



Research report

Motor-evoked potentials reveal functional differences between dominant and non-dominant motor cortices during response preparation

Belinda J. Poole, Marius Mather, Evan J. Livesey, Irina M. Harris and Justin A. Harris*

School of Psychology, University of Sydney, Australia

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ABSTRACT

Transcranial magnetic stimulation (TMS) of the motor cortex produces motor-evoked potentials (MEPs) in contralateral muscles. The amplitude of these MEPs can be used to measure the excitability of the corticospinal tract during motor planning. In two experiments, we investigated learning-related changes in corticospinal excitability as subjects prepared to respond in a choice reaction-time task. Subjects responded with their left or right hand to a left or right arrow, and on some trials the arrow was immediately preceded by a warning cue that signaled which response would be required. TMS was applied to the motor cortex during the warning cues, and MEPs were measured in the dominant or non-dominant hand. We observed changes in corticospinal excitability during the warning cue, but these depended on which hand the subject was preparing to respond with, and how experienced they were with the task. When subjects prepared to respond with the non-dominant hand, excitability increased in the non-dominant hemisphere and decreased in the dominant hemisphere. These changes became stronger with task experience, and were accompanied by behavioral improvements in the task. When subjects were preparing a dominant-hand response, the non-dominant hemisphere was suppressed, but this effect disappeared as subjects gained experience with the task. There were no changes in the dominant hemisphere before dominant-hand responses. We conclude that preparing to respond with the non-dominant hand involves temporarily reversing an asymmetry in excitability that normally favors the dominant hemisphere, and that this pattern is enhanced by learning during the task.

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Most of our daily behaviors involve selecting and executing motor actions without much effort or thought. Simple acts involve complex neural operations that coordinate and plan movement to ensure that the correct behavior is ultimately

selected and executed (Cisek, 2007; Bestmann & Krakauer, 2015). Researchers have used non-invasive brain stimulation techniques, in particular transcranial magnetic stimulation (TMS), to examine in human subjects how the motor system

* Corresponding author. School of Psychology The University of Sydney, Sydney 2006, Australia.

E-mail address: Justin.Harris@sydney.edu.au (J.A. Harris).

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modulates corticospinal activity when interacting with a dynamic environment. TMS can be used to probe the excitability of the corticospinal tract by measuring motor-evoked potentials (MEPs) in selected muscles (Bestmann & Duque, 2016).

During a reaction-time (RT) task in which subjects make a speeded response to a signal, motor activation unfolds within the time between the onset of the signal and the initiation of the movement (Wong, Haith, & Krakauer, 2014). In a simple RT task, in which subjects have to make a single movement (such as pressing a key with their right index finger) in response to a “go” signal, corticospinal excitability increases in the relevant part of the motor system just prior to movement. For example, Chen, Yaseen, Cohen, and Hallett (1998) found increased MEP amplitude in the right hand starting about 100 msec before the onset of muscle activity during a cued movement in that hand (see also Leocani, Cohen, Wassermann, Ikoma, & Hallett, 2000; Kennefick, Maslovat, & Carlsen, 2014). Leocani et al. (2000) also showed that corticospinal excitability increased in the relevant motor system immediately before movement in a choice-RT task that requires subjects to make one of two movements (e.g., with the left versus right hand), as quickly as possible, in response to one of two signals. At the same time, these authors observed a decrease in MEPs elicited from the opposite hemisphere (ipsilateral to the selected movement), suggesting that execution of a unilateral movement also involves inhibition of the opposite hemisphere (see also, Klein, Duque, Labruna, & Ivry, 2016). These observations fit with the hypothesis that multiple motor actions are represented in parallel, and a motor response is selected once it reaches a given threshold (Cisek, 2007; Bestmann & Duque, 2016). At this time, activity is suppressed in motor systems that produce non-selected movements, in order to prevent those movements from reaching selection threshold.

