



When unintended movements “leak” out: A startling acoustic stimulus can elicit a prepared response during motor imagery and action observation

Dana Maslovat, Romeo Chua, Nicola J. Hodges*

School of Kinesiology, University of British Columbia, BC, Canada

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ABSTRACT

Covert forms of practice, such as observation and imagery, have been shown to involve neurophysiological activation of the motor system, and a functional equivalence between covert and overt processes involved in action execution has been proposed (Jeannerod, 2001). We used a startling acoustic stimulus (SAS), which has been shown to trigger prepared movements involuntarily at short latencies via an increase in cortical activation, to probe the similarity of these processes and elicit movement responses in imagery and observation trials. Startle trials were interspersed with control trials while participants ($n=16$) performed or imagined a right hand key lift or observed a model perform the key lift. During physical movement trials, intended movements were triggered by the SAS at a short latency ($RT=78$ ms) in comparison to control trials ($RT=110$ ms). During imagery and observation, unimanual partial movements (assessed by force change and muscle activation) were elicited by the SAS, providing novel behavioural evidence for a functional similarity between covert and overt movement preparation processes. Examination of the magnitude of the reflexive startle response (an index of motor preparation) during imagery and observation also revealed similarities to physical movement trials. We conclude that covert and overt movements involve similarities in motor preparation and neural pathways, and propose that movements do not normally occur during imagery and observation due to low level neural activation.

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1. Introduction

In an attempt to better understand movement preparation and execution, researchers have examined the processes involved in overt (physical) movements as well as covert “actions” such as motor imagery and action observation. There is considerable evidence implicating the involvement of the motor system during imagery and observation (see Fadiga, Craighero, & Olivier, 2005; Jeannerod & Frak, 1999 for reviews), and the discovery of a common neural network involved in both covert and overt movements, known as the mirror neuron system (MNS) (see Iacoboni, 2005; Jeannerod, 2001; Rizzolatti & Craighero, 2004; Rizzolatti & Fabbri-Destro, 2010 for reviews), has provided additional support for motor system activation during imagery and observation.

A variety of neurological measures have led to the suggestion that the involvement of the motor system is related to specific preparation of the observed or imagined movement. For example, brain activation patterns during observation and imagery of gymnastic movements are similar and highly related to the actual

execution of the actions being viewed or imagined, suggesting a common neural system for these processes (Munzert, Zentgraf, Stark, & Vaitl, 2008). Transcranial magnetic stimulation induced motor evoked potentials (which are thought to index movement preparation) are comparable during observation, imagery and actual hand movements (Clark, Tremblay, & Ste-Marie, 2003; see also Kumru, Soto, Casanova, & Valls-Sole, 2008), and the observation and imagery of hand movements has also been shown to generate a lateralized readiness potential (a measure of the preparation of a specific unilateral response) consistent with the laterality of the hand being imagined or observed (Kruczoch, Mathews, Dean, & Sterr, 2009; Touzalin-Chretien & Dufour, 2008). There is also evidence for a desynchronization of EEG mu rhythms during observation of precision grip movements, a process that occurs during active movement and is thought to be involved in motor preparation (Muthukumaraswamy & Johnson, 2004; Muthukumaraswamy, Johnson, & McNair, 2004). The similarity in neural activation patterns between action, observation, and imagery has resulted in the hypothesis that the motor system is part of a simulation network that can be activated during overt, observed, and imagined movements (Jeannerod, 2001).

While it is clear that there is activation at various levels of the motor system during imagery and observation, it is not yet understood if this activation is indicative of identical processes

* Correspondence to: School of Kinesiology, University of British Columbia, War Memorial Gymnasium 210-6081, University Boulevard Vancouver BC, Canada, V6T 1Z1. Tel.: +1 604 822 5895; fax: +1 604 822 6842.

E-mail address: nicola.hodges@ubc.ca (N.J. Hodges).

occurring during covert and overt practice (see Holmes & Calmels, 2008 for a review). In fact, differences have been noted between imagined, observed, and executed movements in cortical activation (Carrillo-de-la-Peña, Galdo-Álvarez, & Lastra-Barreira, 2008; Macuga & Frey, 2012; Munzert et al., 2008; Solodkin, 2004), spinal activation (Baldissera, Cavallari, Craighero, & Fadiga, 2001), autonomic nervous system levels (Demougeot, Normand, Denise, & Papaxanthis, 2009), as well as time to complete a movement (Rodriguez, Llanos, Gonzalez, & Sabate, 2008). In addition to the uncertainty regarding the equivalence between preparatory processes involved in imagery, observation and physical movement, it is also unclear as to why activation of the motor system does not produce overt movement during covert actions. Two possible explanations have been offered for the absence of motor output during imagery and observation (Hohlefeld, Nikulin, & Curio, 2011; Jeannerod, 2001). One suggestion is that motor output is blocked from reaching the motor neuron pool by an inhibitory mechanism generated in parallel to the motor activation. Alternatively, it has been proposed that motor activation during covert actions is at a reduced or subliminal level such that it is insufficient to fire motor neurons. Support for the inhibition hypothesis has been provided by a case study involving a patient with bilateral lesions in the parietal lobe (an area associated with movement initiation and inhibition) who unknowingly executed “imagined” movements (Schwoebel, Boronat, & Branch Coslett, 2002). Similarly, increased activation has been found in inhibitory brain areas during observation (Brass, Derrfuss, & von Cramon, 2005; Brass, Zysset, & von Cramon, 2001). However, single neuron recordings in monkeys have failed to show “gating” of premotor cortex output, leading to the conclusion that movement inhibition is likely not the mechanism when movements are not executed, indirectly supporting the subliminal activation hypothesis (Kaufman et al., 2010). Indeed, low level EMG activation during imagery lends direct support for the subliminal activation hypothesis during covert preparation (Bonnet, Decety, Jeannerod, & Requin, 1997; Guillot et al., 2007; Wehner, Vogt, & Stadler, 1984; see Guillot & Collet, 2005 for a review). It is also possible that both inhibition and low level activation operate at the spinal level such that subthreshold corticospinal activation and movement inhibition occur in parallel (Jeannerod, 2001; see also Prut & Fetz, 1999).

