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An improvement in perception of self-generated tactile stimuli following theta-burst stimulation of primary motor cortex

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Abstract

Recent studies have shown that self-generated tactile sensations are perceived as weaker than the same sensations externally generated. This has been linked to a central comparator mechanism that uses efference copy to attenuate the predictable component of sensory inputs arising from one's own actions in order to enhance the salience of external stimuli. To provide a quantitative measure of this attenuation, a force-matching task was developed in which subjects experience a force applied to their finger and are then required to match the perceived force by actively pushing on the finger using their other hand. The attenuation of predictable sensory input results in subjects producing a larger active force than was experienced passively. Here, we have examined the effects of a novel rTMS protocol, theta-burst stimulation (TBS), over primary motor cortex on this attenuation. TBS can alter the excitability of motor cortex to incoming activity.

We show that application of a 20 s continuous train of TBS, that depresses motor cortex, significantly improves performance in a force-matching task. This suggests that the TBS intervention disturbed the predictive process that uses efference copy signals to attenuate predictable sensory input. A possible explanation for the effect is that TBS has a differential effect on the populations of neurones that generate motor output in M1 than on those neural structures that are involved in generating an efference copy of the motor command.

Keywords: Attenuation of sensory input; Efference copy; Motor cortex excitability; Sensory suppression; Transcranial magnetic stimulation (TMS)

1. Introduction

It has been proposed that predicting the consequences of one's own actions is a key feature in sensorimotor control. By using an 'efference copy' of the motor command (Holst & Mittelstaedt, 1950) together with an internal model of the environment (Wolpert, Ghahramani, & Jordan, 1995; Wolpert & Miall, 1996) a prediction of the consequences of one's actions can be generated. Such prediction can be used to maintain perceptual stability, control actions in the presence of feedback delays or perform mental practice (for a review see Cullen, 2004).

The prediction of the sensory consequences can also be compared to the actual sensations arising during movement. This comparison can be used to distinguish between sensations that are self-generated and those arising from external sources. Moreover, removing the predicted sensory feedback from the actual feedback provides a signal that reflects unexpected changes in the world and may enhance the salience of externally generated sensations. Consistent with such a mechanism, a number of studies have shown that self-generated tactile sensations are perceived as weaker than the same sensations externally generated (Bays, Wolpert, & Flanagan, 2005; Bays, Flanagan, & Wolpert, 2006; Blakemore, Wolpert, & Frith, 1998; Weiskrantz, Elliott, & Darlington, 1971).

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A recent study has investigated sensory attenuation in the perception of self-generated forces (Shergill, Bays, Frith, Wolpert, 2003). A torque motor generated a small constant force on a subject's left index finger, and the subject was then required to reproduce the force they had experienced. When subjects used their right index finger to push on the left index finger to reproduce the experienced force, they produced substantially more force than they had passively experienced. This is consistent with attenuation of the experienced force during direct action of one part of the body on another. In contrast, when they used a joystick in the right hand to control the torque motor to reproduce the experienced force, a novel mapping between actions and sensation in which prediction is unlikely to occur, they could faithfully reproduce the force. Although such sensory attenuation has been investigated psychophysically and shown to be time-locked to the expected time of contact between body parts (Bays et al., 2005), little is known about the neural mechanisms that underlie such a comparison between predicted and actual sensory feedback.

The aim of the present study is to assess the involvement of primary motor cortex (M1) in this mechanism by measuring tactile attenuation before and after administration of a novel transcranial magnetic stimulation (TMS) protocol, theta-burst stimulation (TBS), over MI. Theta-burst stimulation over primary motor cortex has recently been shown to produce long lasting effects on the excitability of the motor cortex as reflected in an increase or decrease in the amplitude of motor evoked potentials (MEP) after TBS (Huang, Edwards, Rounis, Bhatia, & Rothwell, 2005).

If the efference copy signal is a copy of the motor output generated by those population of neurones within MI that can be affected by TBS, then changes to the excitability of MI should affect both the efference copy and the actual motor command equally, and no discrepancy will result. We would therefore expect sensory attenuation to be unaffected.