A further detail to this picture has been provided in a recent experiment by Klein et al. (2016) that compared the recruitment of excitatory and inhibitory processes in the left and right hemispheres of right-handed subjects as they prepared to respond with their right or left hand. While both hemispheres showed equivalent increases in excitability just before a contralateral movement, the hemispheres differed in how much they were suppressed prior to ipsilateral movement. There was stronger suppression of the left (dominant) hemisphere just before a movement with the left (non-dominant) hand than of the right hemisphere prior to a right-hand response. This suggests that performing a response with the non-dominant hand requires stronger suppression of the dominant hemisphere, whereas performing the same response with the dominant hand requires less suppression of the non-dominant hemisphere.

As reviewed above, immediately before the execution of a movement there is a build-up of excitation in the corticospinal system controlling that movement and a suppression of excitability in other corticospinal pathways (especially in the dominant hemisphere before movement of the non-dominant hand). The experiments we present here, like other recent research reviewed below, focus on changes in corticospinal excitability during earlier stages of movement planning, before the motor system has committed to execution of an action. Our experiments investigate whether there is any

asymmetry between the two hemispheres in how corticospinal changes unfold during planning, and whether the changes themselves evolve with task experience and learning.

Many experiments have shown that, during early stages of motor preparation when subjects are planning an upcoming movement, corticospinal pathways not selected for movement are suppressed (Duque, Greenhouse, Labruna, & Ivry, 2017). Most of these experiments use choice-RT tasks in which subjects are first presented with a warning cue that informs them which response they must make (e.g., with left vs right hand), but execution of the response must be withheld pending arrival of a go signal. During the fore-period when the warning cue is present, corticospinal excitability is suppressed in the hemisphere ipsilateral to the upcoming response (Mars, Bestmann, Rothwell, & Haggard, 2007; van den Hurk et al., 2007; Duque, Lew, Mazzocchio, Olivier, & Ivry, 2010; Lebon et al., 2015; Bestmann & Duque, 2016). This suppression in ipsilateral cortex is similar to the response selection processes identified immediately before execution of a signaled movement (Leocani et al., 2000; Klein et al., 2016). However, according to Klein et al., there is no difference between dominant and non-dominant hemispheres in the amount each is suppressed during planning for an ipsilateral movement, unlike the difference those researchers observed between hemispheres leading up to movement execution.

In contrast to the increase in corticospinal excitability observed in the contralateral hemisphere immediately before execution of a movement, many studies have observed a suppression of excitability in that hemisphere during the fore-period while a warning cue is present (Duque & Ivry, 2009; Duque et al., 2010; Labruna et al., 2014; Greenhouse, Sias, & Labruna, 2015; Lebon et al., 2015; Klein et al., 2016). This decrease in corticospinal excitability is seen relative to excitability measured during an empty inter-trial interval, when subjects have no response requirement, and is interpreted as evidence for *impulse control* mechanisms whose function is to prevent the build-up of neuronal activity in premotor areas during the fore-period (e.g., Cisek & Kalaska, 2005) from causing the premature release of a planned response (Duque et al., 2010, 2017; Bestmann & Duque, 2016).

While the majority of studies have reported suppression of MEPs during the fore-period in the hand selected for the upcoming response, two studies have observed the opposite—an increase in MEP amplitudes in the selected hand (Mars et al., 2007; van den Hurk et al., 2007)—which is consistent with changes in corticospinal excitability seen immediately before response execution. These particular studies differ in a number of ways from those reporting evidence for impulse control. For one thing, the warning cues used by Mars et al. and van den Hurk et al. were 100% valid predictors of the impending response, whereas experiments showing impulse control included occasional catch trials in which the warning cue was not followed by the response signal (but see Klein et al., 2016 for evidence of impulse control in one group of subjects tested with 100% valid warning cues). Thus the need to withhold a planned response on catch trials may contribute to the conditions that invoke impulse control mechanisms. The experiments by Mars et al. and van den Hurk et al. can also be distinguished by factors that could cause some suppression of corticospinal activity during baseline

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