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REVIEW ARTICLE

Investigating Central Mechanisms Underlying the Effects of Action Observation and Imagery Through Transcranial Magnetic Stimulation

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ABSTRACT. Sport and exercise psychologists provide some interventions for clients based on limited direct evidence and partial understanding of the mechanisms that underpin their efficacy. The authors review a recent technique, transcranial magnetic stimulation (TMS), which offers a tested procedure for investigating cortical activity during observation and imagery processes. They provide a detailed description of the TMS protocol and highlight some of the key studies that inform sport and exercise psychology research. Finally, the authors offer some thoughts on the direct application to practice.

Keywords: action observation, corticospinal facilitation, movement imagery, transcranial magnetic stimulation

Mental skills training through, for example, the practice of action observation and movement imagery techniques has been shown consistently to improve sporting performance (e.g., Callow & Hardy, 1999; Ram, Riggs, Skaling, Landers, & McCullagh, 2007; Ramsey, Cumming, & Edwards, 2008; Smith & Holmes, 2004). Further, it is now widely accepted that action observation and movement imagery processes, defined here as a combination of first-person perspective visual and kinaesthetic imagery, involve the similar aspects of central motor representations to those accessed during the execution of action (Jeannerod, 1994). Indeed, changes in neural activity can be detected in similar brain regions and interpreted to reflect that the different processes share similar motor representations.

Unfortunately, the sport and exercise psychology literature predominately contains subjective reports and behavioral measures and only a small number of studies have directly investigated the central mechanisms through which observation and movement imagery improve sporting performance (e.g., Fourkas, Bonavolonta, Avenanti, & Aglioti, 2008; Holmes, Collins, & Calmels, 2006; Lotze, Scheler, Tan, Braun, & Birbaumer, 2003). For this reason we propose that transcranial magnetic stimulation (TMS), a noninvasive method of stimulating the brain and peripheral nervous system using induced currents (Barker, Jalinous, & Freeston, 1985), offers sport and exercise psychology researchers a valuable technique that enables them to examine the central mechanisms underlying movement imagery and action observation.

More specifically, in the present article we review (a) methodological issues to consider when using TMS, (b) research that has used TMS to investigate action observation and movement imagery, and (c) implications of using TMS techniques in sport and exercise psychology.

TMS Methods

The TMS coil, consisting of one or more tightly wound copper coils and typically covered with molded plastic, activates the human brain through the principle of electromagnetic induction. As described by Faraday's law, the application of a time-varying magnetic field within a stimulating coil held over the scalp can induce an electric current in the underlying cortical tissue. When applied over the hand representation of the primary motor cortex (M1), the stimulation activates the corticospinal system to produce muscle contractions in the hands and fingers in the contralateral side of the body. The compound action potentials associated with these muscle contractions are easily recorded using skin surface electromyographic (EMG) electrodes and are normally termed *motor evoked potentials* (MEP; see Figure 1).

Various parameters of the MEP can be studied: the size of the MEP (amplitude, duration, and area), onset latency (time between the cortical stimulation and onset of the MEP in the target muscle), stimulation thresholds, and silent period. The peak-to-peak amplitude of the MEP is the most commonly reported measurement and is used as a marker of corticospinal excitability at the time of stimulation (Rossini et al., 1994). Increased levels of corticospinal excitability are reflected by a facilitation of the MEP, specifically an increase in peak-to-peak MEP amplitude, a shortening of the onset latency, and a decrease in motor threshold (discussed subsequently). If the target muscle is active at the time of stimulation, then a variable period of EMG absence typically follows the MEP. This inhibitory phenomenon is termed the *silent period*. The initial component of the silent period (<50 ms) is generated by predominately spinal inhibitory mechanisms whereas the later components (>50 ms) reflect a long-lasting inhibition that originates within the motor cortex (Inghilleri, Berardelli, Cruccu, & Manfredi, 1993). An important characteristic of MEPs is their spontaneous inter- and intra-individual

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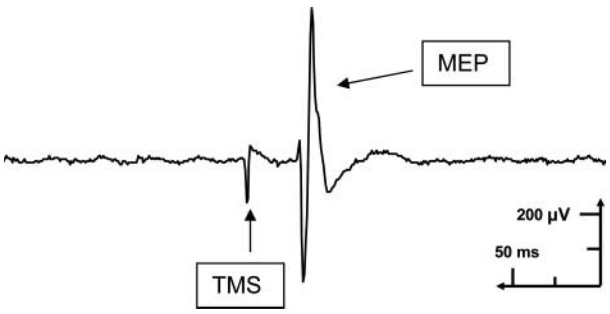

FIGURE 1. Motor evoked potentials following TMS of the motor cortex. The magnitude of the response is typically measured as the peak to peak amplitude of the MEP recorded from the surface EMG activity.

variability in amplitude from one stimulus to the next, even if the stimulus intensity is kept constant. The exact reason for this is presently unknown (Kiers, Cros, Chiappa, & Fang, 1993), but highlights that in order to obtain a reliable estimate of MEP amplitude a reasonably large number of responses (approximately 10–15) should be obtained.

Types of Coils

Different designs of stimulating coils exist and the coil shape determines the properties and the size of the induced magnetic field. The original design of the stimulating coil was circular, and although it produces an effective activation of the motor cortex it has a very limited capacity to target specific muscles. This is because the strength of the induced electric field is minimal underneath the center of the coil and maximum underneath its windings. As the coil diameters are generally large (e.g., 80–100 mm), the windings span a considerable area of the skull surface. Figure-eight shaped coils that comprise two small circular coils aligned in the same plane have a maximum electric field strength underneath the central overlapping section. This allows for a more focal stimulation that is more suitable for mapping cortical representations of muscles (Wassermann, McShane, Hallett, & Cohen, 1992). It should be noted, however, that even when using the figure-eight coil, stimulation normally elicits MEPs in several muscles at the one time. This reflects the considerable overlap of different muscle representations within M1 (Sanes & Donoghue, 2000).

