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Suppression of Vibrotactile Discrimination by Transcranial Magnetic Stimulation of Primary Somatosensory Cortex

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**Abbreviated title:** Suppressed vibrotactile perception with TMS of SI

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Abstract

We employed transcranial magnetic stimulation (TMS) over the primary somatosensory cortex (SI) in human subjects to investigate the extent to which inactivating SI disrupted the discrimination of vibrotactile stimulation at frequencies that give rise to the tactile sensations of flutter (30Hz) and vibration (200Hz). Discrimination at the 30Hz standard following application of TMS to SI was reduced in seven of the eight subjects, and at the 200Hz standard was reduced in all eight subjects. The average change in discrimination following TMS was about 20% for both low and high frequencies of vibrotactile stimulation. The results of this study provide functional evidence in favour of a serial model of information processing in primary and secondary somatosensory cortical regions in humans.

Keywords: tactile, flutter, vibration, SI, SII, TMS
Introduction

The tactile sense of flutter-vibration is associated with activation of two populations of mechanoreceptors: Meissner corpuscles subserving the sensation of *flutter* and most sensitive to vibrotactile stimuli in the range 5-40Hz, and Pacinian corpuscles subserving the sensation of *vibration* and responsive to vibrotactile stimuli in the range 50-300Hz (Talbot et al., 1968). Activity in these two receptor populations is transmitted with little alteration to the somatosensory regions of the cerebral cortex, however the extent to which the primary (SI) and secondary (SII) somatosensory regions contribute to the processing of flutter-vibration remains unclear. Studies in the anaesthetised cat using single cell electrophysiology (Bennet et al., 1980; Ferrington and Rowe, 1980) and metabolic mapping and optical intrinsic signal imaging (Tommerdahl et al., 1999), and single cell recording in the primate (Zhang et al., 2001) suggest a differential representation of the frequency of vibrotactile stimulation in SI and SII: with neurons in SI predominantly responsive to lower frequencies of tactile vibration and in SII predominantly responsive to higher frequencies. A difference in the cortical representation of vibrotactile frequency has also been reported in human subjects in two studies that employed functional magnetic resonance imaging (fMRI) of SI and SII (Francis et al., 2000; Harrington and Downs, 2001). Although these two studies used different frequencies of vibration, 30Hz and 80Hz in the study by Francis et al. and 35Hz and 150Hz in the study by Harrington and Downs, both reported a differential representation of low and high vibrotactile frequencies in SI and SII respectively. However it should be stressed that in both studies the vibrotactile stimulation resulted in some activation of both SI and SII, suggesting a degree of overlap in the frequency representation in both SI and SII, at least for the vibratory frequencies used.
In the present study we investigated if the reported differences in the representation of vibrotactile frequency in SI and SII in human subjects could be observed at a behavioural level. A number of studies have shown that transcranial magnetic stimulation (TMS) of SI disrupts the detection and localisation of electrical stimulation of the digits (Cohen et al., 1991; Seyal et al., 1992, 1997), and alters the size of several components of the somatosensory evoked potential produced by electrical stimulation of the median nerve at the wrist (Kujirai et al., 1993). We employed TMS over the SI cortical region in human subjects and measured the extent to which it disrupted the discrimination of vibrotactile stimulation at frequencies in the range that gives rise to the sensations of flutter and vibration.

Methods

All experiments were undertaken at the Faculty of Health Sciences, University of Sydney and were approved by the University of Sydney Human Ethics Committee. Vibrotactile stimulation consisted of sinusoidal vibration delivered perpendicular to the skin surface of the volar pad of the index or middle finger via a 2 mm diameter Perspex probe attached to the shaft of a mechanical vibrator (Gearing and Watson, model GWV4, UK). The vibrator was mounted on an isolated rigid trunnion (Gearing and Watson, T4). The probe tip projected through a 6 mm diameter hole in a rigid Perspex plate (300 mm²) suspended from the rigid trunnion. The plate was positioned parallel to the skin surface and acted as a guard to limit the spread of surface waves across the skin. The probe and the rigid surround were separated by a gap of 2 mm. Sinusoidal waveforms superimposed on a 1 mm indentation were generated by a computer equipped with the LabView application, passed to a linear power amplifier (Gearing and Watson, PA30) and then delivered to the mechanical vibrator.
Transcranial magnetic stimuli (Magstim 200 and BiStim Module; Magstim Co., Dyfed, UK) were delivered predominantly via a figure-of-eight coil however in some cases a round coil (13.5 cm outside diameter) was used. The coil was positioned over the hand/finger region of the left cortical somatosensory area in each subject at a position that corresponded approximately to the C3/C4 position in the International 10/20 EEG system (Harris et al, 2002). Prior to the experiment the TMS threshold for activation of the intrinsic muscles of the hand was determined, and the intensity of TMS employed over SI during experiments was at this threshold for each subject.

