that we inferred muscle activation during AO based on the known anatomical and functional characteristics of the muscles involved, failing to record EMG activity during physical execution of the observed actions. Although our results confirmed the expected pattern of activation for one of our target muscles (i.e., the APB), this was not the case for the other two muscles. It would have been preferable to obtain EMG recordings during actual execution of the actions displayed in our videos. This would have allowed us to determine with more certainty the correspondence between the EMG profile recruited during action execution and that elicited by observation of the same action (Moriuchi et al., 2017; Naish, Houston-Price, Bremner, & Holmes, 2014).

Another potential problem with the present study lies in the TMS stimulation times we selected. In order to optimise the total testing time and not impose excessively long sessions to the participants, we chose to deliver several pulses during each video presentation, rather than only providing one TMS stimulation per trial. As a result, TMS pulses were delivered at intervals of ~1.5 seconds, which represents a higher frequency than what is commonly used in single-pulse TMS experiments. Typically, longer intervals are selected in order to prevent the TMS-induced changes in excitability from carrying over between two consecutive MEPs. It is possible that the short interpulse interval we selected did not allow sufficient time for CE to return to its pre-TMS pulse levels, which may explain why, in some cases, we observed generalised rather than phase-specific facilitation. In addition, since no figure-of-eight coils were available to us at the time of testing, we necessarily had to employ a circular coil. Compared to figure-of-eight coils, circular coils produce a stronger and less focal magnetic field, which might have further reduced the likelihood of finding phase-specific facilitation of MEP amplitudes. Nevertheless, our results still show phase-specificity to some degree, which suggests that the methods employed in the present study were effective in assessing subtle AO-induced modulations in CE.

Finally, it could be argued that the introduction of a sequence learning element into the observation task may have detracted resources from the action-observation system, affecting the results. However, we did find significant facilitation of amplitudes during observation of the reaching and grasping actions compared to observation of a static hand – and this facilitation was also, to some degree, muscle-specific. In addition, error rates for sequence recall were very low overall, suggesting that the learning task is unlikely to have resulted in considerable cognitive effort. Nevertheless, it would have been preferable to include an additional condition which did not require participants to learn the observed sequence. Future studies should compare motor resonance during observational learning of novel movements of different complexities with that observed during sequence learning; this will allow us to determine whether, during sequence learning, the attentional resources needed for the task are detracted from the MNS.

To conclude, the results of the present study contribute to the existing knowledge by showing for the first time that gaze behaviour during observation of transitive actions modulates the accuracy with which observers map others' actions into their own motor repertoire. Although our gaze manipulations did not increase overall levels of corticospinal facilitation compared to when the actions were viewed with natural gaze behaviour, they nevertheless affected the phase-specific motor resonance response. Phase-specific facilitation was enhanced in the APB under conditions of natural gaze behaviour, whereas it increased in the FDI when participants' eyes were directed to a location overlaying the index finger flexor. The strength and the accuracy of the motor resonance response can be regarded as an index of the observer's experience with the viewed action (Calvo-Merino et al., 2005; Cannon et al., 2016), and they are related to the amount of observational learning (Aridan & Mukamel, 2016; Frey & Gerry, 2006; Krüger et al., 2014). Therefore, by finding ways to optimise covert activation of the motor representations of an action, thereby accurately matching the responses of the motor system to the kinematics of the observed action, we may facilitate learning of novel actions. The results of the present study suggest that this could be achieved through the use of exogenous visual guidance. However, the ways in which gaze behaviour and attentional allocation modulate motor resonance need to be investigated further, so as to establish the relative contributions of overt and covert attention to AO-based interventions for the (re)learning of motor skills.

5.6 References

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6 Chapter 6:

Study 4. Observation of a complex whole-body action promotes gaze-linked increases in corticospinal excitability relative to a simple grasping action

6.1 Abstract

Action observation elicits changes in the observer's brain which resemble those resulting from action execution. This effect is known as motor resonance, and it is thought to support a number of functions, including the ability to understand and imitate others' actions. Neuroimaging studies have shown that motor resonance is modulated by the observer's familiarity with an action. In two previous studies, we found evidence of a relationship between gaze behaviour and motor resonance during viewing of simple thumb movements and reach-to-grasp actions, suggesting that the extent of motor resonance may be dependent upon the locus of fixation. The aim of the present study was to investigate the relationship between gaze and motor resonance during observation of a complex goal-directed action and of a comparatively simple action. Novice and expert golfers watched videos of the golf swing and of a reach-grasp-lift (RGL) action while we tracked their eye movements and recorded MEPs from three forearm muscles. Results revealed that gaze behaviour varied according to characteristics of the observed action, and this was manifested in MEP amplitude: in the RGL condition, participants predominantly maintained their gaze on the target, and this was associated with reduced MEP amplitudes. Consequently, viewing of the RGL did not result in significant facilitation of amplitudes from baseline. In contrast, there was a significant increase in MEP amplitudes during observation of the golf swing; amplitudes were positively correlated with time spent looking at the model's arms or adjacent regions. No expertise-related differences were found in either eye movements or motor resonance. Results suggest that, by adopting specific gaze behaviours during action observation, we may maximise motor resonance, a finding which has implications for observational learning and re-learning of motor skills of varying complexity.

6.2 Introduction

Observational learning is thought to depend on the repeated activation of the same motor representations that are recruited during action execution (Ray, Dewey, Kooistra, & Welsh, 2013). In line with this, studies have identified a network of brain areas which show similar responses during action observation and action execution (Fabbri-Destro & Rizzolatti, 2008; Rizzolatti & Sinigaglia, 2016). This network, also known as action-observation network (AON, Cross, Hamilton, & Grafton, 2006) or mirror neuron system (MNS, e.g., Casile, Caggiano, & Ferrari, 2011), is finely tuned to the motor capabilities of the observer (Orlandi, Zani, & Proverbio, 2017). Using fMRI, researchers have shown that experience with an action is reflected in greater activation in a number of cortical regions during observation of that action (e.g., Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Wimshurst, Sowden, & Wright, 2016). Cross, Hamilton and Grafton (2006) trained participants to perform dance sequences for five weeks. Following training, participants observed videos of the practiced sequences as well as of novel, unfamiliar sequences. The authors reported that observation of the practiced sequences elicited greater activation in MNS areas. This increased activity is specifically related to the observer's motor, rather than visual, familiarity with an action. For instance, expert dancers showed greater MNS activation when observing the dance style in which they were trained, compared to an untrained but motorically similar dance style (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005). Similarly, expert female and male ballet dancers exhibited stronger motor resonance during observation of gender-specific dance moves belonging to their own motor repertoire than during viewing of opposite-gender moves that they frequently saw but did not perform (Calvo-Merino et al., 2006). Evidence so far thus indicates that the mirror response depends on the degree to which an observed action is already present in the observer's own motor repertoire, to the extent that motor resonance may be regarded as an index of motor expertise and learning.

Some TMS studies have shown that physical practice and visual familiarity with simple finger movements or single-limb actions result in changes in corticospinal excitability as well as in the cortical representation of a movement (Stefan, Classen, Celnik, & Cohen, 2008; Tyc & Boyadjian, 2011). However, TMS evidence of expertise-dependent modulation of corticospinal excitability during the observation of complex actions is scarce and contradictory. Aglioti and colleagues (Aglioti, Cesari, Romani, & Urgesi, 2008) investigated the effects of motor and visual expertise on motor resonance in the context of basketball free throws. They found that expert players were able to anticipate the fate of the observed shots earlier and more accurately than both novices and expert watchers. Consistent with fMRI findings, this ability was reflected in a selective increase in corticospinal excitability for an intrinsic hand muscle that becomes most active in the latter phase of the throwing action – the abductor digiti minimi. However, there is also evidence of partially muscle-specific facilitation during viewing of live dance sequences in participants with no visual or motor experience of the observed action (Jola & Grosbras, 2013). Jola, Abedian-Amiri, Kuppuswamy, Pollick, and Grosbras (2012) showed live performances of non-dance movements, ballet and Indian dance to participants who were experienced observers of these styles, and to novices; MEPs were recorded from forearm and hand muscles involved in both dance forms. Amplitudes recorded from the ballet spectators were larger during observation of ballet than during viewing of Indian dance, but no differences were found for the Indian dance spectators. Thus, it is not clear whether expertise-related changes in corticospinal excitability follow the same pattern as the changes in neural activation reported by neuroimaging studies.

Gaze and visual attention play a key role in the context of action observation. During the performance of everyday actions, individuals typically direct their eyes only to locations or objects which are relevant to the task at hand, while irrelevant areas are hardly ever fixated (Hayhoe, 2000; Land, Mennie, & Rusted, 1999). Fixations are directed to the target of an action even before movement onset, indicating that oculomotor plans are used to locate objects and guide and monitor movements (Land & Hayhoe, 2001). 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 (Flanagan & Johansson, 2003; Flanagan, Rotman, Reichelt, & Johansson, 2013). Through experience with our environment, we acquire visuomotor representations of actions, which also include information about the properties of objects; these models are used to control and coordinate movement and to predict the future sensory state of events, which results in highly precise and predictive shifts of visual attention (Hayhoe, McKinney, Chajka, & Pelz, 2012). Although visual attention can be shifted covertly, in the absence of overt eye movements (Posner, 1980; Ryu, Kim, Abernethy, & Mann, 2013), visual search behaviour and eye fixations are generally regarded as an index of attentional allocation and information processing (Irwin, 2012; e.g., Shepherd, Findlay, & Hockey, 1986; Treue, 2003). Attending to potentially informative stimuli is thus fundamental for extracting and processing task-relevant information.

The importance of gaze for information pickup is supported by the findings of the present body of work. In Study 1, we demonstrated that attending to task-relevant areas during observational learning can facilitate acquisition of a complex motor skill. In the subsequent studies, we then found evidence of a link between attention and motor resonance. Specifically, in Study 2 we showed that, by asking observers to anchor their gaze on a location directly over the moving effector during viewing of thumb movements, we could maximise motor resonance in the corresponding muscle relative to a condition in which the eyes were free to move. In Study 3, we found that disrupting the natural gaze behaviour typically adopted during observation of transitive actions modulated the phase-specific pattern of motor resonance in two hand muscles. In line with these findings, the pattern of AO-induced facilitation in corticospinal excitability becomes coarser and loses its muscle specificity when actions are presented in the peripheral visual field (Leonetti et al., 2015), or when covert attention is diverted away from the action by the introduction of a secondary task (Puglisi et al., 2017). The evidence available thus far therefore suggests that the beneficial effects of visual guidance for learning may be due to the link between motor resonance and gaze. Observational learning relies on the covert activation of the motor representations of an action, and the way in which we observe an action appears to modulate the extent of this activation. Therefore, considering also that motor resonance is a sign that an observed action has been mapped onto the observer's motor repertoire, establishing what types of gaze behaviour can effectively optimise motor resonance may allow us to maximise the beneficial effects of AO.

As highlighted above, our eye movements when observing an action are modulated by our experience with that action. Studies of skill-related differences in gaze behaviour have shown that experts' gaze patterns differ considerably from those of novices in many domains (Gegenfurtner, Lehtinen, & Säljö, 2011), including surgery (e.g., see Hermens, Flin, & Ahmed, 2013, for a review), helicopter landing (Robinski & Stein, 2013), and sports (A. M. Williams & Davids, 1998). Skilled performers have a greater ability to focus on and interpret relevant cues, whilst ignoring irrelevant information (Balslev et al., 2012; Jarodzka, Scheiter, Gerjets, & van Gog, 2010). They are able to vary the breadth of their attentional focus (Pesce, Cereatti, Casella, Baldari, & Capranica, 2007), and to efficiently switch between different patterns of visual search depending on the sources of information available (Memmert, 2009; A. M. Williams, 2000). For example, in dynamic decision-making tasks where there are multiple response options (e.g., multi-player scenarios), skilled performers exhibit a high visual search rate, characterized by more fixations of shorter duration. In contrast, when response options are relatively limited, experts tend to employ fewer fixations of longer duration (Piras, Lobietti, & Squatrito, 2010; A. M. Williams & Davids, 1998). Such findings have led to a general agreement in the literature that eye movements are an index of learning and skill acquisition (e.g., Hayhoe et al., 2012).

Identification of expertise-related differences in gaze behaviour has led to the development of perceptual training approaches aimed at directing learners' visual attention to key areas or elements of the display. Attentional guidance has been implemented by highlighting task-relevant regions derived from studies on experts' gaze, or by directly superimposing skilled performers' eye movement patterns over the display. These techniques have in some cases been effective in improving the decision making skills of novice performers – both in sport (Abernethy, Schorer, Jackson, & Hagemann, 2012; Ryu, Abernethy, Mann, Poolton, & Gorman, 2013), and domains such as laparoscopic surgery and other medical training (Chetwood et al., 2012; Litchfield, Ball, Donovan, Manning, & Crawford, 2010; Vine, Masters, McGrath, Bright, & Wilson, 2012) and radiography diagnosis. Visual guidance has also been used to accelerate acquisition of novel motor skills. In Study 1, we employed translucent visual cues to highlight areas containing key postural information during observational learning of the golf swing. Our results showed that the performance of the group who received visual guidance improved at a faster rate compared to a free viewing group and a control group, indicating that, by directing novices' attention to informative areas, we may expedite their acquisition of a complex motor skill. The evidence presented so far indicates that visual attentional guidance approaches represent a promising avenue for enhancing, inter alia, motor skill acquisition. Given the apparent efficacy of using experts' gaze patterns to train those of novices, it is a logical and necessary step to examine not only expert-novice differences in gaze as they observe complex motor skill execution, but also the impact of those gaze strategies on motor resonance.

The aim of the present study was to expand our previous results by examining the ways in which eye movements interact with motor resonance during the observation of complex, whole-body actions. In Study 1, we showed that gaze behaviour appears to change, necessarily, as an observed complex action becomes more dynamic in nature. Moreover, the results of Studies 2 and 3 showed that motor resonance may be somewhat contingent on the locus of fixation. Considering these notions, along with modulatory effects of motor expertise on corticospinal excitability (Aglioti et al., 2008), we used TMS to investigate gaze- and expertise-related modulations of corticospinal excitability during observation of a highly coordinative action – the full golf swing. Specifically, we compared differences in novice and expert golfers' gaze behaviour and corticospinal excitability (CE) as they observed a skilled model perform the full golf swing, and contrasted them with their gaze patterns and CE as they viewed a comparatively simple reach-grasp-lift (RGL) action. Based on previous findings that revealed temporal modulation of the motor resonance effect according to observed kinematics (e.g., Gangitano, Mottaghy, & Pascual-Leone, 2001), we anticipated that the pattern of MEP modulations recorded during observation of the golf swing would be tightly coupled with the time course of the action, reflecting time-dependent peaks in activation of forearm muscles during action execution. We also expected this pattern of activation to be more noticeable in expert golfers, due to their greater familiarity with the observed action. In contrast, we anticipated that no expertise-related differences in corticospinal excitability would emerge during the observation of a simple RGL action. Finally, we predicted that there would be expertise- and task-related differences in gaze behaviour – notably, that experts would tend to fixate more on information-rich areas during the golf observation task, and that no such differences would emerge for the RGL task.

6.3 Methods

6.3.1 Participants

The study was approved on behalf of the Brunel University London Research Ethics Committee (Appendix L) and was conducted in accordance with the standards of the Declaration of Helsinki (2008). Subsequent to providing their written informed consent (see Appendix M), a total of 18 participants took part. Of these, ten had 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 handicaps ranging from 0 to 15 (*M* = 6.75, *SD* = 4.56; Appendix N). Participants had normal or corrected-to-normal vision, and were all right-handed, as assessed using the Edinburgh Handedness Inventory (Oldfield, 1971), *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 (Rossi, Hallett, Rossini, Pascual-Leone, & The Safety of TMS Consensus Group, 2009; Wassermann, 1998). None of them reported any discomfort or adverse effects during the TMS protocol.

6.3.2 Experimental stimuli

Videos were recorded using a Canon XF105 HD camcorder (Canon Inc., Tokyo, Japan). Golf swing 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 (Figure 6.1A). The reach-grasp-lift (RGL) videos displayed a side view of a male model's forearm reaching for, grasping and lifting a 2-litre bottle full of coloured water, also viewed from a third-person perspective (Figure 6.1B). Videos started with a 2-second grey screen; each golf swing video lasted approximately 6 seconds, and each RGL video lasted approximately 8 seconds.

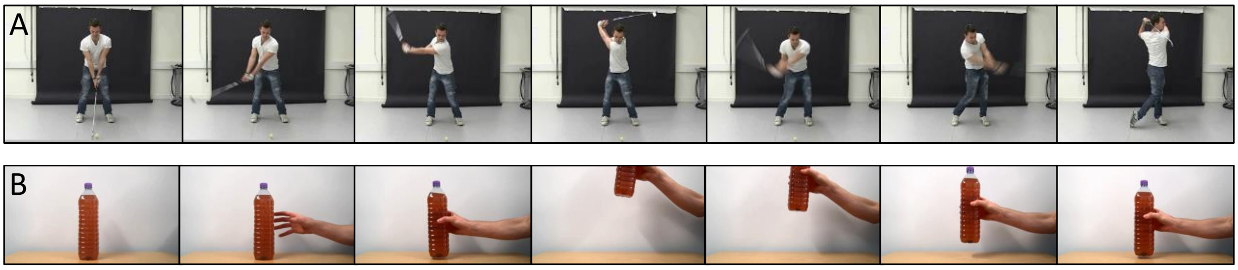

Figure 6.1. Sequential screenshots taken from the golf (A) and RGL (B) videos.

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 x 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.

6.3.3 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 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 on the scalp with side A visible so as to induce a posterior-to-anterior current flow in order to achieve optimal stimulation of the left hemisphere (e.g., see Epstein, 2008). Participants wore a tight-fitting swim cap. The distance between the inter-aural points and that between the nasion and the 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 µV from at least 5 out of 10 consecutive stimulations (Rossini et al., 1994), 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%).

6.3.4 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 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 corticospinal excitability 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; one TMS pulse was delivered in each RGL video at pseudo-random timings during the lifting phase of the action (cf Alaerts et al., 2010). A second block consisted of 120 iterations of the golf swing video, divided into four counterbalanced conditions comprising 30 repetitions, each with a different stimulation time: i) 4000 ms, coinciding with the backswing phase of the action; ii) 4720 ms, coinciding with the forward swing; iii) 4850 ms, coinciding with the acceleration phase; and iii) 5200 ms, coinciding with the follow-through phase. These timings were determined by previous research, which shows that FCR, FCU and ECR activity are differentiated according to the phase of the swing (Marta, Silva, Castro, Pezarat-Correia, & Cabri, 2012). 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 relatively lower in the acceleration, forward swing and follow-through phases, again in descending order. We selected stimulation times to coincide with these peaks so as to determine whether the pattern of AO-induced facilitation followed the same time course of activation as that recorded during action execution. In order to promote participants' attention to the task, a small number of novel videos were interspersed within each of the golf 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. However, it was emphasised that the task of primary importance was to attentively observe all videos.

Past research has shown that the goal of the observation task affects the degree to which mirror neuron areas are recruited (e.g., Decety, 1996); notably, they are recruited to a larger extent when observing with the intention to imitate, when compared to passive viewing or action recognition tasks (Roosink & Zijdewind, 2010). 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 models.

Finally, concurrent motor imagery and action observation have been shown to lead to a greater corticospinal facilitation compared to either in isolation (Sakamoto, Muraoka, Mizuguchi, & Kanosue, 2009; Wright, Williams, & Holmes, 2014). In order to monitor participants' engagement in MI and avoid possible confounds resulting from the interaction between AO- and MI-induced modulations in corticospinal excitability, participants were asked to fill in a brief questionnaire after each block, to determine their engagement with imagery during video viewing (Appendix O). 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 hours. The experimenter regularly monitored the participants' comfort, attentiveness and alertness throughout the protocol.

6.3.5 Data processing and analysis

6.3.5.1 Gaze data.

Gaze data were analysed using Data Viewer (SR Research Ltd., Ontario, Canada). Fixations were defined as eye movements with velocities of less than 30°/s and accelerations below 8,000°/s2; saccades were defined as eye movements with velocities and accelerations above these parameters. For analysis purposes, the golf 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. Study 1). Dynamic interest areas (IAs) were superimposed over the different elements of the videos. For the golf 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 saccade 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.

6.3.5.2 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 microvolts 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 $p > .05$), indicating that there was no overall change in corticospinal excitability over time. Thus, amplitudes recorded in the two baseline periods were averaged so as to get a total baseline measure of corticospinal excitability. 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.