Optimal Scalp Position

At the start of each experimental session it is standard practice to find the optimal scalp position (OSP) for eliciting responses in the target muscle. To do so, repeated stimulations are applied in a systematic fashion, typically 1 cm apart, over the motor cortex using a high stimulus intensity. The OSP (or motor hotspot) is marked as the position that produces MEPs with the highest peak-to-peak amplitudes and shortest onset latencies in the target muscle. A tight-fitting polyester cap worn by the participant can be used to allow the researcher to mark measurements on the head. Recording the position of the OSP in relation to the center of the head (universally identified as Cz, as defined by Jasper's [1958] International 10–20 System) can aid the replication of coil position if repeated TMS sessions are required. Small changes in coil position or rotation can significantly influence MEP amplitudes (Balslev, Braet, McAllister, & Miall, 2007; Boniface, Mills, & Schubert, 1990). For this reason accurate monitoring of coil position is crucial. It is our experience that fixing the coil to the head using a frame significantly aids this process as compared to when the coil is handheld. Newly available image-guided frameless stereotaxic neuronavigation systems, though expensive, reduce experimenter bias and offer the best solution for precise monitoring of coil position (Sparing, Hesse, & Fink, 2010).

Motor Threshold

Once the coil is positioned it is possible to determine the participants' motor thresholds. Resting motor threshold (RMT) is normally defined as the lowest stimulation intensity that induces MEPs of 50 μv (peak-to-peak amplitude) in 50% of 10–20 consecutive trials with the muscle at rest (Rossini et al., 1994). RMT is normally recorded with respect to the maximum stimulator output (MSO) of the magnetic device being used and reported as a percentage of such. Active motor threshold (AMT) can also be determined as the participant performs a small contraction of the target muscle (5–10% maximum voluntary contraction). For this measurement, 50% of MEPs greater than 100 μv are required. AMT values are considerably lower than RMT values, which reflects that the voluntary contraction leads to increased excitability at the cortical and spinal motorneuron levels (Di Lazzaro et al., 1998).

It is important for participants to maintain a constant limb position during any measures of motor threshold because variations in proprioceptive input can also modulate the excitability of the motor cortex (Lewis, Byblow, & Carson, 2001). Attention should also be paid to the interstimulus interval, as the response to a given stimulus can be influenced by prior stimuli. An interstimulus interval of 5–10 s between each successive pulse is recommended to allow the effects of the previous stimulation to subside (Chen et al., 1997).

A wide range of motor thresholds is found within the healthy population. Present evidence suggests that this variation is largely independent of age, gender, and hemisphere but strongly reflects anatomical factors such as individual differences in the distance between scalp and the underlying cortical tissue (McConnell et al., 2001; Stokes et al., 2005). Individual motor thresholds are stable over time and show good reproducibility between sessions (Mills & Nithi, 1997); therefore, the stimulation intensity is commonly normalized to a given percentage of each participant's motor threshold. The intrinsic hand muscles (e.g., first dorsal interosseous [FDI], abductor pollicis brevis [APB]), which are regularly used in studies of action observation and movement imagery, typically have the lowest motor thresholds, reflecting the high density of corticospinal projections to these muscles (Wassermann et al., 1992).

Physiological Basis of the MEP

We presently have a far from complete understanding of how TMS influences brain activity, due to the complexity of the cortical structures that are stimulated; however, the widely accepted mechanism by which TMS activates the motor cortex to produce the MEP is termed the *D- and I-wave hypothesis* (Day et al., 1989; Edgley, Eyre, Lemon, & Miller, 1997). Briefly, this hypothesis proposes that the electrical current induced in the cortex exerts its effects by two very different mechanisms. The electric current may excite corticospinal neurons and their axons directly, giving rise to D- (direct) waves, or excite the corticospinal neurons transsynaptically, giving rise to I- (indirect) waves. Both forms of waves, termed descending volleys, are then transmitted down to the alpha motoneurons in the spinal cord via the large diameter, fast-conducting axons of the corticospinal tract (Di Lazzaro et al., 2004; Edgley et al.). If these descending volleys, individually or via summation, are sufficiently strong, a synchronized discharge of the spinal alpha motoneurons may lead to a subsequent muscle contraction.

The validity of TMS as a method for assessing changes in the excitability of the motor cortex is based on the implications of the D- and I-wave hypothesis. If TMS activates corticospinal neurons in a transsynaptic manner, other processes, such as action observation or movement imagery that elicit a change in cortical excitability, may also modify the extent to which the cortical stimulation excites the corticospinal neurons, which, in turn, may influence the amplitude of the MEP obtained in the target muscle. In contrast, if TMS activates corticospinal axons directly at sites downstream to synaptic input, then the amplitude of the MEP may not reflect the overall balance of cortical excitability at the moment of stimulation. In the following sections, we briefly review how the stimulation intensity and the direction of induced brain current have an important influence on the physiological response to TMS (for more comprehensive reviews of this topic, see Di Lazzaro et al., 2004; Hallett, 2007; Reis et al., 2008).

The onset latencies of MEPs obtained using TMS of high intensity are typically 1–2 ms quicker than those obtained using threshold intensities. Epidural recordings in conscious humans have demonstrated that this is because threshold intensity TMS preferentially activates corticospinal neurons in an indirect transsynaptic manner, whereas high-intensity TMS activates the corticospinal axons directly at a site below the level of the motor cortex (Di Lazzaro et al., 2004). This finding indicates that the amplitudes of MEPs produced using high stimulation intensities are less representative of cortical excitability levels than MEP amplitudes recorded using near threshold intensities of TMS. The practical implication is that it is important to use stimulation intensities that are close to the motor threshold if the purpose of the experiment is to measure cortical excitability.