Vibrotactile discrimination was measured in eight subjects (4 male and 4 female, including the authors) with an age range of 23-48 years. Vibrotactile detection thresholds at 30Hz and 200Hz (standard frequencies) were determined for each subject. Subjects were asked to discriminate in a two-alternative-forced-choice paradigm between a standard and a comparison vibrotactile stimulus that could be of higher or lower frequency. Each stimulus was presented for 200ms, with a 500ms inter-stimulus interval, with the start of the stimulus sequence signaled to the subject by the onset of a light. The frequencies of the two standard stimuli, 30Hz or 200Hz, were chosen to allowing activation predominantly of the Meissner and PC receptors respectively. The frequency of the comparison stimulus was ±15% of the standard stimulus. The amplitude of the comparison stimuli was adjusted for each subject according to their subjective magnitude estimate (determined prior to data collection) of the amplitude of the comparison relative to the standard vibration. A stimulus run consisted of 40 presentations of the stimulus, 20 trials with TMS and 20 trials without TMS, with trials randomly interleaved. In trials with TMS, two pulses were delivered - one 30ms before and the other 5ms after the comparison vibrotactile stimulus. In four of the subjects, control experiments were conducted in which vibrotactile discrimination
employing the 30Hz standard (3 subjects) or the 200Hz standard (1 subject) were carried out with the TMS applied over the frontal cortex.

Results

The stimulus amplitudes used at the standard frequencies of 30 and 200 Hz were determined for each subject, and were appropriate to ensure that the frequency discrimination task was carried out correctly in over 75% of trials in the absence of TMS over SI. The vibratory amplitudes used averaged four times greater than the subjects’ detection thresholds. The mean vibratory amplitude for the 30Hz standard was 82µm (± 1.7 SEM) and for the 200Hz standard was 12µm (± 0.9).

Vibrotactile frequency discrimination at the 30Hz standard was reduced in seven of the eight subjects following application of TMS to SI, and one subject showed no change in discrimination following TMS. Discrimination at the 200Hz standard was reduced in all eight subjects following TMS to SI. Figure 1 shows the discrimination performance of each of the eight subjects for both low frequency (upper graph) and high frequency (lower graph) standards, with and without TMS. The mean discrimination values for the 30Hz standard without TMS was 85% ± 2% and with TMS was 65% ± 5%, and for the 200Hz standard without TMS was 87% ± 3% and with TMS was 66% ± 3%. The reduction in discrimination with TMS in both cases was statistically significantly (30Hz: \( p=0.002 \); 200Hz: \( p=0.0003 \); student \( t \)-test, two-tailed).

The average reduction in discrimination across all subjects, during TMS, relative to discrimination without TMS, is plotted in Figure 2. Also shown in Figure 2 is the effect on discrimination of TMS applied to the frontal cortex. The average change across all subjects for the 30Hz standard (20% ± 5%) and for the 200Hz standard (21% ± 5%) did not differ
significantly \( (p=0.85, \text{ student } t\text{-test, two-tailed}) \). The average change in discrimination in the control condition in which TMS was applied over the frontal cortex was \( 9\% \pm 8\% \), and was significantly different to discrimination at both 30Hz and 200Hz standards (30Hz: \( p=0.01; \) 200Hz: \( p=0.01 \), student \( t \) test, two-tailed).