Significance levels were set at $p < .05$. Where the assumption of sphericity was violated, degrees of freedom are reported using Greenhouse-Geisser correction.

6.4 Results

6.4.1 Gaze data

6.4.1.1 Fixation duration and saccadic amplitude.

Descriptive statistics are reported in Table 6.1. Fixation durations and saccadic amplitudes were analysed using two separate Group (expert/novice) x Condition (RGL/golf) mixed ANOVAs. For fixation duration (Figure 6.2A), 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 than they were in the golf condition. The Group x Condition interaction only approached significance, $F(1,16) = 3.16$, $p = .095$, $\eta_p^2 = .17$. As can be seen in Figure 6.2A, novices tended to show greater reductions in fixation durations from the RGL to the golf condition compared to experts. The main effect of Group was not significant, $F(1,16) = 2.68$, $p = .12$, $\eta_p^2 = .14$. For saccade amplitude (Figure 6.2B), the ANOVA did not reveal any significant main effects or interactions[1].

Two additional Phase (static/dynamic) x Group (expert/novice) mixed ANOVAs were conducted to determine whether the duration of the fixations and the amplitude of the saccades recorded during observation of the golf videos were affected by the phase of the swing. Descriptive statistics are reported in Table 6.2. For average fixation duration (Figure 6.3A), 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 than during the static phase, for all participants. The main effect of Group and the Group x Phase interaction were not significant, $F(1,16) = .23$, $p = .64$, $\eta_p^2 = .01$, and $F(1,16) = .02$, $p = .89$, $\eta_p^2 = .001$, respectively. The ANOVA conducted on the average saccade amplitude (Figure 6.3B) revealed no significant main effects or interactions[2]; however, saccade amplitudes tended to be smaller during observation of the dynamic phase than during viewing of the static phase.

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[1] No significant main effects were found for either Condition, $F(1,16) = .37$, $p = .55$, $\eta_p^2 = .02$, or Group, $F(1,16) = .74$, $p = .40$, $\eta_p^2 = .04$. The Group x Condition interaction was not significant, $F(1,16) = .04$, $p = .85$, $\eta_p^2 = .002$.

[2] No significant main effects were found for either Condition, $F(1,16) = 2.69$, $p = .12$, $\eta_p^2 = .14$, or Group, $F(1,16) = .42$, $p = .53$, $\eta_p^2 = .03$. The Group x Condition interaction was not significant, $F(1,16) = .58$, $p = .46$, $\eta_p^2 = .04$.

6.4.1.2 Dwell times.

Dwell times on the interest areas were analysed separately for the RGL and the golf conditions using two Group x IA mixed ANOVAs. For the RGL videos (Figure 6.4), 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, $F(1,16) = 1.70, p = .21, \eta_p^2 = .10$, nor a Group x IA interaction, $F(1.33,21.27) = .39, p = .60, \eta_p^2 = .02$. Descriptive statistics are reported in Table 6.3.

For the golf video, the Group x IA ANOVA revealed a significant main effect of IA $F(3.51,56.18) = 16.29, p < .001, \eta_p^2 = .50$. Pairwise comparisons using Bonferroni corrections indicated that there were significant differences in dwell times on the different IAs (all significant comparisons are reported in Table 6.4). There was no main effect of Group, $F(1,16) = .30, p = .59, \eta_p^2 = .02$, and no Group x IA interaction emerged, $F(3.51,56.18) = 1.71, p = .17, \eta_p^2 = .10$.

Given the changes in low-level gaze metrics across the two phases of the swing, a Group (expert/novice) x IA (head/hands/arms/shoulders/centre/legs/feet/ball/club) x Phase (static/dynamic) ANOVA was used to determine whether experts 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, $F(3.13, 50.09) = 40.59, p < .001, \eta_p^2 = .72$, suggesting that the differences in dwell times on the various IAs were affected by the phase of swing.

Since the Group factor did not show any significant main effect or interactions[3], 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 IAs except for the feet (Figure 6.5). Specifically, dwell times for the hands, arms, legs, ball and club were longer during the static phase than during the dynamic phase, all $p < .001$. In contrast, participants looked more

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[3] The main effect of Group was not significant, $F(1,16) = 1.01, p = .33, \eta_p^2 = .06$. The Group x IA interaction was not significant, $F(3.38,54.05) = 1.64, p = .19, \eta_p^2 = .09$, nor was the Group x Phase interaction, $F(1,16) = .01, p = .92, \eta_p^2 = .001$. Finally, the Group x Phase x IA interaction was not significant, $F(3.13,50.08) = 1.84, p = .15, \eta_p^2 = .10$.

at the head, shoulders and centre during the dynamic phase compared to the static phase, all $p < .001$.

Table 6.1. *Fixation Duration (ms) and Saccade Amplitude (° of Visual Angle) Recorded in the two Conditions – Descriptive Statistics*

Metric	Condition	Group	*M*	*SEM*	*SD*	*Min*	*Max*
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 6.2. *Fixation Duration (ms) and Saccade Amplitude (° of Visual Angle) during the Two Phases of the Golf Video – Descriptive Statistics*

Metric	Phase	Group	*M*	*SEM*	*SD*	*Min*	*Max*
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

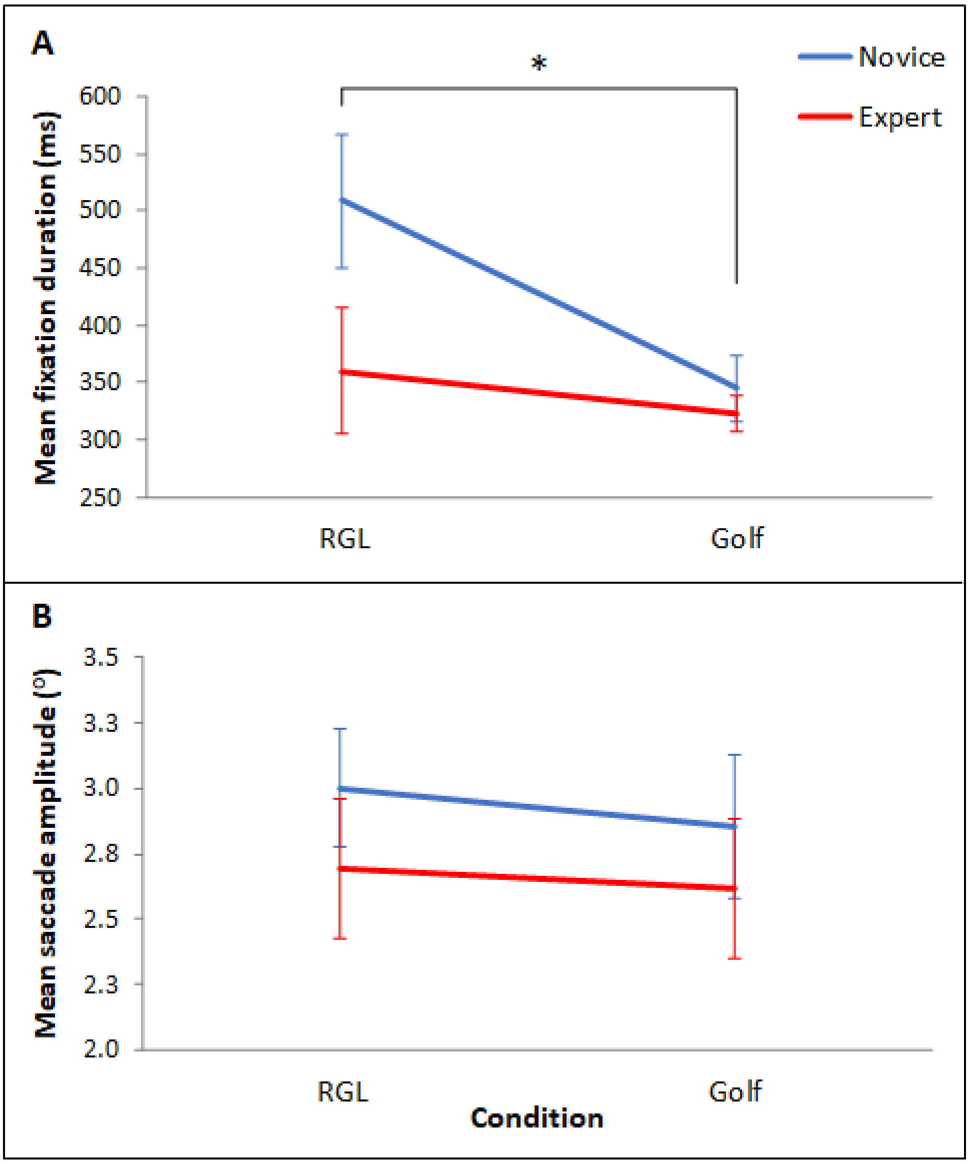

Figure 6.2. Mean fixation duration (in ms; A) and saccade amplitude (in degrees of visual angle; B) across the two groups and the two conditions. Error bars represent standard error of the means; * *p* < .05.

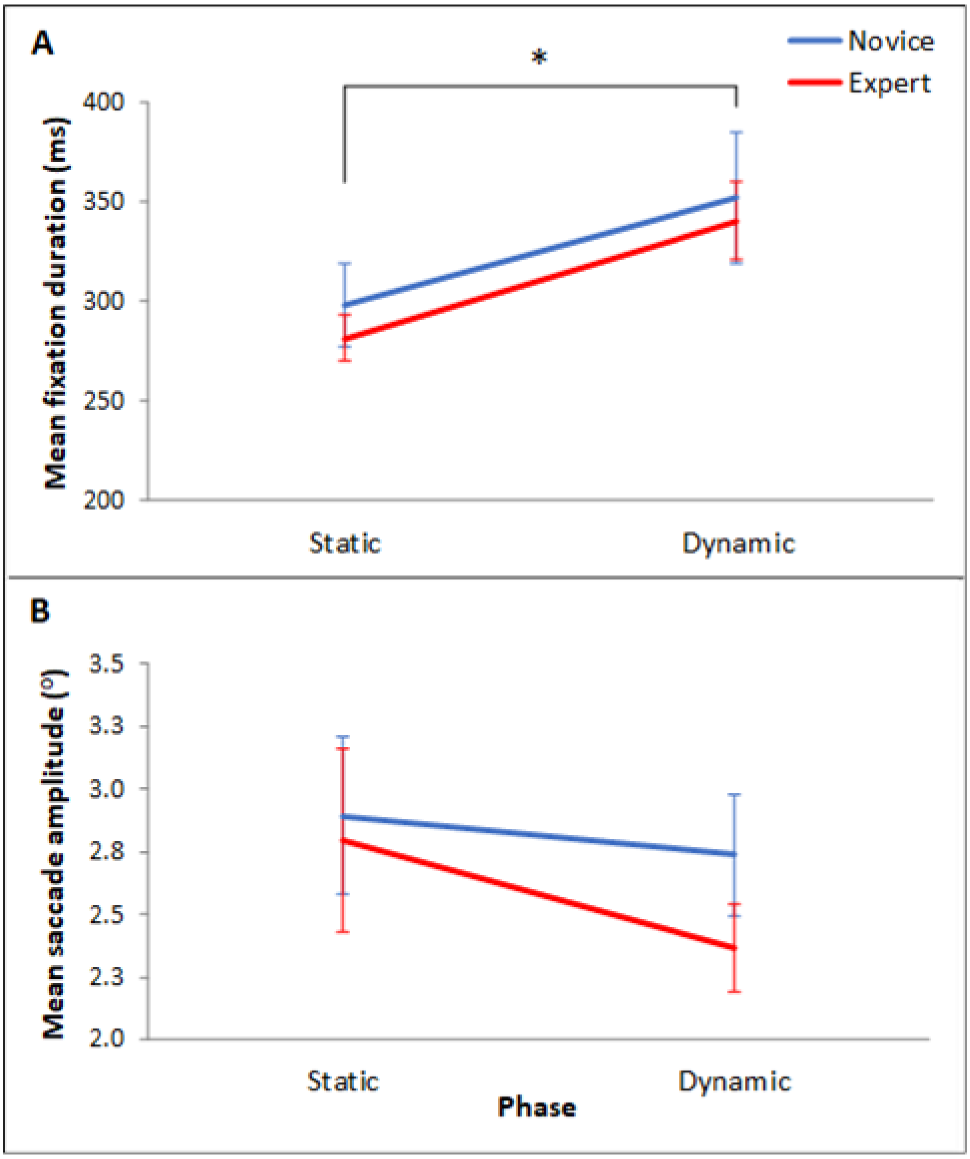

Figure 6.3. Mean fixation duration (in ms; A) and saccade amplitude (in degrees of visual angle; B) for the two groups during viewing of the static and dynamic phases of the golf swing. Error bars represent standard error of the means; * $p < .005$.

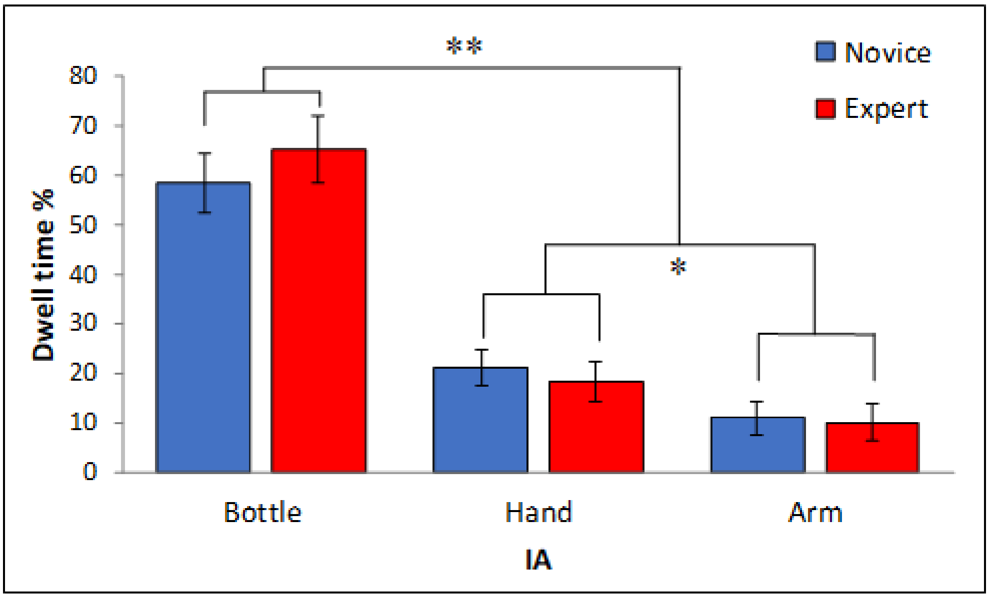

Figure 6.4. Mean dwell time (as a percentage of the total dwell time) on the interest areas during viewing of the RGL videos. Error bars represent standard error of the means; * $p = .03$, ** $p < .001$.

Table 6.3. *Dwell Time on the IAs for the RGL video – Descriptive Statistics*

IA	Group	*M*	*SEM*	*SD*	*Min*	*Max*
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.

Table 6.4. *Differences in Dwell Time on the Various IAs during Viewing of the Golf Video*

Contrasts				95% CI	
IA1	IA2	Mean difference (IA1 – IA2)	Std. Error	Lower Bound	Upper Bound
Head	Ball	12.2**	2.35	3.12	21.28
	Shoulders	9.64*	2.4	.39	18.88
	Feet	14.77**	2.42	5.42	24.12
	Club	13.25**	2.44	3.84	22.66
	Club path	11.95*	2.62	1.56	22.35
Hands	Ball	7.58*	1.86	.40	14.76
	Feet	10.15**	1.6	3.98	16.32
	Club	8.63**	1.57	2.58	14.68
	Club path	7.33*	1.66	.75	13.91
Centre	Ball	12.34**	2.01	4.37	20.30
	Arms	7.22**	.92	3.56	10.88
	Shoulders	9.77**	1.27	4.73	14.82
	Feet	14.91**	1.41	9.33	20.49
	Legs	9.61**	1.78	2.57	16.65
	Club	13.38**	1.49	7.48	19.28
	Club path	12.09**	1.54	5.98	18.2
Feet	Arms	-7.69**	1.41	-13.29	-2.08
	Shoulders	-5.13*	1.18	-9.81	-.46

Note: CI = confidence interval. Only significant Bonferroni-corrected comparisons are reported in the table.
* $p < 0.05$, ** $p < 0.005$.

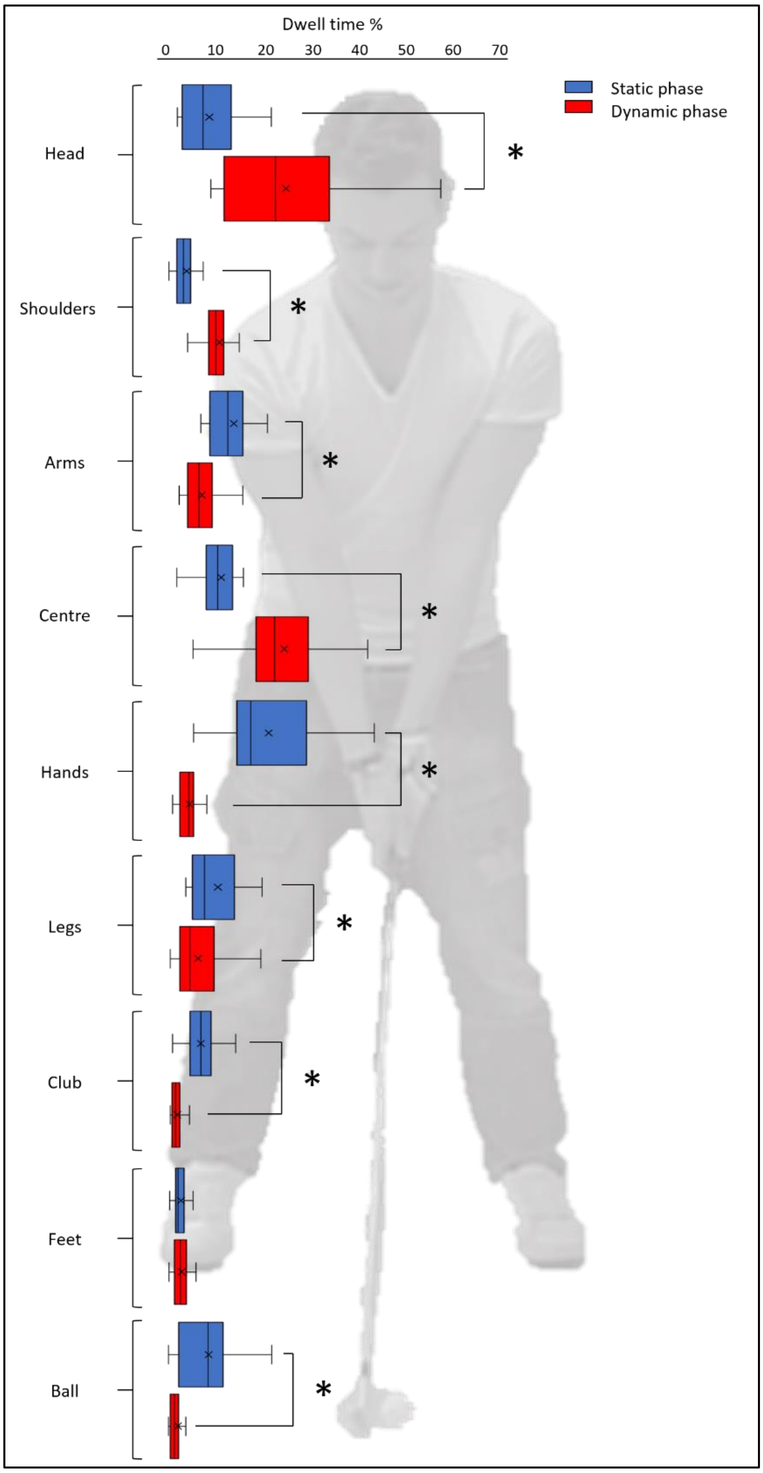

Figure 6.5. Box plots showing dwell times on the IAs (expressed as a percentage of the total dwell time) across the static and dynamic phases. Whiskers represent the lowest and highest values; vertical lines represent the medians; *x* symbols represent the means; * $p < .001$.