The direction of the induced current flow is also an important determinant of the way in which TMS activates the corticospinal system. The electric current induced in the brain is relatively homogenous and flows almost exclusively in a horizontal plane that lies parallel but travels in the opposite direction to that of the stimulating coil (Branston & Tofts, 1990). When using a figure-eight coil, the optimal orientation for achieving indirect transsynaptic activation of the hand area of the motor cortex is when the coil is held tangentially to the scalp with the handle pointing at 45° posterolaterally with respect to the midsagittal axis of the head (Brasil-Neto et al., 1992; Mills, Boniface, & Schubert, 1992). This orientation is referred to as posteroanterior stimulation, as the flow of induced brain current passes perpendicular to the direction of the central sulcus in a posterior-to-anterior direction (see Figure 2).

Investigating the Central Mechanisms of Action Observation and Movement Imagery Using TMS

TMS clearly offers a new approach for researchers in motor learning and sport and exercise psychology to investigate the mechanisms involved in movement-related processes. We propose that TMS techniques, with the rigorous methods discussed previously and contextually relevant designs, can significantly add to the ongoing debate in this important area of research. In the next two sections we consider the research that has used TMS to explore the processes of action observation and movement imagery, two common interventions used by sport and exercise psychologists. We propose that by further investigating the mechanisms underpinning these processes, the applied techniques may be used more optimally.

Action Observation and TMS

As human beings, individuals interact with other individuals on a daily basis. Understanding the meanings of other people's actions is crucial to communication and social interaction; this is especially important in sporting situations. The human mirror system[1] has been proposed to provide some explanation for the underlying mechanisms behind physical activity-related behaviors. For example, according to the direct-matching hypothesis proposed by Rizzolatti, Fogassi, and Gallese (2001), individuals gain a greater understanding of human actions by mapping the visual representation of the observed action onto their own motor representation of the same action, causing the motor system of the observer to resonate during observation of that action. Motor resonance "is revealed either as an overt imitation or as a subliminal activation of the motor structures that would sustain the observed action" (Montagna, Cerri, Borroni, & Baldissera, 2005, p. 1513).

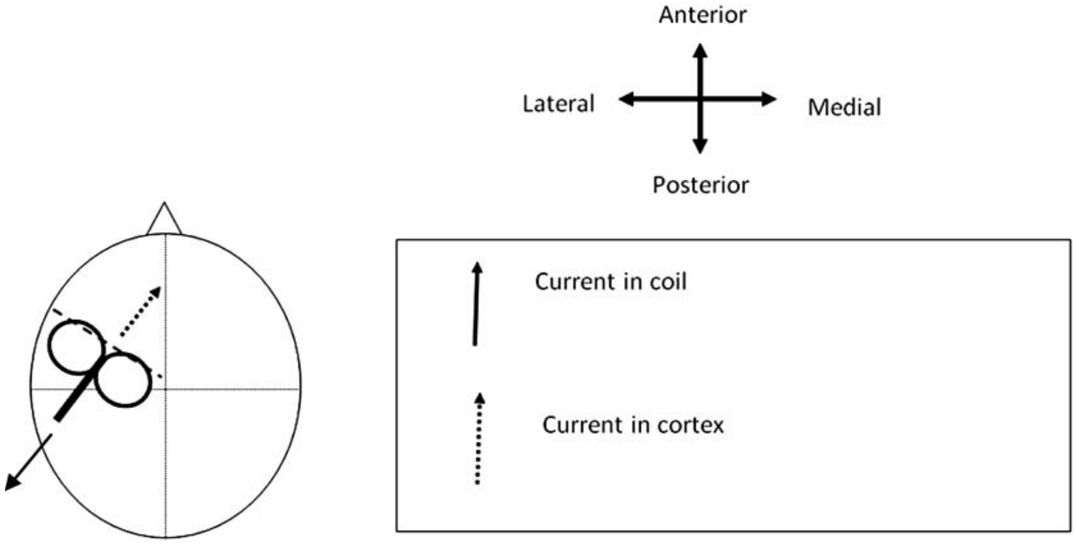

FIGURE 2. An illustration of posteroanterior coil orientation using a figure-eight stimulating coil. This coil orientation provides optimal results when attempting to achieve trans-synaptic activation of corticospinal neurons, giving a good representation of their state of excitability. The coil handle should be held at approximately 45° posterolaterally with respect to the midsagittal axis of the head. Note that the current induced in the coil flows toward the handle, which is in the opposite direction to the current induced in the cortex.

TMS has been used widely in research investigating corticospinal excitability during action observation. The data have shown reliably that observation of an action performed by the self or others, in the absence of any recordable overt movement, modulates the excitability of the corticospinal pathway in humans. This modulation typically results in the increase of the amplitude of MEPs specific to the muscles involved in the observed action. It should be noted that to ensure that the MEPs obtained are a result of action observation, rather than residual muscle activity from actual physical movement, EMG should be constantly monitored. This is important because activation of the muscle of interest causes larger TMS-evoked MEPs (Kiers et al., 1993). Trials showing high EMG muscle activity should be removed from analysis.

In one of the first studies to use TMS in an action observation condition, Fadiga, Fogassi, Pavesi, and Rizzolatti (1995) applied single-pulse TMS to participants' M1. They obtained MEPs from a variety of muscles known to be responsible for controlling the fingers while participants observed one of four conditions: (a) two action observation conditions consisting of an object-directed grasping action and the tracing of Greek alphabet letters in the air, and (b) two baseline conditions in which participants observed either the object alone or a dimming LED on a computer screen. The data showed that the MEP amplitudes obtained as the participants observed both action conditions were higher than those recorded during the two baseline conditions. A further point of interest was the specificity of the response, as this modulation of the MEP amplitude was found only in those muscles of the hand that would have been used to physically perform the observed motor actions. That is, observation of grasping actions and letter drawing increased the amplitude of the MEP obtained in the FDI muscle, but only observation of the grasping action modulated the MEP obtained in the opponens pollicus (OP) muscle, as this muscle is involved in index finger and thumb grasping.