The purpose of this experiment was to probe response preparation processes during movement execution, imagery and observation in order to further understand the mechanisms underpinning covert actions. The methodology we used involved the use of a startling acoustic stimulus (SAS, > 124 dB) which can elicit a prepared action at a short latency, bypassing the usual voluntary initiation processes (see Carlsen, Maslovat, & Franks, 2012; Carlsen, Maslovat, Lam, Chua, & Franks, 2011; Valls-Solé, Kumru, & Kofler, 2008 for reviews). The use of a SAS is a novel methodology used to probe advance preparation. For example, during a simple reaction time (RT) task when pre-programming would be advantageous, replacing the auditory “go” signal with a loud startle tone triggers such diverse movements as arm extension (Maslovat, Hodges, Chua, & Franks, 2011), stepping (MacKinnon et al., 2007), sit-to-stand (Queralt et al., 2008), and head rotation (Oude Nijhuis et al. 2007). A lack of triggering by the SAS is typically attributed to a lack of advance preparation in such paradigms as choice RT (Carlsen, Chua, Inglis, Sanderson, & Franks, 2004), “Go-No Go” RT (Carlsen, Chua, Dakin, Sanderson, Inglis, & Franks, 2008a), and dual-task preparation (Maslovat et al., *in review*). We hypothesized that if motor imagery and action observation engage advance preparatory processes similar to that seen during overt actions a loud startle stimulus would be capable of eliciting such unintended, yet prepared responses.

The use of a SAS also allows for a better understanding of why movements do not occur during imagery and observation. It is

suggested that the SAS increases cortical activation levels via a reticulo-thalamo-cortical pathway (Carlsen et al., 2012). This pathway causes an automatic, involuntary release of a prepared movement, provided that preparatory processes have increased the activation of cortical circuits to a sufficiently high level. If movement inhibition is the cause of a lack of neural activation reaching the motor neuron pool, the involuntary subcortical initiation pathway associated with the SAS should bypass movement inhibitory processes, resulting in triggering of a response similar to that seen during movement execution trials. Alternatively, if low-level activation is the cause of a lack of observed movement, the SAS would increase activation levels such that at least a subset of motor neurons would reach threshold levels, causing neural activation to “leak out” to the muscles in the form of a smaller or partial response. Thus the behavioural response to the SAS not only provides evidence for response preparation during imagery and observation, it also allows for discrimination between the proposed alternatives for a lack of observed movement during covert preparation.

In addition to the direct measure of response preparation (shown by the triggering of a full or partial response), the use of a SAS allows for an indirect measure of action preparation through examination of the reflexive response to the SAS. The magnitude of activation in startle indicators (e.g., activation of sternocleidomastoid muscles in the neck) is assumed to be related to the level of excitability of cortical and subcortical motor centres and an index of the degree of preparation undertaken by the participant (Kumru et al. 2006; Maslovat, Carlsen, & Franks, 2012a). For example, reflexive startle effects are of a greater magnitude when advance preparation can occur in a simple RT paradigm, as compared to a choice RT paradigm when the required response is unknown (Maslovat et al., 2012a). Similar results have been shown in anticipation timing tasks in that as the time nears for the participant to prepare and initiate a response, the startle response amplitude increases (Carlsen, Chua, Inglis, Sanderson, & Franks, 2008b; Carlsen & Mackinnon, 2010). Collectively, these experiments provide evidence that the size of the reflexive startle response is related to movement preparation and thus can be used as a proxy measure of cortical and subcortical excitability. We hypothesized that if response preparation during covert actions occurred in a similar manner to overt movement, the magnitude of activation in the startle reflex indicators would be similar for trials in which a movement was and was not required (i.e., during imagery and observation).

2. Methods

2.1. Participants

All participants were naïve to the hypothesis under investigation and this study was conducted in accordance with ethical guidelines established by the University of British Columbia. Twenty-five right-handed volunteers with no obvious upper body abnormalities or sensory or motor dysfunctions participated in the study after giving informed consent. However, only data from 16 right-handed volunteers (7 male, 9 female; $M=21.3$ yrs, $SD=1.9$ yrs) were employed in the final analysis. Six participants did not show consistent activation in our startle indicator muscle during physical movement trials in which a SAS was presented, and thus were excluded from the analysis. It was critical to ensure a startle response was elicited as engagement of the startle reflex circuitry generally indicates sufficient subcortical activation to produce response triggering (see Carlsen et al., 2011, for more detail).

An additional three participants were excluded for not meeting our baseline trial criteria. To begin the experiment, prior to knowledge of the required tasks, participants depressed 2 telegraph keys with both their right and left hands and were presented with an unexpected startling stimulus (see Section 2.3 for more details). To ensure any unilateral responses we subsequently observed in the experiment were not due to the startle reflex but rather reflected lateralized

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