6.4.2 Motor-evoked potentials

6.4.2.1 Facilitatory effects of action observation.

Raw MEP amplitudes recorded across the four stimulation times during observation of the golf videos were averaged to obtain a total raw MEP amplitude for each of the muscles of interest. Descriptive statistics are reported in Table 6.5. A Group (expert/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 corticospinal excitability, and whether this differed across the two expertise groups (Figure 6.6). 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 recorded during the baseline condition ($M = .21$, $SEM = .02$) were significantly lower than those recorded during the golf observation condition ($M = .29$, $SEM = .03$) $p = .001$, but did not significantly differ from those recorded during the RGL observation condition ($M = .26$, $SEM = .02$). There were no main effects of Group, $F(1,16) = 1.37$, $p = .26$, $\eta_p^2 = .08$, or Muscle, $F(2,32) = .85$, $p = .44$, $\eta_p^2 = .05$, and no significant interactions[4].

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[4] Group x Condition: $F(2,32) = .68$, $p = .51$, $\eta_p^2 = .04$. Muscle x Group: $F(2,32) = .11$, $p = .90$, $\eta_p^2 = .007$. Condition x Muscle: $F(4,64) = .20$, $p = .94$, $\eta_p^2 = .01$. Condition x Muscle x Group: $F(4,64) = .18$, $p = .95$, $\eta_p^2 = .01$.

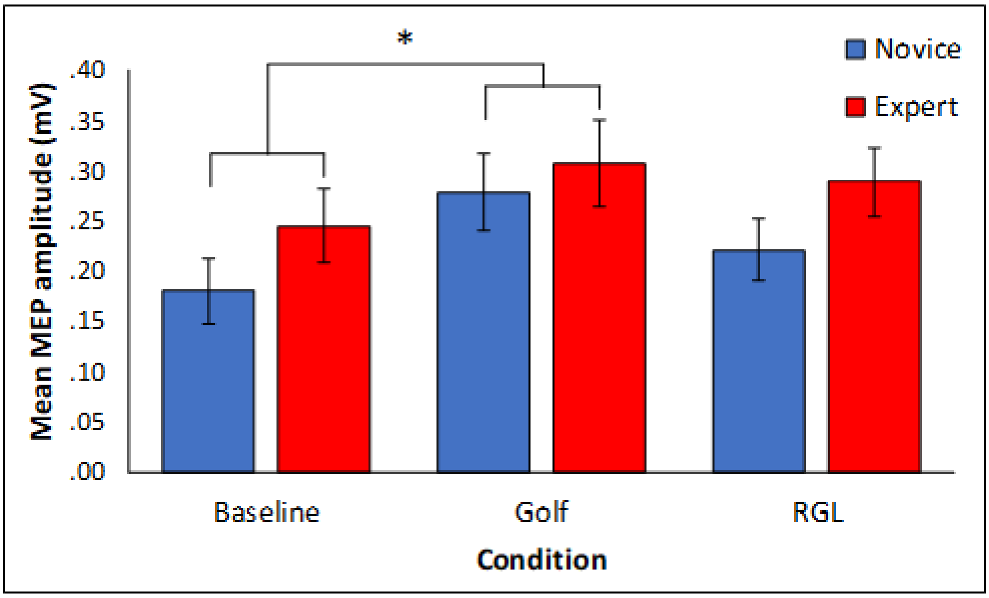

Figure 6.6. Mean raw MEP amplitudes – collapsed across the three muscles – recorded during rest, during observation of the golf videos and during observation of the RGL videos. Error bars represent standard error of the means; * $p = .001$.

6.4.2.2 Golf videos.

A Group (expert/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 between the four stimulation times as well as between experts and novices. This revealed no significant main effects or interactions[5]. Descriptive statistics are reported in Table 6.6.

Previous studies have found that the combination of motor imagery with action observation can elicit greater changes in corticospinal excitability compared to either process in isolation (Sakamoto et al., 2009; Wright et al., 2014). Pearson's correlation was thus used to determine the relationship between the participant's engagement in motor imagery during observation of the golf swing – as indexed by the percentage of clips during which participants had engaged in MI 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[6].

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[5] Group: $F(1,16) = .86$, $p = .37$, $\eta_p^2 = .05$. Muscle: $F(2,32) = .91$, $p = .42$, $\eta_p^2 = .05$. Stimulation time: $F(3,48) = 1.44$, $p = .24$, $\eta_p^2 = .08$. Time x Group: $F(3,48) = .55$, $p = .65$, $\eta_p^2 = .03$. Muscle x Group: $F(2,32) = .98$, $p = .39$, $\eta_p^2 = .06$. Time x Muscle: $F(6,96) = 44$, $p = .85$, $\eta_p^2 = .03$. Time x Muscle x Group: $F(6,96) = 1.08$, $p = .38$, $\eta_p^2 = .06$.

[6] The percentage of clips during which participants had engaged in imagery was not correlated with MEP amplitudes recorded from FCR ($r = -.39$, $p = .11$), FCU ($r = -.08$, $p = .76$), or ECR ($r = -.31$, $p = .21$). The

Table 6.5. *Raw MEP Amplitudes (mV) – Descriptive Statistics*

Muscle	Group	Condition	*M*	*SEM*	*SD*	*Min*	*Max*
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

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reported vividness of the visual image was not correlated with MEP amplitudes recorded from FCR ($r = .11$, $p = .67$), FCU ($r = -.23$, $p = .36$), or ECR ($r = .06$, $p = .83$). The reported intensity of the imagined feeling was not correlated with MEP amplitudes recorded from FCR ($r = .29$, $p = .24$), FCU ($r = .31$, $p = .20$), or ECR ($r = -.02$, $p = .95$).

Table 6.6. *Normalised MEP Amplitudes (%) Recorded During Observation of Golf – Descriptive Statistics*

Muscle	Group	Stimulation Time	*M*	*SEM*	*SD*	*Min*	*Max*
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
		Follow-through	71.54	23.42	74.06	-22.42	179.06
	Expert	Backswing	81.89	37.66	106.51	-14.32	302.87
		Forward swing	61.89	20.90	59.11	-17.21	142.54
		Acceleration	87.82	37.80	106.93	-8.73	270.54
		Follow-through	45.83	24.77	70.05	-39.67	155.41
FCU	Novice	Backswing	64.06	24.93	78.85	-47.23	240.15
		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
		Follow-through	19.25	11.76	33.26	-22.34	76.59
ECR	Novice	Backswing	34.05	14.33	45.33	-11.57	116.11
		Forward swing	68.95	18.43	58.29	10.94	197.32
		Acceleration	76.65	29.56	93.47	-3.05	305.95
		Follow-through	50.54	23.06	72.92	-30.51	197.77
	Expert	Backswing	26.71	10.88	30.78	-3.49	84.75
		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.

6.4.2.3 RGL videos.

A Group (expert/novice) x Muscle (FCR, FCU, ECR) mixed ANOVA was conducted to assess whether there were any differences between novices and experts' normalised MEPs amplitudes recorded from the three muscles. This revealed no significant main effects or interactions. Descriptive statistics are reported in Table 6.7.

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[7].

Table 6.7. *Normalised MEP Amplitudes (%) Recorded During Observation of the RGL Action – Descriptive Statistics*

Muscle	Group	*M*	*SEM*	*SD*	*Min*	*Max*
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.

6.4.3 Correlations between MEPs and gaze

Pearson's correlation was used to determine whether the gaze behaviour adopted by the participants during viewing of the videos was related to normalised MEP amplitudes, as such a relationship has been demonstrated previously (see Study 2).

For the RGL videos, results showed no significant correlations between MEP amplitudes and fixation duration or saccade amplitude[8], respectively. However, dwell time on the bottle was negatively related to amplitudes recorded from the FCU, $r = -.47$, $p = .025$, and

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[7] The percentage of clips during which participants had engaged in imagery was not correlated with MEP amplitudes recorded from FCR ($r = .21$, $p = .41$), FCU ($r = .35$, $p = .15$), or ECR ($r = -.05$, $p = .84$). The reported vividness of the visual image was not correlated with MEP amplitudes recorded from FCR ($r = .40$, $p = .10$), FCU ($r = .39$, $p = .12$), or ECR ($r = .21$, $p = .41$). The reported intensity of the imagined feeling was not correlated with MEP amplitudes recorded from FCR ($r = .36$, $p = .15$), FCU ($r = .46$, $p = .053$), or ECR ($r = .032$, $p = .90$).

[8] No significant correlations were found between fixation duration and amplitudes recorded from FCR ($r = -.29$, $p = .24$), FCU ($r = -.14$, $p = .57$) or ECR ($r = -.11$, $p = .66$). Similarly, saccade amplitude was not significantly correlated with amplitudes recorded from FCR ($r = -.12$, $p = .65$), FCU ($r = .30$, $p = .23$) or ECR ($r = .23$, $p = .35$).

the ECR, *r* = -.45, *p* = .03, and dwell time on the forearm was positively related to ECR MEP amplitudes, *r* = .52, *p* = .014[9].

For the golf videos, no significant correlations were found between fixation duration or saccade amplitude and normalised MEP amplitudes[10]. However, 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, respectively[11].

6.5 Discussion

In the present study, we investigated how gaze behaviour and previous experience with an action modulate motor resonance during observation of two actions of different complexity. We showed expert and novice golfers videos of a RGL action, and videos of a skilled golfer performing a full golf swing. We expected no expertise-related differences in gaze or MEPs to emerge during observation of the RGL video, as such an action is conceivably part of all participants' motor repertoires. In contrast, due to the two groups' varying degrees of familiarity and experience with the action, we expected observation of the golf swing to result in marked group differences in both gaze behaviour and corticospinal excitability.

6.5.1 Gaze data

Analyses of the gaze metrics (i.e., fixation duration, saccade amplitude and dwell time) revealed that, regardless of the participant's familiarity with the observed actions, eye movements were modulated by the characteristics of the action being viewed. Fixation durations were longer during observation of the RGL action than they were during viewing of the golf swing. In a related manner, fixation durations were longer during the dynamic phase

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[9] Dwell time on the bottle was not significantly related to amplitudes recorded from FCR, *r* = -.12, *p* = .31. Dwell time on the forearm was not related to amplitudes recorded from FCR, *r* = .07, *p* = .40, and FCU, *r* = .28, *p* = .13. Dwell time on the hand was not related to the MEP amplitudes recorded from the three muscles (FCR *r* = -08, *p* = .38; FCU *r* = .33, *p* = .09; ECR *r* = .24, *p* = .17).

[10] Fixation duration was not related to the MEP amplitudes recorded from FCR, *r* = -.37, *p* = .13, FCU, *r* = -.23, *p* = .35, or ECR, *r* = -.02, *p* = .95. No significant correlations were found between saccade amplitude and MEP amplitudes recorded from FCR *r* = -.24, *p* = .34, FCU, *r* = .13, *p* = .60, or ECR, *r* = -.07, *p* = .78.

[11] The remaining correlations between MEP amplitudes and dwell time on the interest areas were not significant. **Dwell on the head:** FCR *r* = .32, *p* = .10, FCU *r* = -.002, *p* = .50, ECR *r* = .007, *p* = .49. **Dwell on the hands:** *r* = -.23, *p* = .18, FCU *r* = -.35, *p* = .08, ECR *r* = .22, *p* = .19. **Dwell on the ball:** *r* = -.24, *p* = .17, FCU *r* = -.05, *p* = .42, ECR *r* = .03, *p* = .46. **Dwell on the arms:** *r* = .25, *p* = .16, ECR *r* = .24, *p* = .17. **Dwell on the shoulders:** FCU *r* = .08, *p* = .37, ECR *r* = -.24, *p* = .17. **Dwell on the feet:** *r* = -.22, *p* = .19, FCU *r* = .05, *p* = .42, ECR *r* = -.02, *p* = .47. **Dwell on the centre:** *r* = -.05, *p* = .42, ECR *r* = .15, *p* = .28. **Dwell on the club:** *r* = -.12, *p* = .32, FCU *r* = -.06, *p* = .41, ECR *r* = -.12, *p* = .32. **Dwell on the legs:** *r* = -.36, *p* = .07, FCU *r* = -.24, *p* = .17, ECR *r* = -.23, *p* = .18. **Dwell on the club path:** *r* = -.05, *p* = .42, FCU *r* = -.30, *p* = .11, ECR *r* = .09, *p* = .37.

of the golf swing than they were during the static phase. These results can be explained with reference to the specific task constraints involved in the present study. In fact, eye movements are generally regarded as being shaped both by bottom-up and by top-down factors (Land, 2009). The goal of the observation task, the instructions provided to the observers, and the constraints imposed by the task and the environment, have all been shown to determine the gaze behaviour adopted in specific contexts (Kardan, Henderson, Yourganov, & Berman, 2016; Newell, 1991; A. M. Williams, Janelle, & Davids, 2004). The ways in which these factors may have affected our results are discussed below.

The constraints imposed by the observation task and the observers' intentions are likely to have modulated visual search patterns, both in terms of the duration of fixations and with regard to the loci of participants' point-of-gaze. Dwell time data showed that the golf and the RGL videos elicited two different patterns of gaze behaviour. When observing the common reaching and grasping action, participants predominantly looked at the target, which reflects the gaze strategies typically employed during natural viewing and execution of object-directed actions (Flanagan & Johansson, 2003; Hayhoe & Ballard, 2005; Möller, Zimmer, & Aschersleben, 2015). In contrast, when viewing the golf swing, another transitive but far more dynamic, complex and coordinative action, dwell time on the target – i.e., the ball – was extremely low (*M* = 5.19%, *SEM* = 1.07). In addition, fixation durations were significantly longer during viewing of the RGL video than they were during observation of the golf video.

The differences in the gaze patterns exhibited during observation of the two actions can be ascribed to the different constraints imposed by the actions selected. When observing the simple, single-limb task in the RGL video, participants did not need to extensively scan the visual display. This elicited a naturalistic eye movement pattern which consisted of long-duration fixations directed to the action target and concurrent monitoring of the simple, single-limb action with peripheral vision. The golf videos, in contrast, displayed a very complex action, in which the arms, and legs to a far lesser extent, move simultaneously in a highly dynamic and coordinated manner. As highlighted by coaches, manuals and websites, learning to perform a golf swing requires performers to pay attention to the relative positioning of different elements and anatomical areas, such as alignment of the head, hands and ball, or width of the stance (e.g., Lamanna, 2016; Redford & Tremayne, 1977). Accordingly, in Study 1 we demonstrated that an overt focus of attention on these regions and their spatial interrelationships effectively accelerated novices' learning of the golf swing. Since peripheral vision may not allow effective monitoring of all the relevant information, participants resorted to using a gaze pattern consisting of fixations of shorter duration so as to direct overt attention to more areas and 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 the natural observation of transitive actions. The amount of time participants spent looking at the target might have been further modulated by the degree of similarity between the posture of the models appearing in the two videos and that of the participant. There is evidence that proactive gaze typically emerges when the observer is in a position to actually perform the action. Ambrosini, Sinigaglia and Costantini (2012) showed participants grasping actions while the participants' hands were either freely resting on a table or tied behind their back. The authors found that this restriction severely impaired the proactivity of gaze behaviour that was observed in the hands-free condition, and concluded that "actions are observed best when we are actually in the position to perform them" (p. 263). In the RGL video, the actor's forearm was seen lifting the bottle from a similar desk to that on which the participant's arms were resting, albeit from a viewpoint at ninety degrees to a first-person perspective. It is likely that our participants perceived this action as being within their reaching space, which resulted in proactive, target-directed gaze during observation of the RGL video. In contrast, during observation of the golf video the posture of the model was very different from that maintained by our participants, who were sitting down with their arms resting on a desk in front of them and their heads supported by a headrest. This meant that participants were not in a position to perform the observed action, which reduced target-directed gaze.

Analyses of the fixations recorded during observation of the two phases of the golf swing further illustrate how gaze behaviour was affected by the task constraints. Regardless of expertise, fixation durations were found to be significantly longer during the dynamic phase of the swing compared to the static phase. In addition, saccade amplitudes tended to be smaller in the dynamic phase than they were during viewing of the static phase. This indicates that gaze behaviour changes according to the amount of motion present in the display: when viewing a whole-body action comprising rapid movements, observers tend to implicitly adopt a stiller gaze compared to when the observed scene is relatively static. This quietening of gaze was also evident from the dwell time data for the two phases of the golf swing. Different areas of the display were fixated to varying extents. The most fixated areas tended to be the head, the hands and the centre of the golfer's body. However, the amount of time that participants spent looking at the various IAs was modulated by the phase of the swing. As illustrated in Figure 6.5, gaze became more centralised as the video model progressed from the static to the dynamic phase of the swing; this corroborates the fixation duration data and is in line with the results of Study 1.

Taken together, the fixation duration and dwell time data indicate that, when faced with a complex action consisting of a number of rapidly moving elements, observers tend to adopt a stiller and more centralised point-of-gaze. During the static phase of the swing, participants used short fixations to explore the model's characteristics, probably extracting information with their foveal and parafoveal vision. However, for the dynamic phase, participants' gaze behaviour changed: they employed fixations of longer duration, on more central regions of the model (i.e., head and centre), which indicates an increased reliance on peripheral vision for monitoring and information extraction. Similar findings have been reported by studies that have used multiple object tracking (MOT) tasks, which require observers to monitor and track multiple moving objects amongst an array of identical distractors. Researchers have revealed that in such tasks, participants typically employ a gaze strategy that involves centring the point-of-gaze on a location that represents the centre of mass of the set of moving targets (Fehd & Seiffert, 2010; Zelinsky & Neider, 2008). This *anchoring* of gaze allows monitoring of the moving targets across the display through peripheral vision, and it might represent a beneficial strategy for several reasons. Peripheral vision enables observers to covertly distribute their attention across the visual field, thus avoiding the loss of visual input associated with saccadic eye movements (e.g., Ross, Morrone, Goldberg, & Burr, 2001), to the extent that some researchers specifically recommend anchoring of gaze and using peripheral vision to monitor the visual environment during MOT tasks (Vater, Kredel, & Hossner, 2017). Extrafoveal vision also seems to be preferable in visual search and identification tasks. Nuthmann (2014) used a gaze-contingent display which selectively occluded foveal and parafoveal vision or peripheral vision. Results showed that impairing central vision did not impair search performance; in contrast, occluding peripheral vision affected attentional selection and visual processing. Finally, peripheral monitoring may also be preferable to central monitoring because of the greater sensitivity of the peripheral visual field for motion (Vater et al., 2017), and the higher scanning rate of covert compared to overt attention (Findlay & Gilchrist, 2001). When considering our findings, the golfer's body and golf club can be thought of as an array of multiple moving objects. By anchoring their gaze on a central location, the observer may be able to monitor changes in the model's posture and kinematics more effectively, using peripheral vision in order to do so.

Results also revealed that, as expected, gaze metrics recorded during observation of the RGL video did not differ between the two groups. However, contrary to our predictions, expert and novice golfers exhibited similar gaze behaviours also during observation of the golf video, as indicated by the lack of a main effect of Group in all the analyses conducted. The lack of expertise-related effects on gaze observed here is in contrast to previous findings on perceptual expertise in sports. These typically indicate that skilled performers show more efficient and flexible gaze patterns than their less-skilled counterparts (e.g., Gegenfurtner et al., 2011; Piras et al., 2010; A. M. Williams & Davids, 1998). However, the discrepancy between our results and those of previous studies may be explained by the specific constraints of the task. In fact, studies on expertise-related differences in gaze typically employ anticipation and decision-making tasks. Such tasks require performers to accurately select and process relevant information under severe time constraints so as to rapidly predict and intercept the actions of the opponent (e.g., Piras, Lanzoni, Raffi, Persiani, & Squatrito, 2016; A. M. Williams & Davids, 1998). In contrast, our protocol consisted of an observational learning task which involved repeated observation of the same action across a large number of trials. The time constraints imposed by our task were thus negligible, as participants had the opportunity to explore the visual display extensively across the multiple video repetitions, which may have reduced the likelihood that expertise-related effects would emerge. It should also be noted that, as reported by Mann and colleagues (Mann, Williams, Ward, & Janelle, 2007), expertise effects are more readily observed under ecologically valid, real-world experimental conditions compared to laboratory settings and artificial stimulus presentation modalities, such as video presentation. Thus, it is possible that the stimulus presentation modality employed in the presented study might have prevented the emergence of expertise-related differences in gaze.