Since these first early studies, the use of TMS to understand human representation of action via action observation has increased. For example, Gangitano, Mottaghy, and Pascual-Leone (2001) examined whether the amplitude of the MEPs elicited in the FDI and OP muscles were modulated in relation to temporal aspects of an observed video of a reach-and-grasp movement. TMS was applied to the primary motor cortex while participants observed a hand reaching toward and grasping a ball using a precision grip. The stimulation was delivered at different time intervals corresponding to the following specific phases of the movement: (a) the initial stationary hand position, (b) the beginning of the action when the hand was lifted from the table, (c) during the increase of the grasp aperture, (d) the time of maximal grasp aperture, and (e) when the hand closed on the ball. The data showed that the amplitude of the MEP recorded in the FDI muscle tended to increase throughout the movement, with the largest MEP recorded at the point of maximal grasp aperture. Gangitano, Mottaghy, and Pascual-Leone (2004) explored the effect further by asking participants to observe normal reaching and grasping actions compared to an unusual action, where the hand would close inappropriately and reopen prior to grasping the object. The data replicated that of Gangitano et al. (2001) for the observation of normal action, but showed the MEP facilitation only occurred during the early phase of the observed unusual movement, not during the second segment after the initial closure. It was proposed that this finding suggests that the motor representation predicts the outcome of motor acts before they occur, rather than monitoring and matching the observed movements as they develop in an online fashion. The implications are clear for sporting situations in which motor anticipation and motor deception are important.

In a more recent study, Borroni, Montagna, Cerri, and Baldissera (2005) examined the relationship between MEP amplitudes recorded from two antagonistically paired forearm muscles (the flexor and extensor carpi radialis) while participants observed an experimenter performing a cyclic wrist flexion–extension movement. The amplitudes of the MEPs obtained in both muscles were facilitated in different periods of the observed movement; those recorded from flexor carpi radialis were facilitated when the observed movement was in a period of wrist flexion, and those recorded from the extensor carpi radialis were facilitated during observation of the corresponding wrist extension movement. These findings indicate that the more a muscle is active at a particular point in an observed movement, the greater the MEPs recorded from the muscle at that particular point. This study provides further evidence for the muscle and temporal specificity in the MEP facilitation effect while also demonstrating that the human mirror system seems to respond to simple intransitive actions with no specific object-orientated goal.

These studies indicate that familiarity with the observed action may play an important role in the motor facilitation effect. The ability to actually perform the observed movement, however, may not be essential to modulate corticomuscular excitability. Romani, Cesari, Urgesi, Facchini, and Aglioti (2005) conducted a series of experiments examining the effects of observing biologically possible movements (such as abduction and adduction of the index finger) compared to biologically impossible movements created by shifting the position of the moving digit; the participant would effectively observe the same abduction and adduction movements occurring at points beyond the normally possible range of movement. Surprisingly, MEP facilitation occurred in the associated muscle when observing the normal and impossible movements and this pattern of facilitation was consistent for a number of conditions involving possible and impossible movements. This suggests that facilitation effects are neither limited to movements that are part of the observer's motor repertoire nor limited to normal movements. One problem with this design, however, is that the impossible movements were generated from normal finger movements and simply altered relative to the hand. Therefore, the effects could be explained as a response to local aspects of the observed normal kinematic action profiles. Certainly, more TMS-based studies are needed to test these effects, but the implications for the human movement sciences are, again, evident: imaged and observed actions need not necessarily comprise those that are part of the individual's contemporary history of experiences or present motoric ability. There may also be implications for metaphorical imagery interventions in which the imagined movements can frequently be impossible for humans. These ideas remain to be tested.

The findings from action observation TMS studies have also revealed that the scope of motor representation is not limited to motor acts; it may also play an important role in empathy. As we discussed previously, the observation of an action can demonstrate facilitative effects in the MEPs of specific motor areas. However, Avenanti, Minio-Paluello, Bufalari, and Aglioti (2006) found that the observation of a painful stimulus had an inhibitory effect on MEP amplitude. When participants observed videos of a needle being inserted deep into a hand muscle, the MEP amplitudes obtained in the corresponding muscle of the observer were found to decrease. This effect was once again found to be muscle specific as when participants observed a similarly painful stimulus being applied to the foot area, the amplitude of the MEPs recorded from the two hand muscles remained at baseline levels. A second experiment in which participants observed videos of a needle either penetrating deeply or pricking, superficially, an actor's hand found a negative correlation between participant's perception of pain and the magnitude of the MEPs recorded from his or her FDI muscle. This result provides good evidence that the emotional content of video observation can have significant effects on corticomuscular excitability, suggesting that emotional congruence and meaningfulness may be important in optimizing the use of action observation as an intervention.

Observation, delivered through video media and various movement imagery techniques generally include an auditory component. A relevant issue here is the extent to which action-related sounds contribute to the representation and, potentially, modulates the MEP. While the research in this area is limited, some studies have investigated if action-related sound modulates corticospinal excitability. Fadiga, Craighero, Buccino, and Rizzolatti (2002) recorded MEPs from the tongue muscles as participants listened to words that had either a strong or slight mobilization of tongue-tip action, using words with a double-*r* or double-*f* sound, respectively. The data revealed that the MEP amplitudes resulting from cortical stimulation were higher when participants listened to the words involving a strong, compared to slight, mobilization of the tongue. In a similar experiment, Aziz-Zadeh, Iacoboni, Zaidel, Wilson, and Mazziotta (2004) examined the effect of action related sound on muscle specific facilitation of corticomuscular excitability. Participants listened to hand–finger actions associated with typing and paper being torn, leg–foot actions (the sound of footsteps associated with walking), or a control sound (rumbles of thunder). The data showed that the amplitude of the MEP recorded from the FDI muscle was significantly greater when listening to the hand-related sounds than it was for the leg–foot actions and the control thunder sounds. As in previous studies, assessing congruency between visual representations of action and execution, these results demonstrate a sound specific modulation of corticomuscular excitability that only occurs in those muscles that would actually be involved in executing the action-related sounds. Because action observation and, as we will show in the section below, movement imagery typically include specific reference to auditory cues that are task relevant, the potential for a combined audiovisual facilitation effect seems possible. The exact nature of the specific role of each modality and their interdependence is, at present, unknown.

