BRAIN RESEARCH 1459 (2012) 43–51

Available online at www.sciencedirect.com

SciVerse ScienceDirect

www.elsevier.com/locate/brainres

BRAIN RESEARCH

Research Report

Intracortical modulation of somatosensory evoked fields during movement: Evidence for selective suppression of postsynaptic inhibition

Juha Huttunen[a,*], *Leena Lauronen*[b]

[a]*BioMag Laboratory, HUSLAB, University of Helsinki, Helsinki, Finland*
[b]*Department of Clinical Neurophysiology, Hospital for Children and Adolescents, HUSLAB, University of Helsinki, Helsinki, Finland*

ARTICLE INFO

Article history:
Accepted 11 April 2012
Available online 20 April 2012

Keywords:
Somatosensory cortex
Somatosensory evoked field
Movement
Magnetoencephalography

ABSTRACT

As accurate finger movements depend on guidance by afferent sensory feedback information, it is of interest to examine how the cortical processing of afferent signals is altered during movement states compared with rest. In the present study we evaluated afferent input to the primary somatosensory cortex (SI) in human subjects performing a finger opposition task. We recorded somatosensory evoked magnetic fields (SEFs) in 6 healthy subjects to stimulation of left and right median nerves in a resting condition and during active right-sided finger movements. At the left SI, the SEFs to right (moving hand) median nerve stimulation showed a selective and robust reduction of the P35m deflection during movement compared with rest, while there were only minor non-significant changes in the other SEF deflections, including N20m, which represents the 1st excitatory cortical event after stimulation. In contrast, at the right SI the SEFs to left (non-moving hand) median nerve stimulation were modified in the opposite direction: the P35m deflection was slightly enhanced during right-sided movement, there being no significant changes in the other deflections. The results thus show that the P35m SEF deflection can be selectively reduced during finger movements of the stimulated hand, and selectively enhanced if the movement is being performed with the fingers of the opposite hand. Because N20m was not changed, the modulation took place at the cortical level rather than in the afferent pathways. As the P35m SEF deflection likely represents postsynaptic IPSPs at SI, the results suggest that postsynaptic inhibition to somatosensory impulses from the moving part of the body is suppressed. Comparison of the present results with recent intracellular studies in behaving mice suggests that the P35m reduction specifically corresponds to a reduction in the activity of parvalbumin-containing fast-spiking inhibitory interneurons during movement. The results provide evidence that precision movements can be executed without this type of cortical postsynaptic inhibition.

* *Corresponding author at:* HUSLAB, BioMag Laboratory, Helsinki University Central Hospital, P.O. Box 340, FI-00029 HUS, Finland. Fax: +358 9 471 75781.
E-mail address: juha.huttunen@pp2.inet.fi (J. Huttunen).

0006-8993/$ – see front matter © 2012 Elsevier B.V. All rights reserved.
doi:10.1016/j.brainres.2012.04.023

1. Introduction

Movement and somatic sensation are intimately related. Moving a body part heavily depends on sensory feedback guidance, and sensing objects by means of active touch, in turn, requires the execution of motor sequences. Even relatively simple motor tasks, such as gripping on an object, cannot be successfully performed without sensory feedback (for review, see, *e.g.*, Johansson and Flanagan, 2009).

Clues to understanding how sensory input is integrated into motor programs might be obtained by studying how the processing of afferent signals at the cortex is altered during movement as compared with a resting state. Accordingly, several studies in experimental animal models and in humans have addressed this question by recording afferent responses from the primary somatosensory cortex (SI). In most animal studies the initial excitatory response of SI pyramidal neurones was reduced during movement (*e.g.*, Courtemanche et al., 1997; Fanselow and Nikolelis, 1999; Jiang et al., 1991), which suggests that the modulation may have taken place already in the afferent pathways, before the signals arrive at SI. Similarly, in most human studies utilizing the recording of somatosensory evoked fields (SEFs), the first cortical excitatory response, the N20m deflection, was reduced during active movement of the stimulated hand as compared with rest (Inoue et al., 2002; Kakigi et al., 1995; Schnitzler et al., 1995a). This suggests that, in the settings of these studies, also in humans already the afferent input to the cortex was reduced if the stimulated hand was moving. If there is a possibility of a reduced input to the cortex during movements, it is difficult to evaluate which of the changes observed at later stages of cortical processing are due merely to reduced input, as opposed to task-related changes in intracortical processing. In order to be able to study possible changes in intracortical processing during movement, a paradigm that does not affect the incoming volley needs to be used.