6.5.2 MEP data

Analysis of the amplitudes recorded during baseline and in the two experimental conditions revealed that observation of the golf swing significantly facilitated MEPs from baseline. In contrast, no difference was found between the amplitudes recorded during observation of the RGL action and those recorded at baseline. The absence of corticospinal facilitation in the RGL condition contradicts the results of previous studies which have shown that observing reaching and grasping actions elicits larger MEPs than those that are recorded during rest (e.g., Alaerts et al., 2010; Gangitano et al., 2001). In our view, there are two possible explanations for the present result; the lack of facilitation observed in the RGL condition may reflect the recruitment of inhibitory processes to prevent overt execution of the observed movements, or it may be explained by the gaze behaviour adopted by participants in that condition. Each of these possibilities will be discussed below.

Studies have shown that the internal simulation of others' actions, which is thought to be the basis of our ability to understand and imitate actions, is largely automatic (e.g., Barchiesi & Cattaneo, 2013) – although attention to the specific aspects of the action is key (Bach, Peatfield, & Tipper, 2007). Increased activation of areas comprising the action-observation network (Vogt & Thomaschke, 2007) and facilitation of corticospinal excitability (Alaerts, Heremans, Swinnen, & Wenderoth, 2009; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995) have often been found during the observation of actions, even when only a partial sensory description of the action is available; for example, when listening to action-related sounds (Gazzola, Aziz-Zadeh, & Keysers, 2006). However, there is also evidence of AO-induced modulations consisting of a suppression of mirror activity. Buccino and colleagues (Buccino et al., 2005) found that listening to hand or foot actions induced a muscle-specific reduction of MEP amplitudes compared to baseline. Similarly, action observation can induce decreases in BOLD activity recorded from M1 (Gazzola & Keysers, 2009), as well as in the amplitude of the H-reflex of the muscles involved in the action (Baldissera, Cavallari, Craighero, & Fadiga, 2001). These findings are consistent with the lack of facilitation we found in the RGL condition, and they may be explained with reference to the specific neural mechanisms of excitation and inhibition that are recruited during the observation of others' actions. During AO, the MNS is highly involved in a fast and automatic internal simulation of the observed act, which results in subliminal activation of the muscles involved. In order to prevent overt execution of the movements, inhibitory mechanisms come into play to suppress this subliminal activation; this can then lead to a lack of facilitation or sometimes even to a suppression of corticospinal excitability (Hardwick, McAllister, Holmes, & Edwards, 2012; Villiger, Chandrasekharan, & Welsh, 2011). Evidence in support of these inhibitory mechanisms comes from two studies that have used direct extracellular recordings in monkeys and humans, respectively. Kraskov, Dancause, Quallo, Shepherd and Lemon (2009) recorded the activity of pyramidal tract mirror neurons in the monkey's brain. The majority of neurons exhibited the typical mirror response of discharging during both the execution and the observation of actions. However, a large number of pyramidal tract neurons fired during action execution but showed complete suppression of discharge during action observation. A similar set of *suppression* mirror neurons was later discovered in the human brain (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). These cells, which exhibit opposite responses to those of typical mirror neurons, may play the key functional roles of distinguishing between the actions of others and those of the self, and of inhibiting unwanted self-movement resulting from observation-execution matching processes (Kraskov et al., 2009; Mukamel et al., 2010).

The idea that action observation can elicit either facilitation or inhibition of mirroring activity is gaining support in the literature (e.g., Ferrari, Bonini, & Fogassi, 2009; Kraskov, 2012; Murakami, Restle, & Ziemann, 2011). The specific direction of the AO-induced modulations in corticospinal excitability may depend on a number of factors, including the goal of the observation task and the intentions of the observer (Buccino et al., 2004). In a recent study by Hardwick and colleagues (2012), participants observed transitive and intransitive hand actions; following the observation, they were required to either imitate the action (imitate condition) or to provide true or false judgements about it. The results showed that observation in order to answer a question about the action resulted in a significant facilitation of corticospinal excitability compared to baseline. In contrast, MEPs recorded in the observe-to-imitate condition did not significantly differ from baseline. Since the stimuli used in the two conditions were identical, the lack of facilitation cannot be explained by the absence of motor resonance activity; the same applies to our findings, as observation of grasping actions has previously been shown to increase corticospinal excitability (Alaerts et al., 2010; Gangitano et al., 2001). Therefore, it is likely that when individuals observe an action with the intention to imitate it, inhibitory processes come into play to counteract the excitatory effects of action observation and prevent overt movement (but see Wright, McCormick, Williams, & Holmes, 2016). Such processes are thought to play a fundamental role for selective imitation during action observation (Bien, Roebroeck, Goebel, & Sack, 2009) by preventing the activated motor representations from reaching the threshold at which they are overtly executed (Brass & Heyes, 2005). As is typical for TMS studies, we instructed participants to refrain from moving and we reminded them to keep relaxed throughout the protocol. These instructions may have enhanced the need to suppress subliminal muscle activation so as to avoid overt movement, resulting in a modulation of the AO-induced effects on the excitability of the target muscles (Hardwick et al., 2012; Villiger et al., 2011).

Finally, the observer's posture has previously been reported to modulate the AO-induced effects on the corticospinal system. Specifically, when observers adopt a posture that is congruent with that of the model there is a stronger activation of the corresponding motor representation, which is reflected in larger MEP amplitudes, compared to when the observer and model's postures are incongruent (Alaerts, Swinnen, & Wenderoth, 2009; Urgesi, Candidi, Fabbro, Romani, & Aglioti, 2006). This is consistent with the discovery of a class of mirror neurons in the monkey's brain that exhibit view-dependent responses to action observation (Caggiano et al., 2011). In the present study, the RGL video displayed the right forearm of an actor reaching for, grasping and lifting a bottle that was placed over a table. Although our participants were required to remain relaxed and to maintain their head and chin on the support, which restricted their movements, they were nevertheless in a position to actually perform the RGL action, which had been filmed while the actor was sitting down in front of the desk. During observation of the RGL video, participants thus maintained a posture that was congruent with that of the model, which likely elicited an even greater activation of the motor representations for the observed action. This, in turn, enhanced the need to counteract these excitatory mechanisms with inhibition so as to prevent overt imitation of the action. In contrast, the golf swing 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 corticospinal excitability which did not reach the threshold for overt execution. The modulations in MEP amplitudes recorded during this condition were thus not sufficient to trigger the inhibitory mechanisms that are recruited to prevent overt imitation, which was reflected in facilitation of corticospinal excitability.

Interindividual variability may also be a key factor in determining the response of the observer's corticospinal system to action observation. In Study 2, we found that viewing of thumb movements elicited the typical AO-induced pattern of corticospinal facilitation in the majority of our participants. However, one-third of participants exhibited the opposite response – an inhibition of MEP amplitudes during AO compared to baseline. Interindividual variability in the way in which the MNS responds to the observation of others' actions has in some cases been found to be even higher. Ray, Dewey, Kooistra and Welsh (2013) reported that action observation resulted in either no modulation or a reduction in MEP amplitudes in approximately half of their participants. The individual's tendency to imitate an observed action, as well as his or her ability to counteract this tendency by recruiting inhibitory mechanisms, may thus determine the way in which the motor system responds to action observation. Accordingly, this may explain the discrepancy between studies that have found facilitation and those that have reported no facilitation or even a suppression of MEP amplitudes (see Naish, Houston-Price, Bremner, & Holmes, 2014, for a recent review).

It is also possible that the pattern of corticospinal excitability modulations observed in our two conditions may have been affected by participants' gaze behaviour. Visual attention plays a key modulatory role in the activity of the AON (Bach et al., 2007); in line with this, the results of Study 1 showed that attending to relevant aspects of an action can facilitate learning. In Study 2, we were able to further clarify the mechanisms in which overt visual attention, as indexed by point-of-gaze, affects mirroring of others' actions. We found that, by fixating on a point which maximised the amount of transfoveal motion during observation of thumb adduction/abduction movements, we could maximise facilitation of MEP amplitudes, suggesting that foveal vision may be preferable for eliciting motor resonance (see also Leonetti et al., 2015; and Maranesi et al., 2013). In the present study, analysis of gaze behaviour shows that 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 (Flanagan & Johansson, 2003; Möller et al., 2015). 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 (Johansson, Westling, Backstrom, & Flanagan, 2001; Rayner, White, Kambe, Miller, & Liversedge, 2003). Since our video displayed a side view of the action scaled up so as to occupy the whole display, this meant that during the RGL action, the forearm was at an eccentricity of ~12° from central vision. The forearm could thus only be perceived through peripheral vision, which may have resulted in the lack of motor resonance effects. It may be argued that this explanation cannot account for the presence of facilitation in the golf video, as dwell time on the arms was very low also in this condition. However, the golf videos displayed a full-body view of the golfer; the distance between the golfer's forearms and his head or the centre of his body was 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 (which were the most fixated areas during observation of the dynamic phase of the swing, during which MEPs were recorded) the arms were always within the field of parafoveal vision.

The present study does not allow us to determine the relative contributions of gaze and of inhibitory mechanisms to the observed changes in corticospinal excitability. Increased excitability during observation of simple transitive actions still seems to be the prevalent finding in the literature. Since target-looking represents a behaviour which is normally adopted by participants, it can be assumed that participants in the previous studies which have found increased facilitation were also looking at the target of the action. It may therefore seem more likely that suppression mechanisms may be responsible for the present 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 is in line with the overall findings of the present thesis, and it reinforces the notion that gaze behaviour can modulate the automatic effects of action observation.

Contrary to our predictions, amplitudes recorded during observation of the golf swing did not significantly differ across the four phases of the swing, for either group of participants. Based on previous neuroimaging and neurophysiological findings (e.g., Aglioti et al., 2008; Calvo-Merino et al., 2005; Calvo-Merino et al., 2006), we had predicted that experts' motor representations of the golf swing would be more attuned to the observed action. We expected this to be reflected in a muscle- and phase-specific pattern of corticospinal facilitation, which matched that recorded during actual execution, in skilled golfers but not in our novice participants. While the corticospinal excitability of the three target muscles differed across the four stimulation times, and this differed between novices and experts (Fig. 6), it was observed that i) differences were not significant, and ii) the time pattern of activation did not match that which would be expected during action execution (Marta et al., 2012). The non-specific facilitation found in the present study may again be explained by the eye movement behaviour adopted by participants. Our dwell time results showed that, when considering the whole of the golf swing trials, the most fixated areas were the centre of the golfer's body, and his head. In contrast, gaze was only maintained over the golfer's arms for about 10% of the total dwell time; this proportion was further reduced to around 7% when taking into account the gaze metrics recorded during observation of the dynamic phase of the swing, which is when we delivered the TMS pulses and collected the MEPs. Thus, the golfer's arms were sufficiently close to point-of-gaze so as to be perceived through parafoveal vision, which resulted in an effective facilitation of MEPs compared to baseline. Despite this, the fact that the arms were not directly fixated may have resulted in an inability to accurately map the observed action onto the observers' motor repertoire in both groups. This would be consistent with the degradation of motor resonance that has been reported when viewing actions through peripheral vision (Leonetti et al., 2015). The degree of phase-locked facilitation may also depend on the complexity of the observed action (Smyth, Summers, & Garry, 2010) 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 (see Naish et al., 2014, for a review). In one of the few studies to date that have explored motor resonance during observation of a highly skilled, whole body action, i.e., the basketball free throw (Aglioti et al., 2008), expertise-related modulations of MEP amplitudes were observed in a hand muscle involved in the observed action (the ADM), but not in a forearm muscle equally involved in the action (the FCU). This might indicate that, unlike the fine-grained motor representation of the highly specialised finger muscles, the representation of the forearm muscles may be too coarse to be susceptible to fine phase-specific modulations of MEP amplitudes.

Contrary to our predictions, 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 method of presentation of the action to be imitated. Jola and Grosbras (2013) 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 to the size of the stimulus, as a whole-body action, when 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 experts' motor system might have been more finely tuned to the observed act, allowing potential skill-related differences to emerge. This is a possibility that warrants further investigation. Finally, our skilled golfers group included individuals with widely varying handicap ratings, which ranged from 0 up to 15. It cannot be ruled out that this variability may have contributed to the observed lack of expertise-related effects. To avoid this confound, investigations of skill-related differences should distinguish between more subtle classifications of expertise, for example by comparing responses across novice, national level, European PGA Tour, and PGA Tour players.

6.5.3 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 corticospinal excitability and rule out any changes in excitability due to differences in visual input per se, the visual input provided to the participants during the baseline condition should be as similar as possible to that involved in the experimental conditions (e.g., see Loporto, McAllister, Edwards, Wright, & Holmes, 2012; and Wright et al., 2014). It may have been preferable to include other baseline measurements of excitability by recording MEPs during observation of static images of the golf and RGL actions; however, we decided not to do so to avoid increasing the number of TMS stimulations delivered to the participants. In addition, rather than assuming the extent of muscle activation based on existing anatomical knowledge, 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 a number of ways. The golf video depicted a whole-body view of the action, which involved a large amount of visual information. In contrast, in the RGL video participants saw a side view of only the actor's hand and arm movement and the target. It would have been preferable 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 – which is something that needs to be determined in future research.

The spontaneous recruitment of motor imagery (MI) processes during action observation may represent an additional problem, especially when the goal of the observation task is to imitate. It is generally accepted that action observation and motor imagery recruit a number of largely overlapping neural areas (Eaves, Behmer Jr., & Vogt, 2016; Hardwick, Caspers, Eickhoff, & Swinnen, 2017). To control for the possible confounds arising from this, upon completion of the two AO conditions we asked participants to report whether they had engaged in imagery, and if so, to rate the intensity of the imagined feeling and the vividness of their mental image. We found that participants' MI ratings were not correlated to MEP amplitudes for any of the target muscle or in either condition. However, all participants reported using motor imagery during observation of the golf swing, and over 70% reported using MI also during observation of the RGL action. This suggests that imagery processes may spontaneously be recruited during action observation, in particular when the action at hand is complex and the task is to learn about it and imitate it. Since previous studies have shown that concurrent motor imagery and action observation can result in a stronger facilitation of M1 excitability compared to either process alone (Sakamoto et al., 2009; Wright et al., 2014), it cannot be ruled out that modulations in CE may have been affected by the MI processes spontaneously recruited by our participants while observing with the intention to imitate. This also represents a problem for previous TMS studies on action observation, as the issue of whether participants engage in imagery during AO has largely been neglected so far. Future studies need to take this possible source of confound into account; one way to more effectively rule out such confounds may be to explicitly instruct participants to refrain from engaging in imagery during action observation.

Finally, the lack of skill-related differences in gaze contradicts the results of previous studies as well as our predictions. However, our analyses of fixation duration did reveal a trend towards a Group x Condition interaction: as can be seen from Figure 6.2A, fixation duration was drastically modulated by the type of action for our novice participants, decreasing considerably from the RGL to the golf condition. In contrast, expert participants' fixation durations were only marginally smaller during viewing of golf than they were during viewing of the RGL action. Expertise- related differences in gaze during action observation and observational learning of motor skills need to be further investigated. This will enable us to determine whether the skill-related perceptual advantages typically observed in expert performance also extend to contexts beyond those of anticipation and decision making, and to establish how eye movement behaviour is affected by the specific constraints and requirements of the task.

6.5.4 Conclusion

The present study advances existing work on gaze behaviour and neurophysiological changes during action observation, and it complements the rest of the findings reported in the present body of work. In the first study, we showed that gaze behaviour is modulated by the amount of motion present in the display; our participants spent progressively less time viewing the various interest areas as the model's actions became more dynamic. In the present study, we provide further evidence in support of this modulation. In addition, we expand upon these findings by showing that, with increasing speed and force of the observed action, gaze behaviour becomes increasingly still and centralised. This seems to be an implicit strategy that may necessitate the use of peripheral vision to pick up relevant information, and it has implications for observational learning. The results of the present study also provide further evidence of gaze-related modulations in motor resonance, extending the results of Studies 2 and 3 to the observation of transitive actions of different complexity. During observation of a RGL action, there was no significant facilitation of corticospinal excitability from baseline, and target-looking was associated with reduced MEP amplitudes in the forearm muscles. During viewing of a complex, whole-body action, MEP facilitation was positively related to the time spent looking at central areas close to the model's arms. This indicates that overt attention to the effectors of an action seems to be important for effective recruitment of the observer's motor system, consistent with our previous findings. Future research should explore the effects of instructing learners to anchor their gaze and reduce the extent of their eye movements during AO, so as to determine whether such a strategy can facilitate information extraction and observational learning of motor skills of different complexity. Should the results support the efficacy of gaze anchoring, this approach could become incorporated into AO-based training aimed at teaching novel motor skills via observation, as well as into motor rehabilitation programmes involving the repeated observation of actions as a means to aid motor recovery. However, directing gaze to improve sports performance may be problematic. Williams (1987) showed participants video-modelled throwing actions, and found that observers could be classified as *saccaders*, *trackers* or a combination of the two, based on the gaze pattern that they adopted. When participants were instructed to observe the actions using a different strategy from their preferred one, this resulted in performance decrements. In a related manner, in Study 3 we found that disruption of natural gaze behaviour during AO resulted in modulation of the phase-specific motor resonance response otherwise observed in a thumb muscle. Thus, gaze training may have to be tailored to the preferences of the individual, which highlights the need for researchers to further investigate how eye movement patterns differ as a function of expertise and individual preference in various contexts, including during observational learning of novel actions. Contrary to our predictions, we failed to find any expertise-related differences in either gaze or corticospinal excitability. In our view, this resulted from the combined effects of the goal of the task, the specific constraints involved and the modality of presentation of the actions. Nevertheless, our results highlight the need to further investigate motor resonance during the observation of complex actions, as evidence so far is scarce and contradictory.

6.6 References

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7 Chapter 7:

Discussion

7.1 Introduction

This chapter will briefly summarise the aims of the present work before providing an outline of the main research findings. The implications of the findings will be discussed. The limitations of the present research will be considered, and possible directions for future research will be suggested.

7.2 Aims of the Thesis

The primary aim of the present body of work was to investigate the relationship between gaze and information pickup during action observation (AO). Specifically, the aim of Study 1 was to explore whether, by exogenously directing novices' visual attention to key areas of a model's body, we could accelerate observational learning of a complex motor skill – the full golf swing. Golf novices watched videos of an expert model performing the golf swing, with or without visual guidance (VG). A combination of performance and process data were collected, including eye movement recordings, expert evaluations of golf swing execution and explicit rule formation data.

The aim of the remaining studies was to explore the relationship between motor resonance during action observation – as indexed by the amplitude of TMS-evoked motor-evoked potentials (MEPs) – and gaze behaviour. To this end, we implemented a novel approach in which eye movements and MEPs were simultaneously recorded.

In Study 2, we investigated a putative modulatory effect of the observer's point-of-gaze on motor resonance as they viewed intransitive finger movements. Participants watched videos of thumb and little finger adduction-abduction movements, while moving their eyes freely, or with their gaze fixated on predetermined loci at varying distances from the moving digit. The amplitude of MEPs recorded in each condition and their relationship to various gaze metrics were analysed.

Expanding further on this, our aim in Study 3 was to examine the interactions between gaze behaviour and motor resonance in the context of transitive action observation, as real-world movements often comprise a combination of both transitive and intransitive movements. Participants observed videos that depicted a series of reach-to-grasp actions in which an actor's arm could be seen to reach towards multiple targets sequentially, under three conditions. In a free viewing condition, participants viewed the action as they would naturally. In the remaining two conditions, a translucent visual guide was used to direct participants' gaze either to the targets, or to an intrinsic hand muscle involved in the action – the first dorsal interosseous (FDI) muscle.

In Study 4, we explored the interaction between gaze and corticospinal facilitation during observation of a complex whole-body action – the golf swing – and of an everyday reach-grasp-lift (RGL) action. Previous research indicates that both gaze and mirror activity are modulated by an individual's motor familiarity with the observed action; hence, a secondary aim of the study was to determine whether gaze and MEP amplitude during AO are affected by the observer's motor experience of the action. Skilled and novice golfers viewed videos of a RGL action and of an expert model performing a golf swing. MEPs were recorded from three forearm muscles, all of which are involved in the execution of both tasks.

7.3 Summary of the Research Findings

The results of Study 1 showed that simple exogenous visual guides consisting of translucent colour patches superimposed over the display were effective for directing learners' gaze. Participants who received visual guidance spent longer gazing at the cued areas than those in a free viewing (FV) group and continued to look at these areas after the cues had disappeared. Importantly, the results also showed that, by directing novices' gaze to relevant aspects of a complex motor skill, we might accelerate their observational learning of that skill. Compared to a FV and a control group, the VG group showed immediate improvements in their performance of the golf swing following the intervention. In addition, we found that gaze behaviour was modulated by the dynamics of the observed model: when the model began the swing action, there was a reduction in the time spent looking at the cued areas, relative to the static phase of the action (i.e., the setup phase).