The research in this area has focused mainly on the evidence for a human mirror system; however, the continued use of TMS to support this research base provides confidence for the validity of the technique in action observation research. As we discuss in the next section, TMS is also being used increasingly in movement imagery research to investigate a similar phenomenon.

Movement Imagery and TMS

In contrast to the action observation literature, TMS research in movement imagery is limited, possibly because of the methodological difficulties in controlling the covert behavior (for a review, see Holmes & Calmels, 2008). It is likely, however, that there is some shared neural substrate between motor execution, action observation and movement imagery (Holmes, Cumming, & Edwards, 2010). Therefore, in a similar way to the action observation studies discussed previously, movement imagery also offers opportunities for TMS research. Indeed, some studies have already demonstrated that engaging in movement imagery is associated with a measureable muscle specific change in corticomuscular excitability.[2] In Fadiga et al.'s (1999) study, participants imaged a forearm flexion and extension movement in time to an auditory stimulus while single pulse TMS was applied over the hand area of motor cortex. The amplitudes of the MEPs recorded from the biceps brachii during imagery of forearm flexion were significantly greater than those recorded during imagery of forearm extension. In contrast, the amplitudes of the MEPs recorded from the OP muscle were not affected by the movement imagery task. This suggests a similar effect to that occurring during action observation in that corticomuscular excitability was only found when the muscles involved in the physical task were imaged to perform as force-generating agonists. In a second experiment, participants were required to image their hand opening and closing, effectively holding the hand with the palm exposed, and then creating a fist in time with an auditory stimulus. The participants received stimulation over either their left or right motor cortex while imaging performing the task with either the contralateral or ipsilateral hand. During stimulation of the left motor cortex, MEPs recorded from the OP of both hands were facilitated only during imagery of the hand closing, and MEP magnitudes were significantly greater on the contralateral (right hand) compared to the ipsilateral (left hand) side. When the right hemisphere was stimulated, OP MEPs were facilitated only during imagined hand closing. This effect, however, only occurred in the contralateral (left) limb. Again, this evidence demonstrates that MEP facilitation only seems to occur when the muscle involved is acting as a force-generating agonist. The discrepancy between the results for the different hemispheres suggests that the left motor cortex may play a more dominant role in motor imagery. It should be noted that the extent of the muscle activity during imagined movements was not sufficient to cause physical movement, but there was significant corticospinal activity. In a similar study, Facchini, Muellbacher, Battaglia, Boroojerdi, and Hallett (2002) applied TMS to M1 whilst participants imaged thumb abduction movements. Consistent with Fadiga et al.'s findings, the results showed a rapid increase in M1 excitability during the motor imagery condition. In contrast, however, the increase only involved the contralateral hand. Facchini et al. attributed this disparity to the task, which "involved the whole hand, and thus was likely to be more effective in recruiting a larger population of corticospinal cells across both motor cortices" (p.150). In a more detailed study of imagery processes using TMS techniques, Stinear, Byblow, Steyvers, Levin, and Swinnen (2006) examined changes in corticospinal excitability during kinaesthetic imagery (imagining the feeling that movement of the task creates) and third-person perspective visual imagery (an individual imagining seeing him- or herself performing the task) in a similar thumb movement task. The authors reported greater involvement of M1 in the movement imagery process during the kinaesthetic imagery condition. This is consistent with previous findings using other neurophsysiological techniques (fMRI, e.g., Porro, Cettolo, Francescato, & Baraldi, 2000; EEG, e.g. Stecklow, Infantosi, & Cagy, 2010). Taken together, this evidence provides further support for a central mechanism to explain movement imagery's effects rather than the now outdated peripheral psychoneuromuscular theories.

Relationship Between Vividness of Movement Imagery and MEP Amplitude

Individuals vary in their ability to produce vivid movement images. In sport psychology, this imagery characteristic has often been measured using self-report questionnaires, such as the Vividness of Movement Imagery Questionnaire–Revised (VMIQ-2; Roberts, Callow, Hardy, Markland, & Bringer, 2008). These questionnaires are also used to measure vividness change after imagery-based interventions. TMS therefore provides an opportunity for a promising new method for assessing changes in the vividness of movement imagery following interventions to complement self-report data. A preliminary analysis of data from studies in our own laboratories indicated that the peak-to-peak amplitude of MEPs recorded during a movement imagery task show a moderate to strong correlation with the internal visual and kinaesthetic component scores of the VMIQ-2 (correlation coefficients in the range of 0.4–0.5). This indicates that change in the self-reported vividness of movement images may be reflected in changes in MEP amplitudes during movement imagery tasks, providing further validation for questionnaire measures such as the VMIQ-2. More recent research (Williams, Morris, Pearce, Loporto, & Holmes, 2011) has suggested that the movement image meaning and context are also important factors for consideration. It is possible, therefore, that *r* values of 0.4–0.5 may be underestimates of the relationship between MEP amplitudes and highly vivid and meaningful movement images. This proposal remains to be tested.

Comparing the Effects of Action Observation, Movement Imagery, and Motor Execution Using TMS

We have shown that when TMS activates corticospinal neurons in an indirect, or transsynaptic, manner it is then that the MEP amplitude obtained during stimulation reflects the overall balance of cortical excitability at the moment of stimulation. This is important for any study of action observation or movement imagery because proponents of the mirror system would hypothesize that the activity in the motor areas of interest and related to the covert behavior are additive to the TMS indirectly induced activity, thereby resulting in an MEP facilitation when compared to control conditions. Most TMS research in action observation and movement imagery has been applied over M1. Neuroimaging studies, however, suggest that the two main brain areas of the human mirror system are the inferior parietal lobule (IPL) and the ventral premotor cortex (PMv), including the caudal part of the inferior frontal gyrus (IFG). However, Fadiga, Craighero, and Olivier (2005) proposed a mechanism whereby robust cortico–cortico connections connect M1 and premotor cortex. Therefore, it is believed that during action observation, and possibly movement imagery, M1 excitability is increased through activation of the premotor areas that connect to the primary motor cortex (Rizzolatti, 2005).

