

Sensorimotor Integration

Toshiaki Wasaka and Ryusuke Kakigi

Abstract A motor program for controlling one's own movement requires sensory signals from the target body parts. The information for movement is provided by sensory feedback, as well as the integration of sensory information and motor command, all of which are critical for motor control. Recent studies suggested that cortical activity related to sensory response and perception is modified by movement executing mechanisms. However, this raises the question of how this system integrates motor command and sensory information whenever the intended movement is in progress. In this chapter, we review findings of sensorimotor integration and introduce results of our own studies using magnetoencephalography.

Keywords Corollary discharge · Efference copy · Motor command · Somatosensory information · Visual information

1 Introduction

Movement is the only way of interacting with the world. Indeed, all communication, including speech, gestures and writing, is mediated via the motor system. The motor areas play a crucial role in the coordination of movement, and the sensory areas have a functional role in monitoring the state of movement. To control our action, the human brain uses sensory signals to determine future actions. The existence of

T. Wasaka (✉)

Nagoya Institute of Technology, Gokiso, Syowa, Nagoya, Aichi 466-8555, Japan
e-mail: wasaka.toshiaki@nitech.ac.jp

T. Wasaka · R. Kakigi

Department of Integrative Physiology, National Institute for Physiological Sciences,
38 Nishigonaka, Myodaiji, Okazaki, Aichi 444-8585, Japan

interactions between motor commands and sensory information processing has been investigated using electroencephalography, magnetoencephalography (MEG) and functional magnetic resonance imaging (fMRI).

Sensory feedback from body parts is used to adjust and correct movement in course to the varying environmental constraints. Preceding and during movement, the motor and higher-order brain systems regulate sensory information at several processing stages. This chapter will begin with an explanation of the neural model concerning sensorimotor integration. This will be followed by research topics of neural modulation in the sensory system, especially somatosensory areas, during execution of voluntary movement including our own recent findings. Finally, the functional role of sensorimotor integration will be discussed.

2 The Neural Mechanism of Sensorimotor Integration

Cortical mechanisms such as corollary discharge (Sperry 1950) and efference copy (von Holst and Mittelstaedt 1950) modify sensory information processing during movement generation and execution. These mechanisms are used to keep track of the expected result of the motor command, and to update the current state. The central idea of corollary discharge is that the oculomotor system sends some information about the motor signal to the visual system when it initiates a movement, and this signal blocks the transient shift of the retinal image of the visual world during saccadic periods. Corollary discharge also plays an important role in auditory, vocalization, skeletomotor and somatosensory systems (Crapse and Sommer 2008). Human studies have provided insights into its functional role in two operations: resolving ambiguity in the origin of sensory information and enabling proper motor performance.

Corollary discharge transiently modulates self-generated sensory responses and can help distinguish between self-generated and externally generated sensory information. Recently, interesting research was conducted on the somatosensory system. Everyone knows you cannot tickle yourself, yet if someone else touches your side, you may suddenly feel ticklish. The neural mechanism of this phenomenon was examined using brain imaging techniques. Compared to self-produced stimuli, more activity in somatosensory areas was found when the stimulus was externally delivered (Blakemore et al. 1998). When a movement is self-produced, its sensory consequences can be accurately predicted, and this prediction can be used to attenuate the sensory effects of the movement. The sensory prediction is made by an internal forward model of the motor system (Wolpert et al. 1998). By comparing the predicted with the actual sensory feedback, it is possible to distinguish the sensory consequences of our movements from sensory signals due to changes in the outside world. This neural mechanism has a functional role in controlling voluntary movement based on sensory information.

3 Sensorimotor Integration in the Somatosensory Areas

When we execute voluntary movement, somatosensory information processing, during its course from the peripheral to the somatosensory areas, is influenced by many mechanisms mediated by a network comprising motor and higher-order brain systems. This phenomenon has been reported as changes in the short- and long-latency components of somatosensory evoked potentials (SEPs) and somatosensory evoked magnetic fields (SEFs).