In Study 2, we found that observation of finger movements did not significantly facilitate MEP amplitudes compared to the baseline condition, in which participants viewed a static hand. However, the data also showed that MEP amplitudes were largest when participants were required to fixate their gaze on a location directly over the moving thumb's trajectory. In addition, for the FV condition, MEP amplitude was negatively related to saccadic amplitude, which might reflect the inhibition of visual input which is known to accompany saccadic eye movements.

In Study 3, we extended the previous findings to the observation of goal-directed hand actions. Results revealed that observation of reach-to-grasp actions elicited significantly larger MEP amplitudes than did viewing of a static hand. Analyses of gaze data revealed that during FV, participants predominantly looked at the targets. When the VG was placed on the targets (VGT), although saccade amplitudes were larger, gaze behaviour resembled that adopted during FV, as reflected in the comparable dwell times for all the interest areas. In contrast, directing gaze to the FDI disrupted natural gaze behaviour: compared to the FV condition, fixation duration and dwell time on targets decreased, whereas dwell time on the hand and hand path increased. Importantly, we found that this disruption of gaze, by the introduction of an effector-based visual guide, was associated with a reversal of the mirror response: the phase-specific facilitation of APB amplitudes, which was present in conditions FV and VGT, disappeared in condition VGM. The opposite pattern was found for the FDI: during natural viewing and when the eyes were directed to the targets, facilitation of FDI MEP amplitudes was generic (i.e., not phase-locked to the action), but phase-specific facilitation emerged in condition VGM. Consistent with Study 2, MEP amplitudes were related to both the features and the location of participants' fixations. Saccadic amplitude was negatively related to MEP amplitude, although this was observed only in the VGM condition, that is, when gaze was disrupted. In condition FV, amplitudes were negatively related to dwell time on the hand path. In condition VGT, APB amplitudes were positively correlated with dwell on the targets.

In Study 4, we found that observation of the golf swing, but not of the reach-grasp-lift (RGL) action, elicited significant facilitation of MEP amplitude compared to an eyes-closed baseline, for both groups. Consistent with Study 1, gaze behaviour was affected by the characteristics of the action. Notably, fixation durations were longer during viewing of the RGL video than of the golf swing, as well as during the dynamic, relative to the static, phase of the swing. Furthermore, in the dynamic phase, participants looked at fewer areas of the display, focusing mainly on the model's head and his midriff – relatively static parts. Thus, gaze became more centralised and relatively static. Results also revealed that, in line with our previous findings, the extent of motor facilitation was associated with the location of participants' overt attention. During viewing of the RGL action, MEP amplitudes were negatively related to the amount of time spent looking at the bottle, and were positively related to dwell time on the forearm. During observation of the golf swing, higher dwell times on the centre, arms and shoulders were associated with larger MEP amplitudes. Finally, contrary to our predictions, no expertise-related differences were found for either gaze or motor resonance.

7.4 Implications of Research Findings

The present work contributes to the existing knowledge in a number of ways. Firstly, we were able to show for the first time that, by directing novices' attention during observation of a complex motor skill, we can accelerate learning of that skill (Study 1). We argued that the beneficial effects of visual guidance for learning may be accounted for by the relationship between gaze behaviour and motor resonance – a relationship that was uncovered in our remaining studies, and which had not been demonstrated previously. In addition, our findings advanced our understanding of how eye movements are modulated by the characteristics of the observed action, and of the various factors that can modulate corticospinal excitability during AO. Therefore, the results of the present thesis have important implications for future theory, practice and research in the context of action observation.

7.4.1 Theoretical implications

Demonstrations are widely used for teaching motor and sports skills to novices, but it has been argued that the effectiveness of such approaches may depend on the learner's ability to focus on task-relevant aspects of the modelled action (Boucheix & Lowe, 2010; Hodges & Franks, 2002). Although there have been attempts to use perceptual training programmes that comprise visual attentional guidance to improve athletes' aiming skill (Causer, Holmes, & Williams, 2011; Panchuk, Farrow, & Meyer, 2014) and anticipation abilities (e.g, Hagemann, Strauss, & Canal-Bruland, 2006; Savelsbergh, Van Gastel, & Van Kampen, 2010), the use of this approach for aiding observational learning of motor skills has largely been neglected to date. We provide the first evidence that, by directing observers' gaze to relevant aspects of a modelled action, we may facilitate information pickup, and consequently their learning of complex motor skills. The results of Study 1 showed that, even in the absence of visual guides, participants who watched the model improved their execution of the swing at retention compared to the control group, who did not receive the golf demonstration. This is consistent with previous research showing that observation of a model typically improves movement form and coordination (Ashford, Bennett, & Davids, 2006; Horn, Williams, & Scott, 2002). However, we also found that only those participants who had received the visual guidance achieved immediate performance improvements in the post-test. It should be noted that our participants had limited-to-no previous experience with the golf swing. Therefore, the visual guides may have facilitated learning by eliminating the need to 'search' the visual display in order to identify and focus on task-relevant aspects of the action. According to the Information Reduction Hypothesis (Haider & Frensch, 1996; 1999), this represents one of the hallmarks of skilled performance; with practice, individuals gradually learn to identify and process only the sources of information that are relevant to the task at hand. Our findings can be explained in terms of this theoretical framework: the visual guides, which were placed over key areas of the model's body, automatically directed participants' attention to these areas, thus acting as a sort of information-reduction mechanism.

Overall, our findings provide convincing evidence in support of the fundamental role of visual attention for effective learning via observation. Theoretical accounts of observational learning have consistently identified attentional processes as being fundamental to effective extraction, processing and retention of information. Within social-cognitive accounts (Bandura, 1971; 1977; 1986), effective learning by observation requires attention to the key features of the action. The aspects of the action which are attended to during AO are coded so as to form a symbolic representation of the action, which is then used for action rehearsal and reproduction. Consistent with this, our Study 1 results showed that participants who maintained their attention on the areas highlighted by the visual guide, which contained key information for achieving a correct execution of the golf swing, showed immediate improvements in performance. In contrast, such improvements were not seen in the group who had observed the same model, but in the absence of visual guidance. Since both groups of participants were exposed to the same demonstration, this difference in performance can be explained by the VG group's increased attention to the highlighted areas.

The results of Studies 2, 3 and 4, in which we found evidence of a relationship between overt visual attention and motor resonance, allow us to elucidate further on the beneficial effects of VG for learning. According to mirror-based accounts of action understanding (Iacoboni et al., 1999; Rizzolatti & Sinigaglia, 2010), the mirror neuron system (MNS) is responsible for translating visual information into motor knowledge, which enables individuals to recognise, understand and imitate the actions of others. This involves the formation of motor representations corresponding to the observed actions. These representations are then activated during viewing and execution of the action (e.g., Alaerts et al., 2010; Borroni & Baldissera, 2008; Gangitano, Mottaghy, & Pascual-Leone, 2004), and the extent of activation reflects the observer's familiarity with the skill and his or her ability to perform it (Buccino et al., 2004; Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008). The relationship between overt visual attention and motor resonance uncovered in our TMS studies may account, at least partly, for the beneficial effects of VG on learning. By directing learners' attention to key aspects of the action, our visual guides are likely to have facilitated participants' perception and processing of information pertaining to the action. This, in turn, resulted in more expeditious and accurate mapping of the action into their motor repertoire, which was reflected in improved performance in the post-test.

Collectively, the results of the present thesis show that gaze behaviour is modulated by the characteristics of the observed action. In Study 4, we found that participants employed shorter fixations during viewing of the golf swing than they did when observing the RGL action. The golf swing video, which displayed a whole-body view of a model golfer performing a full swing, conveyed considerably more complex information to process than the single-limb RGL action. Therefore, during viewing of the golf swing, our novice participants employed shorter fixations in order to attend to all potentially relevant areas of the display. Accordingly, there is evidence that, when faced with complex visual displays involving multiple information sources, performers tend to resort to a more extensive visual search behaviour comprising many fixations of short duration – albeit this is a more prominent characteristic of expertise (Roca, Ford, McRobert, & Williams, 2013; Stevens et al., 2010). Motion has been identified as another key factor that can modulate gaze behaviour (e.g., Mital, Smith, Hill, & Henderson, 2011). We expand upon this by providing the first evidence that eye movements are inhibited during observation of a highly coordinative and dynamic whole-body action. In Study 1, when the model began the swing action, there was a reduction in the time spent looking at the cued areas, relative to the static phase of the action (i.e., the setup phase). We speculated that this was likely to be a result of the fact that, when the golfer initiated the backswing, participants' eyes were drawn by the motion. However, since we only analysed dwell time on the highlighted areas, we could not determine with certainty whether that was the case. Study 4 allowed us to further understand this: by recording low-level gaze metrics we were able to show that during viewing of the dynamic phase of the golf swing, participants' gaze became more still and centralised. This apparently automatic gaze behaviour may represent an ideal 'strategy' for perceiving fast-moving stimuli, consistent with the eye movements strategies observed during multiple-object tracking tasks (Fehd & Seiffert, 2010; Zelinsky & Neider, 2008). Due to the inherent limitations of our oculomotor system, we cannot simultaneously track multiple moving stimuli with the fovea, especially when the stimuli appear in spatially diverse locations (Carrasco, 2011). However, as suggested by the zoom lens theory of attention (Eriksen & St. James, 1986), the breath of attentional focus can be varied in size depending on the requirement of the task. This implies that, when the task involves monitoring and perception of a number of moving stimuli, the adoption of a central 'anchor' may enable the observer to broaden their covert attentional focus in order to perceive and extract information via their peripheral vision, which is known to be specialised for motion perception (cf. Vater, Kredel, & Hossner, 2017).

7.4.2 Applied implications

Our Study 1 results have important implications for current practice in sport and motor skill learning. The ability to focus only on task-relevant information represents one of the hallmarks of expert performance in many domains (Gegenfurtner, Lehtinen, & Säljö, 2011; Hayhoe, McKinney, Chajka, & Pelz, 2012; Mann, Williams, Ward, & Janelle, 2007). Therefore, AO-based approaches comprising VG may serve to accelerate the development of expertise. Our results also have implications for motor rehabilitation. There is evidence that the combination of traditional physical therapy with repeated and systematic observation of everyday actions leads to greater improvements in the patient's motor function compared to physical rehabilitation alone (e.g, Ertelt et al., 2007; Pelosin, Bove, Ruggeri, Avanzino, & Abbruzzese, 2013). However, AO-based therapy can impose very high attentional demands on the patient (Buccino, 2014). Simple exogenous forms of visual guidance may reduce the attentional demands of the task, which could in turn optimise the effects of the AO treatment.

Our findings suggest that VG-based approaches may represent an effective way of facilitating the acquisition and refinement of sports skills, as well as the relearning of previously acquired motor skills. Such approaches would constitute a time- and cost-effective adjunct to physical practice and motor rehabilitation, as they can be regarded a form of *covert motor training* which could be implemented easily and without supervision. Future studies should aim to identify what types of attentional guidance are most effective in facilitating learning in different domains, and researchers should investigate the long-term effects of VG-based interventions on observational learning of skills of varying complexity.

An underlying assumption in TMS research is that greater levels of motor resonance during action observation may result in more efficient learning (Wright et al., 2018). This notion is supported by evidence that the extent of corticospinal excitability (CE) is related to the learning process, as it has been reported that MEP facilitation is highest during the early stages of learning (Sakamoto, Moriyama, Mizuguchi, Muraoka, & Kanosue, 2012). Therefore, by finding ways to maximise the extent of covert motor activation during AO, we may be able to optimise the motor learning process. Recent evidence suggests that motor resonance is modulated by attention (Betti, Castiello, Guerra, & Sartori, 2017; Donaldson, Gurvich, Fielding, & Enticott, 2015), which suggests that by directing learners' overt attention to specific aspects of the action we may increase corticospinal facilitation. Although there have been some attempts to investigate the relationship between attention and CE, the lack of simultaneous eye movement and MEP recordings to date had not allowed us to directly determine the specific ways in which overt attention interacts with motor resonance during AO. The present work advances existing knowledge by providing the first direct evidence of a relationship between gaze behaviour and motor resonance. The specific ways in which this relationship manifests itself appear to depend on the interplay between different factors, such as the characteristics of the viewed action and the specific muscles from which MEPs are recorded.

In Study 2, we found that during observation of simple, intransitive actions, fixating the eyes on a location which maximised the participants' perception of biological motion elicited larger MEPs than did observing the action with natural gaze. This indicates that, by exogenously guiding observers' gaze, we may maximise the extent of the motor system engagement with the observed action, which in turn may benefit learning. Reducing eye movements and maximising the amount of motion perception across the fovea may represent a beneficial strategy for increasing motor resonance when observers are faced with simple actions involving limited amount of information. The results of Studies 3 and 4, however, indicate that the relationship between gaze and motor resonance is modulated by other factors as the observed action becomes more complex. During viewing of transitive reach-to-grasp actions (Study 3), dwell time on the hand path was negatively correlated with MEP amplitude, reflecting the fact that during these fixations, participants were not directly looking at the action. In addition, longer dwell times on the targets were associated with larger MEPs in one of the intrinsic hand muscles involved in the action (i.e., the APB). This is consistent with the results of a very recent experiment (Wright et al., 2018) in which it was found that, during observation of grasping, MEP amplitudes were highest when gaze was directed to the target, and the number of fixations on the target (a ball) was a significant predictor of MEP amplitude in the target-focused condition. Furthermore, our results showed that phase-specific facilitation for the APB was present only when participants' gaze was directed to the targets. When we guided participants' attention away from the target and onto the FDI, however, phase-specific motor resonance emerged in the FDI. This indicates that, by focusing overt attention over the target of the pinch grip action, we may have improved perception of the affordances provided by the object (cf. Wright et al., 2018), which could have triggered motor representations of the required action. Directing gaze to the FDI, in contrast, reduced the participants' perception of thumb kinematics, whereas it increased perception of information pertaining to the fixated muscle. In fact, throughout the pinching action, the APB was closer to the targets than it was to the FDI; this is consistent with evidence showing that, when actions are viewed through peripheral vision, corticospinal facilitation becomes coarse and non-specific (Leonetti et al., 2015).

In Study 4, however, the amount of time that participants spent looking at the target during observation of a reach-grasp-lift action was not associated with larger MEP amplitudes in the forearm muscles. On the contrary, the results of Study 4 revealed that MEP amplitudes were positively correlated with dwell time on the forearm, and negatively correlated with dwell time on the bottle. This apparent discrepancy, in our view, can be explained by the characteristics of the displayed action. During observation of a pinch grip, by directing overt attention to the target we may facilitate perception of the object's affordances – thereby increasing the observer's attention to the kinematic requirements of the action – relative to when the eyes are fixated on an effector (cf. Wright et al., 2018). In Study 4 we used a different action, in which the actor's hand reached for the bottle, grasped it using a whole hand grasp and then lifted it from the table; we also recorded MEPs from the muscles of the forearm instead of from the hand. In this case, focusing the eyes on the target might possibly have resulted in better perception of the hand kinematics pertaining to the type of grasp required, due to the proximity between the hand and the bottle. However, it is unlikely that focusing on the target would have enabled accurate extraction of information pertaining to the forearm muscles and the associated kinematic requirements, as these muscles were too distant from the target of the action to be accurately perceived. Therefore, focusing of gaze on the target of an action may represent a beneficial strategy for instances in which the target is sufficiently close to the muscles of interest, but in other cases it may be more beneficial to focus on other aspects of the action.

The above proposition finds support in the results of Study 4. These showed that, during viewing of the golf swing action, the amplitude of MEPs recorded from the forearm was positively related to gaze dwell time on the model's arms and shoulders, and on the centre of his body. The visual display involved a whole-body view of the golfer, which subtended a smaller visual angle than the RGL action. The positive correlation between MEP amplitude and dwell time on the centre, shoulders and arms of the model can be explained by the fact that fixation on these areas allowed maximal perception of the arms motion through foveal and parafoveal vision.

Collectively, the results of the present thesis suggest that, when observing complex actions involving fast, highly coordinated movements, it may be beneficial to direct observers' gaze to selected, more centralised, locations. This strategy could facilitate accurate perception and monitoring of the action. Centring gaze on specific locations may allow observers to distribute covert attention, resulting in more effective use of peripheral vision; it may also reduce saccadic eye movements and the associated loss of visual input, thereby maximising motor resonance. This would apply particularly to the observation of complex and dynamic actions, as suggested by the fact that gaze behaviour naturally tends to change according to the amount of motion (Studies 1 and 4). In addition, the results of Study 2 indicate that the advantage of a centralised gaze for facilitating resonance may also apply to the observation of simple intransitive actions. Anchoring of gaze has been shown to benefit performance on MOT tasks (Vater et al., 2017); thus, it may represent a beneficial strategy also for perceiving biological motion and extracting relevant information.

The specific forms of visual guidance provided to participants should be tailored not only to the features of the action, such as the amount of motion, the speed of the action and its complexity, but also to the observer's preferences. Research has shown that leading individuals to adopt a gaze strategy different from their preferred one can exert detrimental effects on performance (Williams, 1987). We provide further evidence in support of this notion. In Study 3, in which the task involved observation of sequential reach-to-grasp actions, participants mainly looked at the targets, which is consistent with proactive, target-directed gaze behaviour typically employed by observers when viewing transitive actions (e.g., Ambrosini, Costantini, & Sinigaglia, 2011; Flanagan & Johansson, 2003; McCormick, Causer, & Holmes, 2013). However, when participants were required to adopt a different gaze behaviour (i.e., in the VGM condition), a negative correlation between MEP amplitude and saccade amplitude emerged; a relationship which was absent in the other conditions. Previous studies have consistently shown that, through experience with a task, individuals acquire gaze strategies which are tailored to the task requirements. Since the action selected in Study 3 consisted of a common reaching and grasping action, when participants observed the action naturally (i.e., as they did in the FV and, to some degree, in the VGT conditions), they were able to look at the scene in such a way as to maximise information extraction and minimise the loss of visual input associated with saccadic eye movements. In contrast, when natural gaze behaviour was disrupted, the ability to efficiently observe the action was reduced.

7.4.3 Methodological implications

The present thesis introduced a novel methodology which involves the concurrent use of TMS and eye tracking. By simultaneously recording gaze and MEPs, we were able to demonstrate that, during AO, there is a relationship between the location and the characteristics of participants' eye movements and the extent of corticospinal facilitation. From a methodological perspective, this has important implications for future research on action observation. TMS studies have largely neglected the role of gaze during AO processes. The novel approach employed in the present body of work can be easily implemented by using a desktop-based eye tracker (and depending on camera location, possibly also a head-mounted one) while delivering TMS pulses. We recommend that future TMS studies should employ this methodology. This will allow us to shed light on a number of contrasting or puzzling findings that have been reported so far, and to disentangle the contributions of overt attentional allocation from other modulating factors which collectively determine the extent of the motor resonance response. For example, Study 4 results showed that during viewing of the RGL video, there was no significant facilitation of CE from baseline, which probably resulted from the fact that gaze was mainly directed to the bottle rather than the hand or arm. It is interesting to compare these results to those reported by Valchev et al. (2015), who found that motor resonance was modulated by the weight of an object that was being lifted and which was hidden from view. This suggests that, since participants could not look at the target, they inevitably directed their eyes to the arm, resulting in accurate facilitation of MEPs. However, the lack of gaze data does not allow us to determine this. Future studies should attempt to further elucidate the ways in which gaze and attention interact with motor resonance by recording MEPs and eye movements concurrently, and by manipulating gaze and attentional allocation.

In addition, the present work has contributed to furthering our understanding of the ways in which motor resonance is modulated by factors such as the characteristics of the action and the specific muscles from which MEPs are recorded. Our results showed that observation of simple intransitive movements did not significantly facilitate CE compared to the baseline condition (Study 2), in which participants observed a static hand. In contrast, viewing of reach-to-grasp sequences of actions resulted in significant facilitation of MEP amplitude (Study 3). This is consistent with previous evidence which indicates that meaningful and transitive actions are more effective than intransitive or meaningless movements in eliciting motor resonance (Decety et al., 1997; Enticott, Kennedy, Bradshaw, Rinehart, & Fitzgerald, 2010; Grèzes & Decety, 2001; Newman-Norlund, van Schie, van Hoek, Cuijpers, & Bekkering, 2010). These results also provide further evidence in support of MNS involvement in understanding the actions of others and their goals (e.g., see Iacoboni, 2005; Rizzolatti & Sinigaglia, 2010; and Rizzolatti & Craighero, 2004).