In one of the first attempts to compare MEP magnitudes in the three behavioral conditions, Clark, Tremblay, and Ste-Marie (2004) separated action observation into two further conditions of either passive observation in which the participant simply observed a movement, or in a condition requiring observation to imitate. In this latter condition participants observed an action in order to perform it for themselves at a later time. All conditions showed a significant increase in MEP magnitude and significant decrease in MEP latency compared with the baseline conditions, mentally counting backwards and a postbaseline activity check. Although performing actions physically led to the greatest difference from the baseline conditions, there was no difference in the level of facilitation between passive observation, observation to imitate, and movement imagery of the action. Preliminary analysis of data from ongoing experiments in our laboratories have produced findings similar to those of Clark et al. This is an interesting finding for sport and exercise psychologists, not only suggesting that action observation and movement imagery show changes in corticospinal excitability, but also confirming that both behaviors share at least some neural substrate with the physical execution of action. The possibilities for combining the two processes in multiple intervention strategies to support physical practice would seem sensible.

Comparing the Effects of Action Observation and Movement Imagery in Sport Using TMS

The advance of the cognitive neurosciences and the introduction of noninvasive psychophysiological techniques have made it possible to investigate the intact human brain and, as we have shown, this has contributed greatly to advances in knowledge in the field of sport and exercise science. Unfortunately, however, there are only a limited number of TMS studies that have been conducted investigating action observation and movement imagery in the sporting brain. In one of the only sports action observation TMS studies, Aglioti, Cesari, Romani, and Urgesi (2008) measured the corticospinal excitability of elite basketball players, expert basketball watchers, and novices while they observed a series of basketball shots, soccer kicks, and static images. The results showed increased modulation of corticospinal excitability in the elite and expert groups for their area of expertise, suggesting activation of the motor system during observation of domain-specific actions. In a second study, Fourkas et al. (2008) used TMS techniques to consider neuroplastic changes in skilled tennis players. A number of important findings emerged: (a) kinaesthetic components of movement imagery modulated corticomuscular excitability, (b) tools associated with performance (in this case the tennis racket) influenced kinaesthetic imagery and associated corticospinal facilitation, and (c) normalized MEP markers of kinaesthetic imagery were greater for more experienced tennis players. Although some of these claims have been theorized (e.g., Holmes & Collins, 2001) or supported through psychometric markers (e.g., Hardy & Callow, 1999), the direct corticospinal facilitation concurrent with the more subjective data is new to sport and exercise psychology and significantly increases the understanding of a frequently used intervention. We encourage more research in this area.

Single Versus Paired-Pulse Techniques in TMS

All the experiments presented in this review so far have used a method that stimulates motor cortex using a single pulse TMS technique and have, as the only marker, the MEP obtained in peripheral muscles. The limitation of this approach is that the increase in corticomuscular excitability, as represented by the increased MEP amplitude, may have occurred through many different neuronal pathways. As a consequence, these studies raise further questions about the mechanisms by which the interventions may modify corticomuscular excitability. With regards to action observation, Fadiga et al. (2005) suggested at least two mechanisms by which the facilitatory effect could occur. Data from primates (as discussed previously) show a strong interconnectivity between premotor area F5 and primary motor area M1, a similar potential cortico–cortical mechanism may also be present in humans to allow the activity of mirror neurons in the premotor cortex to increase the excitability of motor cortex. Similarly, however, the facilitation effect could be due to connections between the premotor cortex and the spinal cord. Regardless of the exact mechanism, the evidence provided here suggests that the mental simulation of actions is associated with muscle-specific changes in corticomuscular excitability on a trial-by-trial basis.

To address this important methodological and mechanistic concern, a paired-pulse TMS method has been proposed (Kujirai et al., 1993). This method offers the potential to provide two TMS pulses, at short interstimulus intervals, through a single stimulating coil. The ability to change pulse intervals and to control the power level of each stimulus allows the experimenter to evaluate the effects of an initial conditioning stimulus on the amplitude of the MEP elicited by a subsequent test stimulus. One form of the paired-pulse technique is to use a subthreshold conditioning stimulus and a suprathreshold test stimulus. If the intensity of the first conditioning pulse is set to 80% of the motor threshold and the interstimulus interval is set between 1 and 5 ms, then this pulse will act to reduce the MEP elicited by the subsequent test pulse and is a valid approach for probing intracortical excitability (Kujirai et al.).

Patuzzo, Fiaschi, and Manganotti (2003) used this paired-pulse TMS technique to investigate the effects of action observation and movement agency on corticomuscular excitability and intracortical inhibition. The participants observed either their own hand or an experimenter's hand perform finger movements via previously recorded videos. Further conditions included movement imagery of the same action and two baseline conditions: looking at a blank white screen and observing the movements of a computer-generated geometric shape. Significant increases in MEP amplitude compared with baseline conditions were observed in the observation and imagery conditions. This finding not only provides further evidence of similarities between action and observation, but also suggests that the ownership of the movement (whether a movement is attributed to one individual or another) is not important to MEP facilitation. As a result of the paired-pulse TMS technique, the authors were able to make stronger claims for the effects being due to changes at a cortical rather than a spinal level.

Investigating Changes in Cortical Plasticity Using TMS

The studies reviewed in the previous section indicate that TMS can provide useful markers of corticomuscular excitability during action observation and movement imagery. TMS can also be used to assess the use of mental skills training that may be associated with more permanent changes in neural activity due to various forms of cortical plasticity. Although sport and exercise psychologists make elaborate claims for behavior change as a consequence of their interventions, direct evidence for such change is frequently lacking. TMS may provide an effective route through which to address this concern.