Sensorimotor integration in the somatosensory areas occurs via two major mechanisms: (1) modulation of SEPs/SEFs can be carried out by inhibitory interaction between the given sensory signals and the efferent signals induced by the motor command from the motor related areas (centrifugal mechanism), and (2) modulation can be exerted by interaction between the given sensory afferents that produce SEPs/SEFs and the afferent signals evoked by the movement, i.e., afferent signals from the muscles and joints (centripetal mechanism) (Jones et al. 1989).

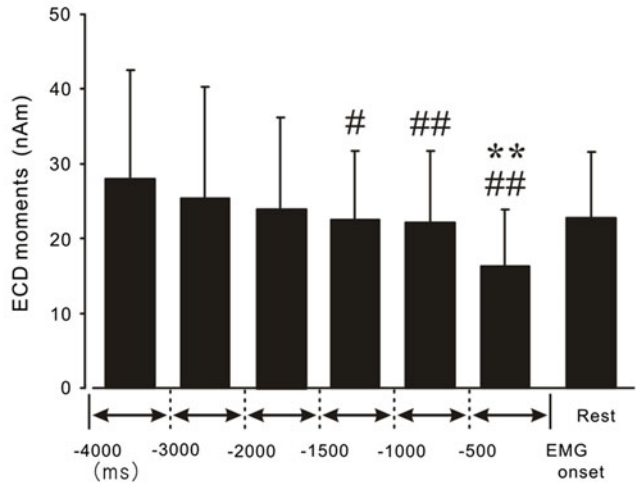
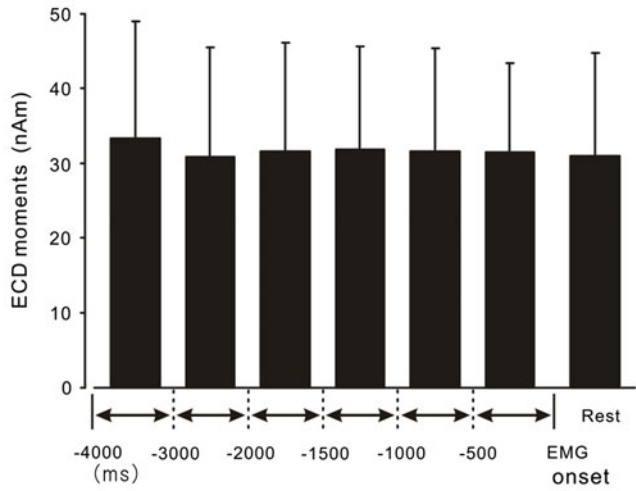
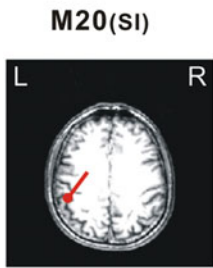
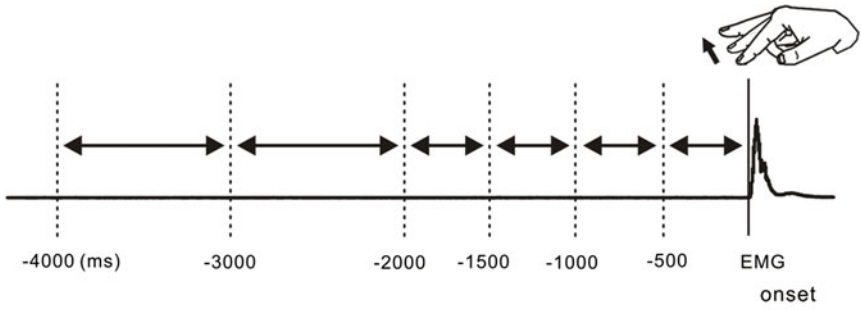
With regard to the modulation of somatosensory cortices produced by voluntary movement, change in SEP/SEF amplitude was found not only during movement (Rushton et al. 1981; Kakigi et al. 1995; Nakata et al. 2003; Nakajima et al. 2006) but also just prior to it (preparatory period) (Cohen and Starr 1987; Kida et al. 2004, 2006). In previous studies, pre-movement modulation of somatosensory information processing has been investigated using reaction time tasks (Starr and Cohen 1985; Bocker et al. 1993; Murase et al. 2000). However, a reaction time task evokes various cognitive brain activities, such as expectancy, motivation and attention, which may change the sensorimotor activities. In fact, the neuronal effect of attention on somatosensory information processing has been addressed with various methods, including single unit recordings in monkeys (Hyvarinen et al. 1980; Iriki et al. 1996), SEPs/SEFs (Desmedt and Tomberg 1989; Garcia-Larrea et al. 1995; Mauguiere et al. 1997; Mima et al. 1998) and fMRI (Johansen-Berg et al. 2000; Staines et al. 2002). By using a self-initiated voluntary movement task without external cues, one can observe the temporal modulation of somatosensory cortical activities with respect to movement onset and elucidate the neural interactions between somatosensory and motor areas in detail.