The results of Study 4 showed that observation of a RGL action did not result in significant facilitation of MEP amplitudes from baseline; this contradicts the results of Study 3, in which observation of reach-to-grasp actions did result in significant MEP facilitation. It should be noted that the two studies differed in terms of the baseline condition that was employed. In Study 3, the baseline condition involved observation of a static hand resting on a desk. In contrast, baseline levels of CE in Study 4 were recorded while participants kept their eyes closed. Since in the latter experiment we showed participants two actions that were very different from each other, this ‘neutral’ baseline was chosen so as to make it a suitable reference point for both experimental conditions. It has been argued that, in order to obtain reliable measures of the modulations of MEP amplitude resulting from AO, visual input should be kept as similar as possible across all the conditions, including during baseline measurements (Loporto, McAllister, Edwards, Wright, & Holmes, 2012; Wright, Williams, & Holmes, 2014). Some authors specifically warn against the use of eyes-closed baseline conditions, suggesting that this does not allow us to determine whether the changes in CE that are found during AO are actually due to the recruitment of mirror processes resulting from action perception, or whether they are merely a result of the presence of visual stimuli (e.g., Enticott et al., 2010). In a similar vein, it could be argued that the discrepancy between the results of Studies 3 and 4 may have resulted from the differences in the baseline conditions employed. However, this is unlikely for two reasons. Firstly, if the observed differences had been due to the different visual input provided at baseline, then we would have expected to see greater facilitation of MEP amplitude when the baseline condition involved no visual input – as participants kept their eyes closed – compared to when it consisted of a static hand. In contrast, the results of Studies 3 and 4 revealed the opposite pattern. Furthermore, in Study 2, where we used a static hand as a baseline – thus maintaining visual input as similar as possible throughout – we nevertheless did not find significant facilitation from baseline. This indicates that the type of baseline condition used does not result in MEP amplitude modulations per se.

In our view, there are two important differences between Studies 3 and 4 which could account for the apparently contrasting findings reported above. In order to ensure high levels of engagement with the observation task, in Study 3 we asked participants to learn the observed sequence of reach-to-grasp actions. Facilitation of CE in the muscles involved in the action may have been promoted by the inclusion of this attentional manipulation task, as attention to the action seems to be necessary for motor resonance to emerge (Betti et al., 2017; Donaldson et al., 2015). In contrast, when no additional task was present – as during viewing of the RGL video in Study 4 – participants’ levels of attention might have decreased, consequently inhibiting the recruitment of AO processes.

It is likely that the emergence of motor resonance was also modulated by the muscles we selected. The cortical representations of the intrinsic hand muscles are known to be comparatively much larger and more detailed than those of the forearm muscles. Accordingly, it has been argued that the mirror response may be muscle-dependent to some degree. In Study 3, when we recorded from the finger muscles, we did find significant facilitation of CE during observation of goal-directed single limb actions; however, such facilitation did not reach statistical significance when we looked at the forearm muscles, in Study 4. Therefore, we argue that the cortical representations of more proximal muscles may be too coarse to be modulated by the observation of common single-limb actions. Rather, activation of the coarser representations of these muscles via observation may require viewing of a more dynamic and forceful action, in which the target muscles are recruited to a larger extent compared to a simple RGL action. In line with this notion, motor resonance in the forearm muscles was present during observation of the golf swing, a highly coordinative and vigorous action.

The fact that we recorded from the forearm rather than the hand muscles may also have accounted for the lack of expertise-related differences in motor resonance during observation of golf (Study 4). In one of the few TMS studies that investigated skill-related modulations of CE (Aglioti, Cesari, Romani, & Urgesi, 2008) during observation of a complex and skilled action, such modulations were observed in an intrinsic hand muscle (ADM), but not in an extrinsic forearm one (FCU). Therefore, our findings suggest that viewing of dynamic whole-body actions can activate the coarse cortical representations of the forearm muscles involved in the action – but also that these representations may nevertheless be too coarse for subtle experience-dependent modulations to emerge. Interestingly, Bunday and colleagues (Bunday, Lemon, Kilner, Davare, & Orban, 2016) recently found that muscle-specific motor resonance emerged during observation of an arm and hand performing a grasping action. However, grasp-specificity was no longer present when the video displayed the whole body of the action. This suggests that the fact that our golf condition, which also displayed a whole-body view of the golfer, may have precluded the emergence of subtle skill-related differences.

These findings have implications for TMS studies, as they suggest that selection of the muscles of interest should be tailored to the specific aims of the investigation. For instance, when exploring how an observer's familiarity modulates the motor resonance response, it may be preferable to record from hand muscles rather than from more proximal ones, so as to promote the emergence of subtle skill-related modulations. The visual display should not only comprise whole-body views of the action; zoomed-in videos showing the movements of specific effectors should also be included. The responses recorded during observation of the two perspectives could then be compared so as to further understand how the characteristics of the visual display interact with the observer's expertise. In contrast, when using AO as a way to promote motor system activation in patients with motor impairments, it may be preferable to select actions which require a greater amount of force or which involve dynamic and coordinated movement of multiple limbs, so as to maximise the extent of motor resonance. Future studies should aim to investigate these possibilities.

7.5 Limitations and Future Research Directions

There are some limitations to the present body of work. In Studies 1 and 4 we failed to measure the perceived amount of cognitive effort required for the task. In Study 1, we found that observational learning of the golf swing was facilitated by the inclusion of visual attentional guidance during AO. Inclusion of a cognitive effort measure would have enabled us to determine whether the visual guides facilitated learning by reducing the cognitive resources required to actively 'search' the visual display in order to identify and extract relevant information. Alternatively, the visual guides may have provided a 'visual anchor' which enabled learners to diffuse their covert visual attention in a more efficient way, facilitating processing of information via parafoveal and peripheral vision. Eye tracking measures do not allow us to determine the aspects of the action to which covert attention is allocated; therefore, our explanations above remain speculative. Future research should aim to distinguish the relative contributions of covert and overt visual attention to motor resonance, by adopting different types of attentional manipulations and different task instructions. This could be done by asking participants to perform an attentionally demanding task at fixation while they are engaged in an AO task. For example, participants could be required to maintain their eyes either on the action, or on a fixation cross, which would briefly flicker at random times, and which would be placed so as not to overlap the modelled action. Following observation, participants should answer questions about either the action or the fixation cross, such as, "*Was the last action you saw the same or different from the previous one?";* or "*Did the fixation cross flicker in the last trial?"*. By simultaneously recording gaze and AO-induced MEPs, as well as the percentage of correct answers, we would then be able to determine the extent to which modulations in CE during observation of biological motion were a result of overt and/or covert attentional processes.

An additional problem, which may represent an endemic issue in TMS studies of AO, is that our participants might have spontaneously recruited motor imagery (MI) processes while engaging with the observation task. There is evidence that the combination of MI and AO elicits larger facilitation than does either process alone (Sakamoto, Muraoka, Mizuguchi, & Kanosue, 2009; Wright et al., 2014), a phenomenon that may have affected our findings. We attempted to account for this somewhat in Study 4, by asking participants to estimate the percentage of clips during which they had engaged in MI and to rate the ease with which they imagined the action in the visual and kinaesthetic modalities. Our analyses did not reveal any correlations between the MI variables and MEP amplitudes. However, all participants reported that they had engaged in imagery of the golf action, and some had also engaged in imagery of the RGL action. It is possible that self-report measures of imagery may not be sufficiently subtle to accurately measure engagement in MI processes, which may explain the lack of significant correlations between these crude assessments of MI engagement and motor resonance. Interindividual variability in MI ability may also be problematic, as we did not accurately control for this variable. In order to avoid possible confounds arising from these issues, future studies could attempt to use more objective measures of MI abilities, such as a combination of MEP recording, qualitative and chronometric assessments, and participants should be allocated to MI-ability matched groups.

When designing TMS experiments, careful consideration should be given to the choice of control muscles. For instance, in Studies 2 and 3 we selected the abductor digiti minimi (ADM) as a control muscle. Our results showed that, during observation of actions which do not require direct involvement of ADM, the ADM muscle nevertheless exhibited a facilitation that was comparable to that of the thumb abductor (abductor pollicis brevis, or APB). This suggests that the ADM may not represent the ideal control muscle; the similarity in behaviour between APB and ADM may reflect the fact that the two are often coactivated during execution of everyday hand movements (Mason, Gomez, & Ebner, 2001). To avoid any confounds, researchers should ensure that they obtain MEP recordings from several muscles that are differentially active during different phases of the action. An additional limitation of the present thesis lies in the fact that, rather than obtaining recordings of EMG activity during physical execution of the actions that we showed our participants, we inferred the extent of muscle activation based on existing anatomical knowledge. This is common for TMS studies, but in order to determine with certainty the extent of muscle activation and the degree of co-activation between different muscles, researchers should record EMG activity during action execution itself, to act as a reference point for assessing AO-induced modulations of CE.

Consideration should be given also to the frequency of the TMS pulses. Typically, in TMS studies of action observation, a single TMS pulse is delivered during each video presentation. The frequency of pulse delivery is thus rather low, which ensures sufficient time between each pulse for corticospinal excitability to return to the pre-TMS levels. With higher frequencies of pulse delivery, there is a risk that the levels of TMS-induced activation of the corticospinal system may affect the amplitude of subsequent MEPs to some degree. Although short interpulse intervals do not represent a problem when trying to assess overall levels of corticospinal excitability, they may reduce the likelihood of finding subtle phase-specific effects of action observation. This potentially represents a problem for Study 3, where, in order to record MEPs during two phases of a reach-to-grasp action without drastically increasing the total testing time, we employed an interpulse interval of ~1.5 seconds – a higher frequency than is commonly reported. Nevertheless, the findings of Study 3 showed phase-specific facilitation of MEP amplitudes to some degree, which suggests that the frequency we employed was sufficiently low to detect subtle modulations of CE.

7.6 Conclusion

To conclude, the results of the present work highlight the importance of appropriate allocation of visual attention for extraction and processing of relevant information during action observation. The present thesis addresses some of the limitations of the existing research on AO. In the first place, we applied the concept of sports-based perceptual training based on highlighting relevant cues, to the context of observational learning. In so doing, we demonstrated that this type of exogenous attentional guidance can effectively accelerate learning of novel motor skills, which has implications for future coaching and motor skill teaching practices, and for motor rehabilitation. Furthermore, the present thesis introduces a novel method which allows us to tap directly into the ways in which visual attention interacts with a proxy for mirror neuron activity – motor resonance. By simultaneously recording eye movements and TMS-evoked MEPs, we provided evidence that the locus of overt visual attention and characteristics of the eye movement patterns adopted by the observer are two important factors to consider, and that by directing gaze to specific elements of an action, we can maximise motor resonance – something that had not been directly tested before. Future studies should continue to explore the specific visual attentional mechanisms underlying observational learning, and the related neurophysiological correlates, so as to determine optimal gaze strategies in different contexts.

Our findings collectively suggest that visual attentional guidance represents a beneficial addition to observational (re)learning of motor skills. By directing observers’ gaze during AO, we may maximise the extent of covert simulation of the action in the observer’s motor system. Since the underlying assumption is that increased levels of motor resonance during AO may reflect more effective motor learning (e.g, see Wright et al., 2018), the present findings have implications for AO-based approaches to motor skill learning and motor rehabilitation.

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APPENDICES

APPENDIX A:

List of Publications Emanating from the Present Programme of Research

Published Articles

D'Innocenzo, G., Gonzalez, C. C., Williams, A. M., & Bishop, D. T. (2016). Looking to learn: The effects of visual guidance on observational learning of the golf swing. *Plos One, 11*(5), e0155442. doi:10.1371/journal.pone.0155442

D'Innocenzo, G., Gonzalez, C. C., Nowicky, A. V., Williams, A. M., & Bishop, D. T. (2017). Motor resonance during action observation is gaze-contingent: A TMS study. *Neuropsychologia, 103*, 77-86. doi:10.1016/j.neuropsychologia.2017.07.017

Manuscripts in Preparation

D'Innocenzo, G., Di Gruttola, F., Nowicky, A. V., & Bishop, D. T. (2018). *Exogenous guidance of the observer's gaze modulates phase-specific motor resonance during observation of transitive action sequences.* Manuscript in preparation.

D'Innocenzo, G., Nowicky, A. V., & Bishop, D. T. (2018). *Observation of a complex whole-body action promotes gaze-linked increases in corticospinal excitability relative to a simple grasping action.* Manuscript in preparation.

APPENDIX B:

Study 1 – Research Ethical Approval Letter

Head of School of Sport & Education
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Giorgia D'Innocenzo
PhD (Sport Sciences) Researcher
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12th May 2014

Dear Giorgia

RE38-13 Exploring the effects of visually guided learning on the acquisition of a motor skill

I am writing to confirm the Research Ethics Committee of the School of Sport and Education received your application connected to the above mentioned research study. Your application has been independently reviewed to ensure it complies with the University/School Research Ethics requirements and guidelines.

The Chair, acting under delegated authority, is satisfied with the decision reached by the independent reviewers and is pleased to confirm there is no objection on ethical grounds to grant ethics approval to the proposed study.

Any changes to the protocol contained within your application and any unforeseen ethical issues which arise during the conduct of your study must be notified to the Research Ethics Committee for review.

On behalf of the Research Ethics Committee for the School of Sport and Education, I wish you every success with your study.

Yours sincerely

J Bradshaw.

pp Dr Richard J Godfrey
Chair of Research Ethics Committee
School Of Sport and Education

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APPENDIX C:

Study 1 – Participant Information Sheet and Informed Consent Form

Brunel
UNIVERSITY
LONDON

PARTICIPANT INFORMATION SHEET

Study title: Exploring the effects of visually guided learning on the learning of a golf swing

What is the purpose of the study? We aim to investigate the effects of viewing different videos related to golf on your ability to learn the golf swing in the very short-term

Do I have to take part? You don't have to. If you are not willing to participate you will be explained what you would have to do if you were to take part

What will happen to me if I take part? There are no risks involved in the protocol that will be used.

What do I have to do? You will be required to perform 10 golf swings before and after watching a video of a skilled golfer performing a swing. The whole process will take no longer than 20 minutes per participant. While you are watching the video your eye movements will be recorded using a portable eye tracking device. You will also be required to complete a questionnaire and a pen-and-paper test.

What are the possible disadvantages and risks of taking part? The task you will be asked to do will involve physical exercise, which means that you may get slightly tired. However, you will only be required to practise the movement for a maximum of 6 or 7 minutes, and the procedure used is harmless. None of your peers will be able to watch you performing the moves.

Will my taking part in this study be kept confidential? Yes. All data will be made anonymous and you will not be identified in any way. You will not be able to see other participants' performance or details.

What will happen to the results of the research study? The results may be included in a PhD thesis, published in an academic journal or in the media or they may be presented at a conference.

Who has reviewed the study? This has been reviewed by the Brunel University School of Sport and Education Research Ethics Committee, acting on behalf of the University Research Ethics Committee.

Contact for further information

Should you require further information about this study, please do not hesitate to contact Giorgia D'Innocenzo at giorgia.d'innocenzo@brunel.ac.uk. Alternatively, you may contact her PhD supervisor, Dr Dan Bishop, on daniel.bishop@brunel.ac.uk or 07939 526536.

APPENDIX C (Continued)

Brunel
UNIVERSITY
LONDON

Learning the Golf Swing: INFORMED CONSENT FORM

Please tick the appropriate boxes. Thank you.	*YES*	*NO*
Have you read the Research Participant Information Sheet?	☐	☐
Have you had an opportunity to ask questions and discuss this study?	☐	☐
Have you received satisfactory answers to all your questions?	☐	☐
Who have you spoken to?		
Do you understand that you will not be referred to by name in any report concerning the study?	☐	☐
Do you understand that you are free to withdraw from the study:		
• at any time?	☐	☐
• without having to give a reason for withdrawing?	☐	☐
• (where relevant, adapt if necessary) without affecting your future care?	☐	☐
Do you agree to take part in this study?	☐	☐

Signature: Name in capitals:

Date:

<u>Witness statement</u>

I am satisfied that the above-named has given their informed consent.

Witnessed by (signature): *Name in capitals:*

Date:

Researcher name:	Signature:
Supervisor name:	Signature:

APPENDIX D:

Study 1 – Demographic Information Questionnaire

Brunel UNIVERSITY LONDON

About You

Name: ____________________________________

Gender: Male / female **Date of birth**: _____ /_____ /_____

How would you describe your ethnicity *(e.g. 'Black British')***?** _______________________

Are you right-handed, left-handed, or ambidextrous?

1. **Have you ever watched golf?** YES / NO
2. **Have you ever played golf?** YES / NO

   [if 'NO', then please go to Item 5]

3. **At which level do you currently play?** *(e.g. recreational, school, county)*

   ____

   a. For how many years have you competed at this level or above? ______

4. **If different from above, what is the highest level at which you've played?**

   ____

5. **Please list other sports that you play, or have played:**

Sport	Current level	Yrs of competing

6. **Please list your other hobbies (e.g., listening to music, playing an instrument, etc):**

APPENDIX E:

Study 1 – Rule Formation Questionnaire

Brunel
UNIVERSITY
LONDON

Technical points for swinging a golf club

If you had to pass on technical advice about how to execute a golf swing, to someone who had never even held a club before, what would it be? Please list as many technical points as you can think of below, in any order. YOU HAVE 2 MINUTES IN WHICH TO DO SO.

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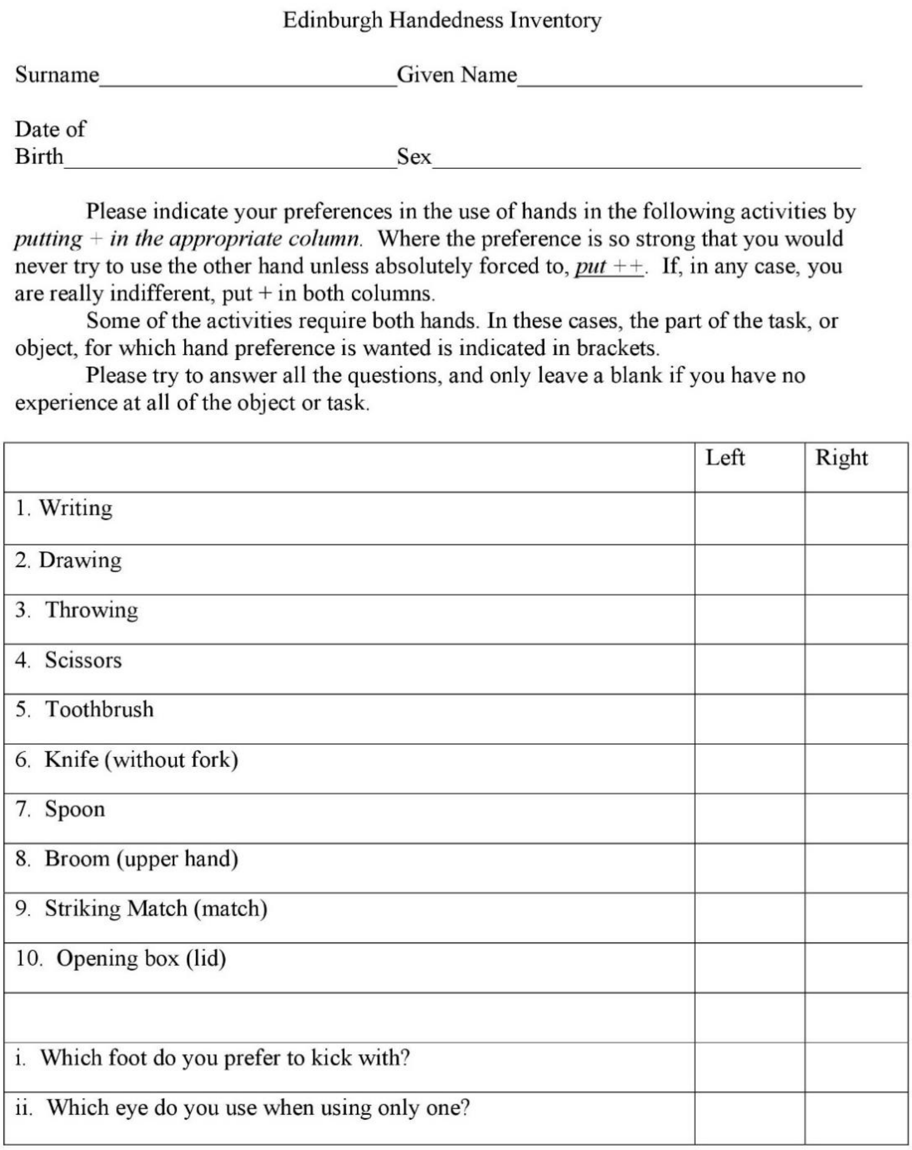
APPENDIX F:

Edinburgh Handedness Inventory



Edinburgh Handedness Inventory

Surname________________________Given Name____________________________

Date of
Birth__________________________Sex___________________________________

Please indicate your preferences in the use of hands in the following activities by *putting + in the appropriate column.* Where the preference is so strong that you would never try to use the other hand unless absolutely forced to, *put ++*. If, in any case, you are really indifferent, put + in both columns.