Pascual-Leone et al. (1995) were one of the first groups using TMS to demonstrate plasticity in the motor cortex associated with mental skills training. They first found the motor hotspot for the long finger flexor (LFF) and long finger extensor (LFE) muscles of the participant's dominant hand. A grid was created around the OSP, allowing the experimenters to map the area of the motor cortex representing the LFF and LFE muscles. The physical practice group participants performed a simple five-finger piano-playing task with their dominant hand, while the mental practice group participants imaged performing the same task without moving their hand or touching the keys. Participants practiced for 2 hr each day over a 5-day period and were tested in their ability to physically perform the task each day by the monitoring of the number of sequence and timing errors. Initially, only stimulation of the OSP elicited MEPs of $>50\ \mu$v from the LFF and LFE muscles. However, after physical or mental practice, stimulation of the areas surrounding the OSP resulted in MEPs of similar magnitude. This effect was not present in a control group, who underwent daily mapping sessions without piano practice, suggesting that training resulted in changes in the size of the cortical motor representations of the muscles involved in the task. Perhaps, unexpectedly, while increases in cortical map size were equal for the physical and mental practice groups, their performance during daily testing sessions differed. The mental practice group took five days to reach the standard that the physical practice group had achieved in three. After a further 2-hr physical training session, the mental practice group achieved the same level of performance as the physical practice group. Taken together, these TMS data suggest that physical and mental practice of a task can increase the cortical representation of the specific muscles involved. This may be due to the generation of new neuronal connections, the renewing of previously established connections, or a combination of both of these factors. Although increases in cortical map size indicate that these changes occur within the motor cortex, the possible contribution of other structures, such as premotor cortex or cerebellum, is unclear. The similarity in the increase in cortical areas suggests physical and mental practice share a common mechanism, which is important for human performance scientists, whereas physical practice was more effective in improving performance of the task. The combination of both types of practice appeared to be most effective.

In a novel TMS study of brain plasticity, Classen, Liepert, Wise, Hallett, and Cohen (1998) discovered that the application of single-pulse TMS to the motor cortex can elicit isolated thumb movements that, within individual participants, display a high level of directional consistency. They used this phenomenon to investigate whether the repetition of simple movements was effective in inducing relatively permanent changes in cortical motor representations. The baseline direction of the TMS-evoked thumb movements was first established before participants repetitively performed thumb movements in the opposite direction for up to 30 min. For example, if the baseline TMS-evoked thumb movements were in an extension and abduction direction, then the participant would repetitively flex and adduct the thumb. The posttraining results showed that the TMS-evoked movements changed toward the recently practiced direction. However, this effect was transient, as it lasted for only several minutes before the TMS-evoked movements returned to their original direction. This directional training also modulated the excitability of thumb muscle representations in M1 in favor of the trained agonist muscle. This finding suggests that the repetitive physical practice of simple movements can induce transient changes in cortical motor representations and that this may reflect the memory encoding of the kinematic aspects of the movement.

There is evidence from behavioral studies that action observation can lead to improved performance (Ram et al., 2007) and that a shared motor representation may be associated with subsequent motor learning. This proposal would be supported by evidence demonstrating that action observation can, without physical practice, lead to the formation or modulation of cortical motor representations. In this regard, Stefan et al. (2005) showed that action observation can modulate changes in motor representations. Utilizing the elegant TMS method of Classen et al. (1998), they stimulated M1 to determine the baseline direction of each participant's TMS-evoked thumb movements. Two of the conditions presented to the participant were (a) physical practice of thumb movements performed in the direction opposite to the preferential TMS-evoked movement bias and (b) observation of an actor's hand performing thumb movements in the direction opposite to the participant's preferential TMS-evoked movement bias. In agreement with the results of Classen et al., the repetitive physical practice performed in the direction opposite to the initial TMS-evoked movement bias induced a change in the subsequent TMS-evoked movements away from the pretraining baseline toward the practiced direction. This kinematic change was also associated with an increase in corticomuscular excitability of the agonist muscle and lasted for at least 10 min (durations of longer than 10 min were not tested in this study). More significantly, the observational training also produced qualitatively similar but less prominent changes in these variables. These results demonstrate that action observation training can modulate cortical motor representations, even in the absence of physical practice. Celnik et al. (2006) also provided compelling evidence, obtained from elderly participants, that cortical motor representations encoded by physical practice can be enhanced by action observation. These findings provide strong support for the efficacy of observation-based interventions used not only by sport and exercise psychologists, but also by practitioners in clinical rehabilitation environments, for example with stroke patients (Ertelt et al. 2007; Holmes & Ewan, 2008).

The modulation effects of action observation on cortical motor representations were also explored by Stefan, Classen, Celnik, and Cohen (2008). They investigated whether the observation of thumb movements presented in temporal synchrony with physical practice could moderate the formation of motor memories. They found that the practice-dependent formation of a motor memory, as shown previously by Classen et al. (1998), was modulated by the concurrent observation of another individual performing a similar motor task. Concurrent observation of thumb movements that were directionally congruent to the participant's physical practice facilitated motor memory encoding whereas the observation of incongruent movements appeared to have little effect. It may be considered that the enhancing effect of congruent action observation occurred through a direct facilitation of the quality of physical practice. However, it should be noted that there is a distinction between using action observation to improve performance during physical practice periods and using action observation to directly improve subsequent physical performance. The physical practice performance did not vary across conditions. Therefore, the enhancing effect of congruent action observation was not due to an improvement in the quality of the physical training movements, but rather a direct improvement in the later performance.

TMS Methodological Concerns

TMS is still a relatively new psychophysiological technique, and although it is a valuable technique for measuring the excitability of a shared motor representation, it is not without its methodological concerns. Addressing some of these issues should allow further work in this area to be highly rigorous.