If efference copy signals do not arise as a copy of the motor output generated from those corticospinal neurones in MI, then an increase or decrease in the excitability of MI will produce a mismatch between the efference copy and the actual motor command sent to the muscles. This will create a discrepancy between the predicted sensory input, based on efference copy, and the actual sensory input related to the motor activity. This kind of discrepancy is usually found when a body part is moved passively by an external force, so predictive processes that normally apply during self-action are likely to be disrupted. For instance, predictive modulation of grip-force is impaired when this kind of sensory discrepancy is introduced, either by amplifying or reducing force feedback (Blakemore, Goodbody, & Wolpert, 1998). Likewise, the central cancellation of self-administered tactile stimuli was reduced when a mismatch between predicted and actual sensory consequences was created by introducing spatial or temporal delays between action and effect (Blakemore, Frith, & Wolpert, 1999).

In the present study, a sensory mismatch caused by an increase or decrease in MI excitability may reduce the normal attenuation of self-generated sensation and hence improve performance on the force-matching task.

2. Methods

2.1. Subjects

Sixteen healthy right-handed subjects (nine males, seven females; 20–31 years) participated in the experiments. They were naive to the specific purpose of the experiments and gave written informed consent. The study was conducted in accordance with the Declaration of Helsinki and the methodology had been approved by the local ethics committee.

2.2. Experimental protocol

We used a recently developed force-matching task that allows us to quantify the sensory attenuation of self-produced stimuli (Shergill et al., 2003). Subjects rested either their left or right index finger in a moulded support. A force sensor (Nano-17 6-axis F/T sensor, ATI Inc.) rested on the tip of the finger at the end of a lever attached to a torque motor (Fig. 1). To start each trial the torque motor applied one of five constant target forces in the range 1–3 N to the tip of the subject's index finger for 3 s. Following an auditory go-signal, subjects were then required to reproduce the force they had just experienced by pressing with their opposite index finger on the resting index finger through the force sensor. After 3 s an auditory stop-signal indicated the end of the trial.

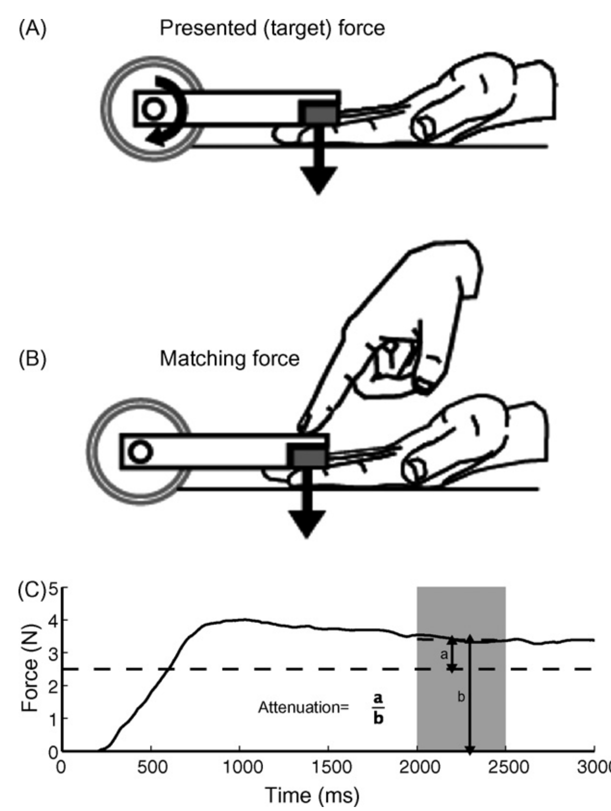

Fig. 1. Illustration of the force-matching paradigm. On each trial the torque motor generated a target force between 1 and 3 N on the either the left or the right index finger for 3 s (A). Subjects were then required to reproduce the force by pushing with their opposite index finger (matching force, B). Each subject used both left and right finger to match the target force (blockwise, in a counterbalanced pseudorandom order). The applied forces were measured using a force transducer mounted in the lever of the torque motor. (C) Sample trace of forces generated by one subject (solid line) during a representative trial with a target force generated by the torque motor of 2.5 N (dashed line). The grey area indicates the interval over which the mean subject-generated force was calculated. The "attenuation index" was then calculated as the percentage of the matching force level by which it exceeded the target force level (a/b).