Some of the activities require both hands. In these cases, the part of the task, or object, for which hand preference is wanted is indicated in brackets.

Please try to answer all the questions, and only leave a blank if you have no experience at all of the object or task.

	Left	Right
1. Writing		
2. Drawing		
3. Throwing		
4. Scissors		
5. Toothbrush		
6. Knife (without fork)		
7. Spoon		
8. Broom (upper hand)		
9. Striking Match (match)		
10. Opening box (lid)		
i. Which foot do you prefer to kick with?		
ii. Which eye do you use when using only one?		

APPENDIX G:

TMS Screening Questionnaire

TMS Screening questionnaire

Please answer the following health-related questions. You should complete this questionnaire only if you know that you are fit and healthy and have read and understood all of the information included in the provided information sheet. If you answer **yes** to any of these questions then you **should not participate** in the study.

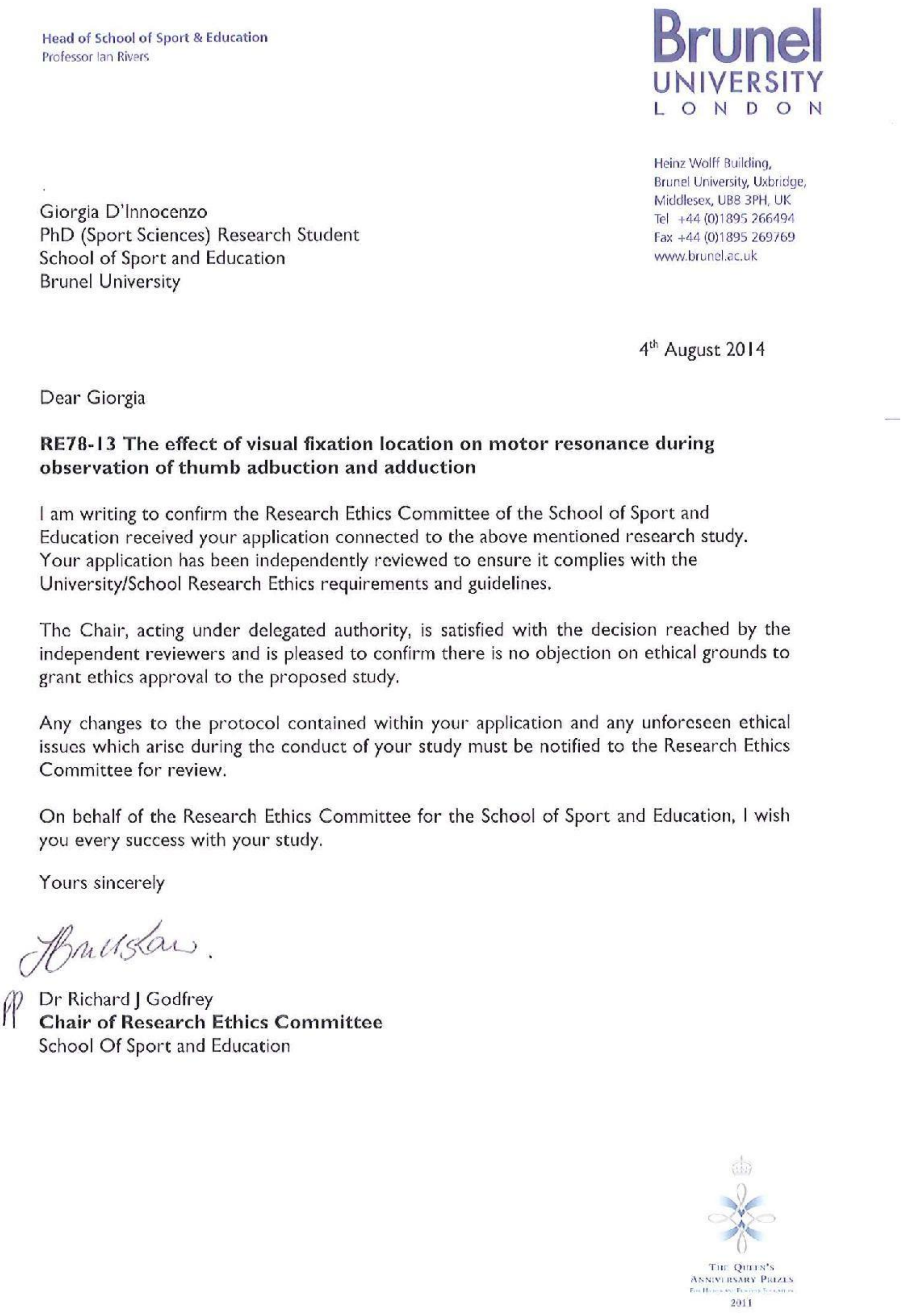
Please circle your responses

Question	
I feel unwell today.	Yes No
I suffer from dizziness/ severe or frequent headaches.	Yes No
I have fainted or passed out one or more times in the last year.	Yes No
I have a low heart rate (bradycardia, less than 55 bpm) and/ or low blood pressure.	Yes No
I have had one or more anxiety/panic episodes in last year.	Yes No
I am on prescribed medication. If yes, please specify.	Yes No
I have an orthopaedic hand or wrist condition (injury to my joints).	Yes No
I have a medical condition.	Yes No
I have a heart condition and /or have a cardiac pacemaker.	Yes No
I have a respiratory problem other than asthma.	Yes No
I have a dermatological condition.	Yes No
I have a (metal) prosthesis or implant in my body.	Yes No
I have had a neurosurgical procedure (operation to the skull).	Yes No
I have an aneurysm clip in my head.	Yes No
I have a neurological condition (including epilepsy).	Yes No
I am pregnant.	Yes No

If you have answered **no** to all of the above questions, then you **may participate** in the study. Your participation is entirely voluntary. You may withdraw at any time from any session for any or no reason. If you have any concerns you are most welcome to address them whenever you feel like it.

APPENDIX H:

Study 2 – Research Ethical Approval Letter



Head of School of Sport & Education
Professor Ian Rivers

Brunel
UNIVERSITY
LONDON

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Middlesex, UB8 3PH, UK
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www.brunel.ac.uk

Giorgia D'Innocenzo
PhD (Sport Sciences) Research Student
School of Sport and Education
Brunel University

4th August 2014

Dear Giorgia

RE78-13 The effect of visual fixation location on motor resonance during observation of thumb adbuction and adduction

I am writing to confirm the Research Ethics Committee of the School of Sport and Education received your application connected to the above mentioned research study. Your application has been independently reviewed to ensure it complies with the University/School Research Ethics requirements and guidelines.

The Chair, acting under delegated authority, is satisfied with the decision reached by the independent reviewers and is pleased to confirm there is no objection on ethical grounds to grant ethics approval to the proposed study.

Any changes to the protocol contained within your application and any unforeseen ethical issues which arise during the conduct of your study must be notified to the Research Ethics Committee for review.

On behalf of the Research Ethics Committee for the School of Sport and Education, I wish you every success with your study.

Yours sincerely

Dr Richard J Godfrey
Chair of Research Ethics Committee
School Of Sport and Education

THE QUEEN'S
ANNIVERSARY PRIZES
2011

APPENDIX I:
Study 2 – Participant Information Sheet and Informed Consent Form

Participant Information Sheet

Study title: The effect of visual fixation location on motor resonance during observation of thumb abduction and adduction.

You are being invited to take part in a research study. Before you decide, it is important for you to understand why the research is being done and what it will involve. Please take time to read the following information carefully and discuss it with others if you wish. Ask us if there is anything that is not clear or if you would like more information. Take your time in deciding whether or not you wish to take part.

Thank you for reading this.

What is the purpose of the study?

It is well known that merely observing another person perform an action activates the same areas of the brain that are involved in the execution of the observed action. The present study aims at testing the notion of an optimal fixation point for the extraction and processing of biological motion information.

Who are we looking for?

We are looking for 16 participants who are healthy, 18 years or older and right-handed.

Do I have to take part?

Participation is entirely voluntary and so it is up to you to decide whether or not to take part. If you do decide to take part you will be given this information sheet to keep and be asked to sign a consent form.

You are free to withdraw at any time of the experiment without giving a reason. Your withdrawal will not have any impact on your status as a student, a member of staff or a visitor to the University.

What will happen to me if I take part?

APPENDIX I (Continued)

If you are willing to participate, you will be asked to attend one session in the laboratory in the Mary Seacole Building at Brunel University. You will also be required to fill out a simple health questionnaire for screening purposes and to make sure you do not put yourself at risk.

The session should last no more than 2 ½ hours and will involve detailed measurements of the excitability of the motor cortex (i.e. the area of the brain that is involved in the planning, control and execution of voluntary movements) and of the resulting motor evoked potentials (i.e. the degree of activation in the target muscle) while you watch a video of simple thumb movements.

Brain Stimulation Techniques: Transcranial Magnetic Stimulation (TMS)

TMS is a technique using a hand held electromagnetic coil positioned over the scalp and it is used to briefly activate the brain area which controls voluntary movement. After each TMS pulse the normal signals from the brain activates the neural pathway leading to your muscles, which will produce brief muscle twitches. The TMS pulses are painless and allow us to monitor changes in brain activity. TMS is a safe and non-invasive technique which has been used for over 25 years in experimental and clinical studies of brain function. Known side effects to either of these techniques during or after the stimulation include transient and mild headache and local discomfort. However, most people do not experience any of these known side effects at all. There are no reported long term side effects of acute application of these techniques.

To measure the small muscle twitches produced by TMS, we also need to use a technique called surface electromyography or EMG which uses self-adhesive electrodes placed on the skin over your hand muscles. This is also a safe technique, which harmlessly allows recording of tiny muscle electrical signals produced prior to muscle twitches.

What are the possible disadvantages and risks of taking part?

It is possible that you may feel discomfort or distress about participating in this study because you may not know anything about the techniques we use. Therefore the researchers will explain the procedure and will familiarize you with these and they will answer any questions you may have.

APPENDIX I (Continued)

The researchers will monitor your comfort throughout the study and will check that you are happy to continue at frequent intervals. When asked or at any time during testing you may request that the researchers stop testing.

What are the possible advantages of taking part?

There are currently no recognised personal advantages or benefits of taking part in this study; however, the study potentially has implications for motor skill acquisition and for the re-learning of previously acquired skills in stroke patients. Potential application for rehabilitation requires initial evaluation in healthy participants.

What if something goes wrong?

Every effort to minimize any discomfort and possible risks and to ensure the safety of all participants during the experiment will be taken. **The researchers will monitor your comfort throughout the study and will check that you are happy to continue at frequent intervals. When asked or at any time during testing you may request that the researchers stop testing.** If at any time you have any concerns regarding the study, do not hesitate to ask one of the researchers or the laboratory supervisor.

Will my taking part in this study be kept confidential?

All data recorded during the study will be anonymous and kept confidential. As the experiment will be conducted in the University laboratory, the data will be stored in the laboratory computer as well as in anonymized format for subsequent analysis. The participant consent form will be the only document that will have your full name and signature on it. This will be securely stored in locked cabinets in the laboratory. Unauthorised individuals will not have access to the data.

What will happen to the results of the research study?

The results may be included in a PhD thesis, published in an academic journal or in the media or they may be presented at a conference.

APPENDIX I (Continued)

This study has been approved by the Research Ethics Committee of the School of Sport and Education, Brunel University.

Contact for Further Information

Should you require further information about this study, please do not hesitate to contact Giorgia D’Innocenzo at giorgia.d’innocenzo@brunel.ac.uk. Alternatively, you may contact her PhD supervisor, Dr Dan Bishop, on daniel.bishop@brunel.ac.uk or 07939 526536.

Thank you for taking time to read this information sheet.

APPENDIX I (Continued)

Participant Consent form

Study title: The effect of visual fixation location on motor resonance during observation of thumb abduction and adduction.

Confidential

Please answer the following health related questions. You should complete this questionnaire only if you know that you are fit and healthy and have read and understood all of the information included in the provided information sheet. If you answer **yes** to any of these questions then you **should not participate** in the study.

Please circle your responses

Question	
I feel unwell today.	Yes No
I suffer from dizziness/ severe or frequent headaches.	Yes No
I have fainted or passed out one or more times in the last year.	Yes No
I have a low heart rate (bradycardia, less than 55 bpm) and/ or low blood pressure.	Yes No
I have had one or more anxiety/panic episodes in last year.	Yes No
I am on prescribed medication. If yes, please specify.	Yes No
I have an orthopaedic hand or wrist condition (injury to my joints).	Yes No
I have a medical condition.	Yes No
I have a heart condition and /or have a cardiac pacemaker.	Yes No
I have a respiratory problem other than asthma.	Yes No
I have a dermatological condition.	Yes No
I have a (metal) prosthesis or implant in my body.	Yes No
I have had a neurosurgical procedure (operation to the skull).	Yes No
I have an aneurysm clip in my head.	Yes No
I have a neurological condition (including epilepsy).	Yes No
I am pregnant.	Yes No

If you have answered **no** to all of the above questions then you **may participate** in the study. Your participation is entirely voluntary. You may withdraw at any time from any session for

APPENDIX I (Continued)

any or no reason. If you have any concerns you are most welcome to address them whenever you feel like it.

Participant's Statement

Please read the form below carefully. If you are unsure of your response please do ask us your enquiries about this study.

The participant should complete the whole of this sheet		
Please initial the appropriate box	YES	NO
Have you read the Research Participant Information Sheet?		
Have you had an opportunity to ask questions and discuss this study?		
Have you received satisfactory answers to all your questions?		
Who have you spoken to?		
Do you understand that you will not be referred to by name in any report concerning the study?		
Do you understand that you are free to withdraw from the study:		
• at any time		
• without having to give a reason for withdrawing		
• without having a negative impact on your status as a University visitor, student or member of the staff		
Do you understand that you will not receive any direct benefit from participating in this study?		
Do you agree to take part in this study?		

APPENDIX I (Continued)

Risk and Discomfort

The use of transcranial magnetic stimulation (TMS) for paired-pulse transcranial stimulation of the brain and the voluntary motor control area is safe and without known long-term risk. This technique has been used throughout the world for over 25 years in both research and clinical screening. Although it is a painless procedure, the activation of muscles using this technique may cause brief discomfort. However, once over the novelty of the sensation of this type of stimulation, it is well-tolerated.

The researchers will monitor your comfort throughout the study and will check that you are happy to continue at frequent intervals. When asked or at any time during testing you may request that the researchers stop testing.

In a small number of cases use of TMS brain stimulation technique may cause a mild headache after your participation in the experiment. These should be mild and not persist. Please do inform us if you experience any such symptoms during or after the experiment.

This study has been approved by the Research Ethics Committee of the School of Sport and Education, Brunel University.

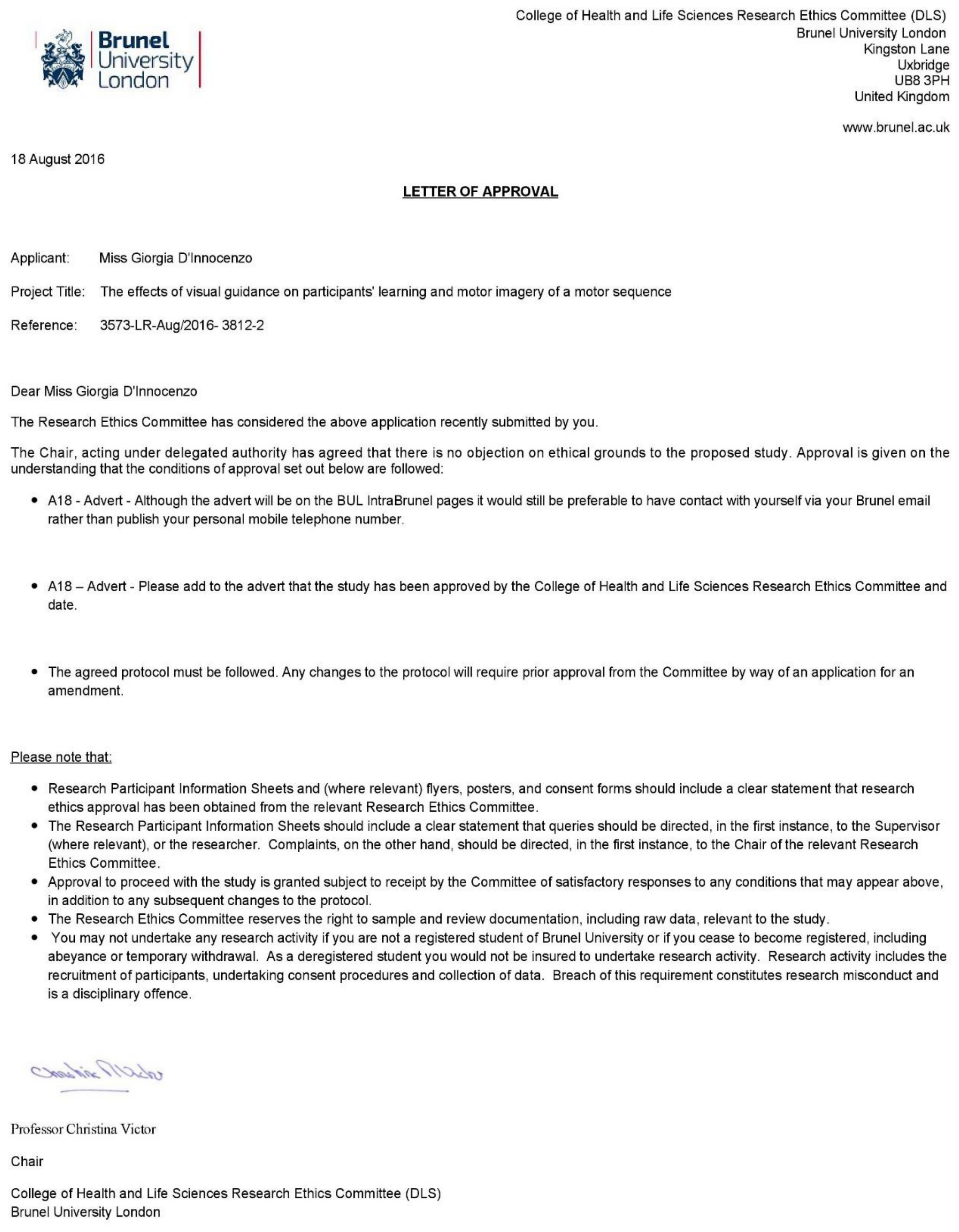
I understand the information provided for me and agree to participate in the practical session for this study and give my consent.

Name: ________________________ Signature: ____________________
Age: ________ Date: _____/________/___________

Witness: ___________________________ Signature: ______________

APPENDIX J:

Study 3 – Research Ethical Approval Letter



College of Health and Life Sciences Research Ethics Committee (DLS)
Brunel University London
Kingston Lane
Uxbridge
UB8 3PH
United Kingdom

www.brunel.ac.uk

18 August 2016

LETTER OF APPROVAL

Applicant: Miss Giorgia D'Innocenzo

Project Title: The effects of visual guidance on participants' learning and motor imagery of a motor sequence

Reference: 3573-LR-Aug/2016- 3812-2

Dear Miss Giorgia D'Innocenzo

The Research Ethics Committee has considered the above application recently submitted by you.

The Chair, acting under delegated authority has agreed that there is no objection on ethical grounds to the proposed study. Approval is given on the understanding that the conditions of approval set out below are followed:

- A18 - Advert - Although the advert will be on the BUL IntraBrunel pages it would still be preferable to have contact with yourself via your Brunel email rather than publish your personal mobile telephone number.

- A18 – Advert - Please add to the advert that the study has been approved by the College of Health and Life Sciences Research Ethics Committee and date.

- The agreed protocol must be followed. Any changes to the protocol will require prior approval from the Committee by way of an application for an amendment.