Stimulus Intensity Issues

In TMS action observation experiments, contrasting results are often obtained and this may be explained by the intensity used for stimulation. As explained in a previous section (see TMS intensity), there are practical implications regarding the choice of the intensity used. The MEP amplitudes recorded using high stimulation intensities are less representative of the ongoing level of cortical excitability than MEP amplitudes recorded using near threshold intensities of TMS. It is therefore interesting to note the variety of intensities used by different researchers and laboratories to investigate the similar phenomena. Some researchers have applied TMS over motor cortex with a stimulation intensity of 110% RMT (e.g., Borroni et al., 2005; Catmur, Walsh, & Heyes, 2007; Gangitano et al., 2004; Molnar-Szakacs, Wu, Robles, & Iacoboni, 2007; Montagna et al., 2005; Takahashi, Kamibayashi, Nakajima, Akai, & Nakazawa, 2008), with others stimulating at the higher intensities of 120% RMT (e.g., Aziz-Zadeh, Maeda, Zaidel, Mazziotta, & Iacoboni, 2002; Buccino, Sato, Cattaneo, Roda, & Riggio, 2009; Bufalari, Sforza, Cesari, Aglioti, & Fourkas, 2010; Fourkas, Ionta, & Aglioti, 2006; Patuzzo et al., 2003; Sakamoto, Muraoka, Mizuguchi, & Kanosue, 2009), 130% RMT (Aglioti et al., 2008; Alaerts, Heremans, Swinnen, & Wenderoth, 2009; Alaerts, Swinnen, & Wenderoth, 2010; Romani et al., 2005; Urgesi, Candidi, Fabbro, Romani, & Aglioti, 2006), and some as high as 150% RMT (Li, Stevens, & Rymer, 2009). The range of intensities used in these experiments is of concern as TMS pulses can evoke different kinds of descending volleys depending on the intensity of the stimulation (Di Lazzaro et al., 2004), which will have an impact on the resulting MEPs obtained during action observation or movement imagery (see previous section on D- and I-waves).

Optimal Scalp Position (Motor Hotspot) Issues

In TMS action observation studies it is very common for experimenters to record MEPs from a number of concurrent muscles (e.g., when recording from various finger and wrist muscles during observation of a reach and grasps action). Researchers tend to determine the OSP for only one of the muscles under investigation (usually the main muscle of interest). Once that position is located, the coil is then positioned over that scalp site and stimulation occurs at that one site throughout the experiment. This is problematic because MEPs are recorded for other muscles, which, as a result of this method, are not being stimulated at their respective OSPs. Often, despite testing muscles that are in close proximity with each other, they differ slightly in their positioning over the motor cortex. Therefore, by not conducting separate experiments, each time using a different muscle's own OSP, the topic of muscle specificity during action observation should be treated with caution. By stimulating a muscle at a site other than its optimal scalp site may affect the muscle's threshold intensity and, therefore, influence the stimulation intensity applied throughout the experiment. The significance of the importance of stimulus intensity is described in the previous section (see stimulus intensity issues).

Control Condition Issues

An increasingly large number of research groups have used TMS to test the observation-execution matching system in humans. However, there have been inconsistencies in the control conditions employed in these studies. For example, many TMS action observation studies (e.g., Alaerts et al., 2009; Gangitano et al., 2001; 2004; Leonard & Tremblay, 2007; Patuzzo et al., 2003) have compared the MEP amplitudes during action observation against observation of a blank screen, with results generally showing larger MEP amplitudes in the action observation condition. Without a static hand condition, however, it is not possible to determine whether the recorded effects are specifically due to the observation of the action per se, as the effects could be due to the presence of an object on the screen irrespective of the type of action, muscles used, or meaning of the action. Although a small proportion of TMS action observation studies have compared action observation to static image controls (e.g., Catmur et al., 2007; Lepage, Tremblay, & Theoret, 2010; Urgesi et al., 2006), these inconsistencies in the control conditions make it difficult to compare findings across laboratories. By using a blank screen or a fixation cross control, researchers are unable to attribute the MEP changes to the observed action. It is, therefore, more revealing and informative to compare the MEP facilitation obtained during action observation to a static control of the same action in order to represent a true facilitation: to report an increase (or decrease) from that static control. Using a static control condition clearly seems to have benefits over a blank screen in action observation studies and would seem to be the obvious control choice. There are, however, studies that have used other novel control conditions to explore the mechanisms of action observation further. As we reported previously, Romani et al. (2005) compared TMS responses during the viewing of either biomechanically possible or impossible movements, the latter, in effect, acting as a novel control condition that allows normal movement comparisons beyond that which blank screen or static control conditions would allow. Other novel control manipulations would be welcomed.

Conclusions

We have presented a review of the optimal TMS methods as they are currently understood to operate. We believe that TMS offers a valid and relatively cost-effective approach for investigating the mechanisms supporting some of the most popular interventions employed in sport and exercise psychology. TMS is a technique that can be used to investigate the involvement of the human motor system during observation and imagery of actions by measuring the excitability of the motor system and discriminating the muscles involved in the motor replica (Craighero, Metta, Sandini, & Fadiga, 2007). Through further carefully designed studies, researchers should be able to refine movement imagery and action observation-based interventions as a direct consequence of the greater understanding of some of the mechanisms associated with TMS techniques.

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NOTES

1. The relatively recent discovery of a group of visuomotor neurons that seem to have a role in action execution, action observation, and possibly movement imagery has been termed the *mirror neuron system*, arguably, a major neuroscience finding of relevance to movement imagery and action observation (Van Gog, Paas, Marcus, Ayres, & Sweller, 2009). Functional magnetic resonance imaging studies have identified a wider network of mirror neurons within premotor, parietal, and temporal areas, which are active during action execution and action observation (for a more comprehensive review, see Rizzolatti & Craighero, 2004). The term mirror system is now commonly used.

2. As with the action observation studies, EMG activity needs to be monitored throughout movement imagery experiments to control for nonexperimental muscle activity at all times. In this way, MEP changes can be attributed to changes in the corticospinal system as a result of the movement imagery.

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