SEFs allow the study of population-level postsynaptic sensory responses at SI in awake human subjects (Hämäläinen et al., 1993). In order to achieve a high enough signal-to-noise ratio, electrical stimulation of a nerve trunk is usually the preferred method to elicit SEFs. After median nerve stimulation at the wrist, a sequence of SEF deflections occur over the contralateral SI, whose origins have been located to cortical neuron populations at SI by means of equivalent current dipole modeling (*e.g.*, Hari et al., 1984; Huttunen et al., 2006). The first cortical response is termed N20m and peaks at about 20 ms, and reflects the initial excitatory postsynaptic potential (EPSP) at SI pyramidal neurons (Ikeda et al., 2005), largely those in area 3b occupying the major part of the posterior wall of the central sulcus; however, other areas, most notably 3a and 1, can also possibly contribute to the SEFs. N20m is followed by a P35m deflection with current flow roughly in the opposite direction. Several lines of evidence suggest that the latter largely represents postsynaptic inhibitory potentials (IPSPs) at SI. First, P35m is very sensitive to repeated stimulation, substantially diminishing in amplitude when the stimulation frequency is increased from once in 5 s to once every second. This type of behavior is strikingly similar to that of postsynaptic IPSPs (*cf.*, Wikström et al., 1995). Similarly, in a paired-pulse situation, it takes much longer for P35m to recover than it does for the excitatory N20m. This feature of P35m is very similar to the behavior of IPSPs, as recorded intracellularly in various animal preparations (*e.g.*, Davies et al., 1990; Deisz, 1999; Olpe et al., 1994; *cf.*, Huttunen et al., 2008). Furthermore, when stimulus trains at 10 Hz are presented, P35m is reduced very rapidly during the first few pulses of a train (Huttunen, 2010), which again is similar to the known behavior of IPSPs in intracellular recordings (*e.g.*, Hellweg et al., 1977; Nacimiento et al., 1964). Finally, administration of the GABA-agonist lorazepam reduces P35m, while enhancing the excitatory N20m (Huttunen et al., 2008), an effect that is expected to occur for IPSPs (*cf.*, Krnjevic and Schwartz, 1967).

In the present study, we show that active finger movements can selectively suppress the P35m SEF deflection when the stimulated hand is engaged in the movements, there being no change in the preceding N20m deflection. This suggests that the afferent input to the cortex was unaltered and the reduction of P35m was due to intracortical mechanisms. The results provide evidence that postsynaptic IPSPs evoked by sensory stimulation, may not be important for the processing of sensory feedback information that is needed for the movement execution. In contrast, the P35m deflection at the opposite SI, in response to stimulation of the non-moving hand, was enhanced, suggesting that postsynaptic inhibition is differently modulated depending on whether the corresponding body part is engaged in an active task or not.

The results have appeared previously in a preliminary form (Huttunen et al., 2000).

2. Results

In the resting condition, the SI SEFs were separable into N20m, P35m and P60m deflections in all subjects. Fig. 1 shows the individual SEF waveforms from the left SI after right median nerve stimulation in the resting and finger opposition conditions, *i.e.*, when the movements were performed with the stimulated hand. The topmost curves in Fig. 1 demonstrate the repeatability of the responses in the resting condition for one subject. Comparison of the responses between rest (solid lines) and movement (dotted lines) shows that N20m was very similar in both conditions for Subjects 1–4 whereas it appeared slightly diminished in the finger movement condition for Subjects 5 and 6. In marked contrast, the P35m deflection was clearly diminished in all

Fig. 1 – Individual SEF planar gradient waveforms from the channel showing maximum signals from the left SI after stimulation of the right median nerve. Top: Reproducibility of the waveforms from 3 different runs in the resting condition for Subject 2. Other waveforms: Individual SEFs in the resting condition (solid lines) and during the right-sided finger opposition task (dotted lines) superimposed. The vertical line marks the time of stimulus delivery.