**Discussion**

The principal finding of the study is that TMS of the primary somatosensory cortex (SI) significantly suppressed the discrimination of low and high frequency vibrotactile stimuli. Previous studies have investigated the effect of TMS over SI on discrimination of low frequency vibration, but there has been no comparison of discrimination of both high and low frequencies. Harris et al. (2002) investigated tactile memory by measuring frequency discrimination for low vibrotactile frequencies (16 - 24Hz) following TMS delivered over SI from 300-1200ms after the presentation of the first stimulus in a stimulus pair, a TMS paradigm substantially different to the one used in the present study. Harris et al. (2002) found that TMS caused significant disruption of discrimination if the pulse was presented within 600ms after the first stimulus. Knecht et al. (2003) investigated vibrotactile frequency discrimination (standard frequency of 20Hz) after a period of repetitive 1 Hz TMS over SI for 5, 10 or 20 minutes. Knecht et al. (2003) found that discrimination was impaired following TMS, with the duration of impairment positively correlated with the duration of the TMS. Other groups have used TMS to investigate processing of spatial tactile information, and have shown that judgments of letter recognition, grating orientation and groove/ridge width, and dot roughness are adversely affected by TMS of SI (Cohen et al., 1997; Zangaladze et al., 1999; Merabet et al., 2004).
In this study the vibratory stimuli were presented for 200ms, which is relatively brief compared to many previous studies that used a stimulus period of at least 1s (for example, Morley & Rowe, 1990; Mahns et al, 2006). The reason for the shorter stimulus period was that it allowed us to “Bracket” the comparison vibrotactile stimulus with TMS of S1, and thereby increase the likelihood of interrupting the cortical processing of the stimulus. TMS to S1 was applied 30ms before and 5ms following the end of the 200ms comparison stimulus. The times of TMS application were chosen based on reported disruption of tactile detection by TMS delivered at different times (Cohen et al, 1991; Seyal et al, 1992, 1997), and our own (unpublished) observations on the effects of TMS of S1 on detection of both low and high frequencies of vibration.

Our finding of a substantial disruption of both low and high frequency vibrotactile discrimination following TMS of S1 suggests that SII may not process high frequency vibration independently of SI. The argument that a functional differentiation exists between the processing of low and high frequency vibrotactile stimuli in somatosensory cortex is based on evidence of a differential representation of low and high frequency vibration in SI and SII respectively (Bennet et al., 1980; Ferrington and Rowe, 1980; Tommerdahl et al., 1999; Francis et al., 2000; Harrington and Downs, 2001; Zhang et al., 2001) and on the basis of a parallel model of direct thalamic input to both SI and SII (Turman et al., 1992, 1995; Zhang et al., 1996, 2001; Kahru and Tesche, 1999). If the differential representation of vibrotactile stimuli is largely correct, our results support a serial processing model in SI and SII. The in series model for processing tactile information holds that the tactile information first passes through SI before reaching SII, such that inactivation of SI will in turn disrupt function in SII. Support for the in series model comes from lesion and single cell electrophysiology studies in non-human primates (Pons et al., 1987;
Garraghty et al., 1990) and investigation in human subjects using functional magnetic resonance imaging (fMRI) and magnetoencephalography (MEG) (Disbrow et al., 2001; Inui et al., 2004).

A potential complicating factor in the interpretation of our data is the extent to which the effects of the TMS could spread beyond SI to affect function in SII. In the human brain, SII is located deep in the lateral sulcus extending onto the insula. The position of SII and the distance from the SI hand region make it unlikely that the single pulse TMS protocol would have a direct effect on SII (Rudiak and Marg, 1994). However, the reciprocal connectivity between SI and SII (Schwark et al., 1992) could provide a means by which TMS of SI could indirectly modulate neural activity in SII. Although we cannot rule this possibility out completely, evidence from single cell recording studies in primate and non-primate species indicate that even with the complete abolition of activity in SI through localized cortical cooling, >90% of neurons in SII retain responsiveness to vibrotactile stimuli (Turman et al, 1992; Zhang et al, 1996).

In summary, the results of this study show that discrimination of both low and high frequencies of vibrotactile stimulation are suppressed by TMS over SI, and provides functional evidence in favour of a serial model of information processing in primary and secondary somatosensory cortical regions in humans.
References


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Figures

Figure 1. Discrimination of low and high frequencies of vibrotactile stimulation. Discrimination with tactile stimulus alone or with tactile stimulus following TMS over SI for each subject for the 30Hz standard (upper graph) and 200Hz standard (lower graph).
Figure 2. Average of the change in discrimination for all subjects for the low and high frequencies of vibrotactile stimulation following TMS over SI and following TMS over the frontal cortex. Error bars are SEM.