Please note that:

- Research Participant Information Sheets and (where relevant) flyers, posters, and consent forms should include a clear statement that research ethics approval has been obtained from the relevant Research Ethics Committee.
- The Research Participant Information Sheets should include a clear statement that queries should be directed, in the first instance, to the Supervisor (where relevant), or the researcher. Complaints, on the other hand, should be directed, in the first instance, to the Chair of the relevant Research Ethics Committee.
- Approval to proceed with the study is granted subject to receipt by the Committee of satisfactory responses to any conditions that may appear above, in addition to any subsequent changes to the protocol.
- The Research Ethics Committee reserves the right to sample and review documentation, including raw data, relevant to the study.
- You may not undertake any research activity if you are not a registered student of Brunel University or if you cease to become registered, including abeyance or temporary withdrawal. As a deregistered student you would not be insured to undertake research activity. Research activity includes the recruitment of participants, undertaking consent procedures and collection of data. Breach of this requirement constitutes research misconduct and is a disciplinary offence.

Professor Christina Victor

Chair

College of Health and Life Sciences Research Ethics Committee (DLS)
Brunel University London

APPENDIX K:

Study 3 – Participant Information Sheet and Informed Consent Form

Participant Information Sheet

Study title: The effects of visual guidance on participants' learning and motor imagery of a sequential motor task

You are being invited to take part in a research study. Before you decide, it is important for you to understand why the research is being done and what it will involve. Please take time to read the following information carefully and discuss it with others if you wish. Ask us if there is anything that is not clear or if you would like more information. Take your time in deciding whether or not you wish to take part.

Thank you for reading this.

What is the purpose of the study?

Previous research has shown that observing another individual perform an action has positive effects on motor learning. The aim of the present study is to investigate the effects of different types of visual guidance during action observation on brain activity, on learning of a novel motor sequence task, and on individuals' ability to mentally simulate sequential actions. Your eye movements will also be recorded.

Who are we looking for?

We are looking for 16 healthy, right handed participants (18 years or older).

Do I have to take part?

Participation is entirely voluntary and so it is up to you to decide whether or not to take part. If you do decide to take part you will be given this information sheet to keep and be asked to sign a consent form.

You are free to withdraw at any time of the experiment without giving a reason. Your withdrawal will not have any impact on your status as a student, a member of staff or a visitor to the University.

What will happen to me if I take part?

APPENDIX K (Continued)

If you are willing to participate, then you will be asked to attend one session in the laboratory in the Marie Jahoda Building at Brunel University London. You will also be required to fill out a simple health questionnaire for screening purposes and to make sure that you do not put yourself at risk.

The entire session should last no more than 2 hours. You will be required to observe, and mentally simulate a number of different action sequences, which will involve reaching for and squeezing some squash balls. Your performance on the task will be recorded and assessed so as to establish the amount of learning. We will record detailed measurements of the excitability of the motor cortex (i.e. the area of the brain that is involved in the planning, control and execution of voluntary movements) while you engage in motor imagery of the motor sequences, using a brain stimulation technique called Transcranial Magnetic Stimulation (TMS). Your eye movements will be monitored throughout, and you will be asked to fill in some questionnaires to allow us to assess your motor imagery ability and your level of alertness.

Transcranial Magnetic Stimulation (TMS)

TMS is a technique in which a hand held electromagnetic coil is positioned over the scalp, to deliver an electromagnetic pulse which briefly excites the motor cortex. Immediately after each TMS pulse is delivered, the associated muscle will 'twitch', as evidence of the increased activation of the brain-to-muscle pathway. The TMS pulses are safe and painless, and the technique has been used for over 25 years in experimental and clinical studies of brain function. Known side effects during or after the stimulation include transient and mild headache and local discomfort. However, most people do not experience any of these side effects at all. There are no reported long-term side effects of acute application of TMS.

To measure the small muscle twitches produced by TMS, we also use a technique called surface electromyography (EMG), in which self-adhesive electrodes will be placed on the skin of your forearm and index finger muscles. This is also a safe technique, which harmlessly allows recording of the tiny electrical signals that underpin the muscle twitches we see.

What are the possible disadvantages and risks of taking part?

APPENDIX K (Continued)

It is possible that you may feel discomfort or distress about participating in this study because you may not know anything about the techniques we use. Therefore, the researchers will explain the procedure and will familiarize you with these; they will answer any questions you may have.

What are the possible advantages of taking part?

There are currently no recognised personal advantages or benefits of taking part in this study; however, the study potentially has implications for motor skill acquisition and for the re-learning of previously acquired skills (e.g., in the case of stroke patients).

What if something goes wrong?

Every effort will be taken to minimize any discomfort and possible risks and to ensure the safety of all participants during the experiment. **The researchers will monitor your comfort throughout the study and will check that you are happy to continue at frequent intervals. When asked or at any time during the study, you may request that the researchers stop testing.** If at any time you have any concerns regarding the study, do not hesitate to ask one of the researchers.

Will my taking part in this study be kept confidential?

All data recorded during the study will be anonymous and kept confidential. As the experiment will be conducted in the University laboratory, the data will be stored in the laboratory computer, in anonymized format for subsequent analysis. The participant consent form will be the only document that will have your full name and signature on it. This will be securely stored in locked cabinets in the laboratory. Unauthorised individuals will not have access to the data.

What will happen to the results of the research study?

The results may be included in a PhD thesis, published in an academic journal or in the media or presented at a conference.

This study has been approved by the College of Health and Life Sciences Research Ethics Committee, Brunel University London.

APPENDIX K (Continued)

Thank you for taking time to read this information sheet.

Contact for Further Information

Should you require further information about this study, please do not hesitate to contact Giorgia D'Innocenzo at giorgia.d'innocenzo@brunel.ac.uk. Alternatively, you may contact her PhD supervisor, Dr Dan Bishop, at daniel.bishop@brunel.ac.uk or on 01895 267513 or 07939 526536. Should you have any concerns or complaints about the study, please contact Professor Christina Victor, chair of College Research Ethics Committee, at Christina.Victor@brunel.ac.uk.

Participant Consent form

Study title: **The effects of visual guidance on participants' learning and motor imagery of a sequential motor task**

Please answer the following health-related questions. You should complete this questionnaire only if you know that you are fit and healthy and have read and understood all of the information included in the provided information sheet. If you answer **yes** to any of these questions then you **should not participate** in the study.

Please circle your responses

Question	
I feel unwell today.	Yes No
I suffer from dizziness/ severe or frequent headaches.	Yes No
I have fainted or passed out one or more times in the last year.	Yes No
I have a low heart rate (bradycardia, less than 55 bpm) and/ or low blood pressure.	Yes No
I have had one or more anxiety/panic episodes in last year.	Yes No
I am on prescribed medication. If yes, please specify.	Yes No
I have an orthopaedic hand or wrist condition (injury to my joints).	Yes No
I have a medical condition.	Yes No
I have a heart condition and /or have a cardiac pacemaker.	Yes No
I have a respiratory problem other than asthma.	Yes No
I have a dermatological condition.	Yes No
I have a (metal) prosthesis or implant in my body.	Yes No
I have had a neurosurgical procedure (operation to the skull).	Yes No
I have an aneurysm clip in my head.	Yes No
I have a neurological condition (including epilepsy).	Yes No
I am pregnant.	Yes No

If you have answered **no** to all of the above questions then you **may participate** in the study. Your participation is entirely voluntary. You may withdraw at any time from any session for

any or no reason. If you have any concerns you are most welcome to address them whenever you feel like it.

Participant's Statement

Please read the form below carefully. If you are unsure of your response please do ask us your enquiries about this study.

The participant should complete the whole of this sheet		
Please initial the appropriate box	YES	NO
Have you read the Research Participant Information Sheet?		
Have you had an opportunity to ask questions and discuss this study?		
Have you received satisfactory answers to all your questions?		
Who have you spoken to?		
Do you understand that you will not be referred to by name in any report concerning the study?		
Do you understand that you are free to withdraw from the study:		
• at any time		
• without having to give a reason for withdrawing		
• without having a negative impact on your status as a University visitor, student or member of the staff		
Do you understand that you will not receive any direct benefit from participating in this study?		
Do you agree to take part in this study?		

Risk and Discomfort

The use of transcranial magnetic stimulation (TMS) for stimulation of the brain and the motor cortex is safe and without known long-term risk. This technique has been used throughout the world for over 25 years in both research and clinical screening. Although it is a painless procedure, the activation of muscles using this technique may cause brief discomfort. However, once over the novelty of the sensation of this type of stimulation, it is well-tolerated.

The researchers will monitor your comfort throughout the study and will check that you are happy to continue at frequent intervals. When asked or at any time during testing you may request that the researchers stop testing.

In a small number of cases, use of TMS brain stimulation technique may cause a mild headache after your participation in the experiment; this should be mild and not persist. Please do inform us if you experience any such symptoms during or after the experiment.

This study has been approved by the College of Health and Life Sciences Research Ethics Committee, Brunel University London.

I understand the information provided for me and agree to participate in the practical session for this study and give my consent.

Name: ________________________________ Signature: _____________________

Gender: M/F Age:________ Date: _____/________/___________

Witness:___________________________ Signature: ______________

APPENDIX L:

Study 4 – Research Ethical Approval Letter

Department of Life Sciences Research Ethics Committeee
Brunel University London
Kingston Lane
Uxbridge
UB8 3PH
United Kingdom

www.brunel.ac.uk

7 January 2016

LETTER OF APPROVAL

Applicant: Miss Giorgia D'Innocenzo

Project Title: Expertise-related differences in gaze behaviour and motor resonance during observation of the golf swing

Reference: 0854-MHR-Jan/2016-1204

Dear Miss Giorgia D'Innocenzo

The Research Ethics Committee has considered the above application recently submitted by you.

The Chair, acting under delegated authority has agreed that there is no objection on ethical grounds to the proposed study. Approval is given on the understanding that the conditions of approval set out below are followed:

- The agreed protocol must be followed. Any changes to the protocol will require prior approval from the Committee by way of an application for an amendment.

Please note that:

- Research Participant Information Sheets and (where relevant) flyers, posters, and consent forms should include a clear statement that research ethics approval has been obtained from the relevant Research Ethics Committee.
- The Research Participant Information Sheets should include a clear statement that queries should be directed, in the first instance, to the Supervisor (where relevant), or the researcher. Complaints, on the other hand, should be directed, in the first instance, to the Chair of the relevant Research Ethics Committee
- Approval to proceed with the study is granted subject to receipt by the Committee of satisfactory responses to any conditions that may appear above, in addition to any subsequent changes to the protocol.
- The Research Ethics Committee reserves the right to sample and review documentation, including raw data, relevant to the study.
- You may not undertake any research activity if you are not a registered student of Brunel University or if you cease to become registered, including abeyance or temporary withdrawal. As a deregistered student you would not be insured to undertake research activity. Research activity includes the recruitment of participants, undertaking consent procedures and collection of data. Breach of this requirement constitutes research misconduct and is a disciplinary offence.

Professor Christina Victor

Chair

Department of Life Sciences Research Ethics Committeee
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APPENDIX M:
Study 4 – Participant Information Sheet and Informed Consent Form

Participant Information Sheet

Study title: Differences in experts' and novices' gaze patterns and brain activity during observation of the golf swing

You are being invited to take part in a research study. Before you decide, it is important for you to understand why the research is being done and what it will involve. Please take time to read the following information carefully and discuss it with others if you wish. Ask us if there is anything that is not clear or if you would like more information. Take your time in deciding whether or not you wish to take part.

Thank you for reading this.

What is the purpose of the study?

It is well known that merely observing another person perform an action activates the same areas of the brain that are involved in the execution of the observed action, an effect known as *motor resonance*. The aim is to investigate expert-novice differences in motor resonance that are elicited during observation of a skilled golfer executing a series of golf swings; your eye movements will also be recorded.

Who are we looking for?

We are looking for 10 participants with no previous experience of playing golf (novices) and 10 expert golfers. Participants must be healthy, 18 years or older and right-handed.

Do I have to take part?

Participation is entirely voluntary and so it is up to you to decide whether or not to take part. If you do decide to take part you will be given this information sheet to keep and be asked to sign a consent form.

You are free to withdraw at any time of the experiment without giving a reason. Your withdrawal will not have any impact on your status as a student, a member of staff or a visitor to the University.

What will happen to me if I take part?

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If you are willing to participate, then you will be asked to attend one session in the laboratory in the Gaskell Building at Brunel University London. You will also be required to fill out a simple health questionnaire for screening purposes and to make sure that you do not put yourself at risk.

The entire session should last no more than 2 hours and will involve detailed measurements of the excitability of the motor cortex (i.e. the area of the brain that is involved in the planning, control and execution of voluntary movements) while you watch videos of an everyday action and of a skilled golfer performing the golf swing, using a brain stimulation technique called Transcranial Magnetic Stimulation (TMS).

Transcranial Magnetic Stimulation (TMS)

TMS is a technique in which a hand held electromagnetic coil is positioned over the scalp, to deliver an electromagnetic pulse which briefly excites the motor cortex. Immediately after each TMS pulse is delivered, the associated muscle will ‘twitch’, as evidence of the increased activation of the brain-to-muscle pathway. The TMS pulses are safe and painless, and the technique has been used for over 25 years in experimental and clinical studies of brain function. Known side effects during or after the stimulation include transient and mild headache and local discomfort. However, most people do not experience any of these side effects at all. There are no reported long-term side effects of acute application of TMS.

To measure the small muscle twitches produced by TMS, we also use a technique called surface electromyography (EMG), in which self-adhesive electrodes will be placed on the skin of your forearm muscles. This is also a safe technique, which harmlessly allows recording of the tiny electrical signals that underpin the muscle twitches we see.

What are the possible disadvantages and risks of taking part?

It is possible that you may feel discomfort or distress about participating in this study because you may not know anything about the techniques we use. Therefore, the researchers will explain the procedure and will familiarize you with these; they will answer any questions you may have.

What are the possible advantages of taking part?

APPENDIX M (Continued)

There are currently no recognised personal advantages or benefits of taking part in this study; however, the study potentially has implications for motor skill acquisition and for the re-learning of previously acquired skills (e.g., in the case of stroke patients).

What if something goes wrong?

Every effort will be taken to minimize any discomfort and possible risks and to ensure the safety of all participants during the experiment. **The researchers will monitor your comfort throughout the study and will check that you are happy to continue at frequent intervals. When asked or at any time during the study, you may request that the researchers stop testing.** If at any time you have any concerns regarding the study, do not hesitate to ask one of the researchers.

Will my taking part in this study be kept confidential?

All data recorded during the study will be anonymous and kept confidential. As the experiment will be conducted in the University laboratory, the data will be stored in the laboratory computer, in anonymized format for subsequent analysis. The participant consent form will be the only document that will have your full name and signature on it. This will be securely stored in locked cabinets in the laboratory. Unauthorised individuals will not have access to the data.

What will happen to the results of the research study?

The results may be included in a PhD thesis, published in an academic journal or in the media or presented at a conference.

This study has been approved by the College of Health and Life Sciences Research Ethics Committee, Brunel University London.

Thank you for taking time to read this information sheet.

Contact for Further Information

Should you require further information about this study, please do not hesitate to contact Giorgia D’Innocenzo at giorgia.d’innocenzo@brunel.ac.uk. Alternatively, you may contact her PhD supervisor, Dr Dan Bishop, at daniel.bishop@brunel.ac.uk or on 01895 267513 or 07939 526536. Should you have any concerns or complaints about the study, please contact Professor Christina Victor, chair of College Research Ethics Committee, at Christina.Victor@brunel.ac.uk.

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Participant Consent form

Study title: **Differences in experts' and novices' gaze patterns and brain activity during observation of the golf swing**

Please answer the following health-related questions. You should complete this questionnaire only if you know that you are fit and healthy and have read and understood all of the information included in the provided information sheet. If you answer **yes** to any of these questions then you **should not participate** in the study.

Please circle your responses

Question	
I feel unwell today.	Yes No
I suffer from dizziness/ severe or frequent headaches.	Yes No
I have fainted or passed out one or more times in the last year.	Yes No
I have a low heart rate (bradycardia, less than 55 bpm) and/ or low blood pressure.	Yes No
I have had one or more anxiety/panic episodes in last year.	Yes No
I am on prescribed medication. If yes, please specify.	Yes No
I have an orthopaedic hand or wrist condition (injury to my joints).	Yes No
I have a medical condition.	Yes No
I have a heart condition and /or have a cardiac pacemaker.	Yes No
I have a respiratory problem other than asthma.	Yes No
I have a dermatological condition.	Yes No
I have a (metal) prosthesis or implant in my body.	Yes No
I have had a neurosurgical procedure (operation to the skull).	Yes No
I have an aneurysm clip in my head.	Yes No
I have a neurological condition (including epilepsy).	Yes No
I am pregnant.	Yes No

If you have answered **no** to all of the above questions then you **may participate** in the study. Your participation is entirely voluntary. You may withdraw at any time from any session for

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any or no reason. If you have any concerns you are most welcome to address them whenever you feel like it.

Participant's Statement

Please read the form below carefully. If you are unsure of your response please do ask us your enquiries about this study.

The participant should complete the whole of this sheet		
Please initial the appropriate box	YES	NO
Have you read the Research Participant Information Sheet?		
Have you had an opportunity to ask questions and discuss this study?		
Have you received satisfactory answers to all your questions?		
Who have you spoken to?		
Do you understand that you will not be referred to by name in any report concerning the study?		
Do you understand that you are free to withdraw from the study:		
• at any time		
• without having to give a reason for withdrawing		
• without having a negative impact on your status as a University visitor, student or member of the staff		
Do you understand that you will not receive any direct benefit from participating in this study?		
Do you agree to take part in this study?		

Risk and Discomfort

The use of transcranial magnetic stimulation (TMS) for stimulation of the brain and the motor cortex is safe and without known long-term risk. This technique has been used throughout the world for over 25 years in both research and clinical screening. Although it is a painless procedure, the activation of muscles using this technique may cause brief discomfort. However, once over the novelty of the sensation of this type of stimulation, it is well-tolerated.

The researchers will monitor your comfort throughout the study and will check that you are happy to continue at frequent intervals. When asked or at any time during testing you may request that the researchers stop testing.

In a small number of cases, use of TMS brain stimulation technique may cause a mild headache after your participation in the experiment; this should be mild and not persist. Please do inform us if you experience any such symptoms during or after the experiment.

This study has been approved by the College of Health and Life Sciences Research Ethics Committee, Brunel University London.

I understand the information provided for me and agree to participate in the practical session for this study and give my consent.

Name: ________________________ Signature: _____________________

Age:________ Date: _____/________/___________

Witness:__________________________ Signature: ______________

APPENDIX N:

Study 4 – Demographic Information Questionnaire

Brunel University London

About You

Are you right-handed, left-handed, or ambidextrous?

1. **Have you ever watched golf?** YES / NO

2. **Have you ever played golf?** YES / NO

[if 'NO', then please go to Item 6]

3. **At which level do you currently play?** *(e.g. recreational, school, county)*

   ____

   a. For how many years have you competed at this level or above? ______

4. **If different from above, what is the highest level at which you've played?**

   ____

5. **What is your handicap rating?** ______

6. **Please list other sports that you play, or have played:**

Sport	**Current level**	**Yrs of competing**

APPENDIX O:

Study 4 – Motor Imagery Questionnaire

Please answer the following questions about the golf videos

- While watching the videos, did you at any point imagine yourself performing the movement?
  YES/NO *[if 'NO', then please go to the next page]*

- For how many clips do you recall doing this?

____

- If you did imagine yourself at any point:
  - How intensely, on average, did you FEEL yourself performing the movement?

No sensation	Mildly intense	Moderately intense	Intense	As intense as executing the action
1	2	3	4	5

  - How vividly, on average, did you SEE yourself performing the movement (i.e. from a third-person perspective)?

No image	Blurred image	Moderately clear image	Clear Image	Image as clear as seeing
1	2	3	4	5

APPENDIX O (Continued)

Please answer the following questions about the bottle videos

- While watching the videos, did you at any point imagine yourself performing the movement?

  YES/NO

- For how many clips do you recall doing this?

____

- If you did imagine yourself at any point:
  - How intensely, on average, did you FEEL yourself performing the movement?

No sensation	Mildly intense	Moderately intense	Intense	As intense as executing the action
1	2	3	4	5

  - How vividly, on average, did you SEE yourself performing the movement (i.e. from a third-person perspective)?

No image	Blurred image	Moderately clear image	Clear Image	Image as clear as seeing
1	2	3	4	5