Our research has focused on the neural mechanisms of sensorimotor integration in the somatosensory areas, especially the centrifugal modulation in the primary somatosensory area (SI) and the secondary somatosensory area (SII), during the preparatory period of self-initiated voluntary movement. The hypothesis is that if motor commands interact with sensory inputs in the central nervous system, neurons in the motor and sensory areas should show a change of activities when these commands are issued.

4 Modulation in the SI During the Preparatory Period of Voluntary Movement

Previously, we reported differential pre-movement modulation of SEP components estimated to be in the SI. There was no significant change in amplitude for the M20, the primary component associated with SI, but there was attenuation of the M35, a subsequent component localized to SI, just before movement onset (Fig. 1) (Wasaka et al. 2003). The change in the amplitude of the M20 during the preparatory period has been controversial. Some authors reported that the amplitude did not change before movement (Starr and Cohen 1985; Murase et al. 2000), while others reported attenuation just before movement (Hoshiyama and Sheean 1998). In contrast, attenuation of the amplitude of the M35 just before movement has consistently been reported (Starr and Cohen 1985; Cohen and Starr 1987; Hoshiyama and Sheean 1998). In general, the M20 is considered to be generated in Brodmann's area 3b of the SI (Desmedt et al. 1987; Allison et al. 1991; Inui et al. 2004). However, the generator for the M35 remains unknown. Inui et al. (2004) reported overlapping activities among multiple cortical areas such as Brodmann's areas 3b, 4 and 1, around 20–30 ms following stimulation of the dorsum of the hand. Source modeling analysis suggested that area 4 of the primary motor area (MI) was involved in generating the M35 (Kawamura et al. 1996). Furthermore, the modulation of SEF components caused by the effect of the interstimulus interval suggested that another potential mechanism responsible for the M35 was inhibitory postsynaptic potentials in the deeper layers in area 3b (Wikstrom et al. 1996). Although we estimated the source of M35 around the SI, further study will be needed to elucidate the generator.

Interestingly, the time course of the M35 modulation, starting from 1500 ms before the movement and the remarkable attenuation just prior to the movement, was similar to that of the activities of movement-related cortical potentials that reflected the neural activities of movement preparation in motor-related areas. In addition, our previous study showed that the extent of the centrifugal mechanism for SEPs was dependent on the amplitude of the negative slope. This result suggested that the centrifugal modulation in the SI was related to the activities of motor related areas (Wasaka et al. 2005b). Subdural recording showed that the supplementary motor area (SMA) and the MI activities in this period were recorded from the cortex of humans (Ikeda et al. 1992). Motor related areas, such as SMA and MI, have extensive cortico-cortical connections to other cortices such as the SI (Jones et al. 1978) and possibly other sensory associated cortices. Intracortical microstimulation of the neurons in the MI in monkeys caused a profound decrease in the magnitude of the short-latency component of somatosensory evoked potentials (Jiang et al. 1990), suggesting that the activities in the motor related areas just before movement could modulate the response in the SI, especially the generator for the M35 component. It is assumed that these electrophysiological changes are associated with a decrease in tactile sensitivity commonly observed before the onset of movement of the limb that received the sensory stimulation (Schmidt et al. 1990).



◀ **Fig. 1** The premovement subperiods and the onset of the rectified EMG. The preparatory period was divided into five subperiods from the onset of EMG to 4000 ms before movement. The time scale is expressed in minus values before the onset of movement. Stimulation of the median nerve was applied at random and the MEG signals following stimulation were averaged separately depending on each subperiod to obtain the premovement somatosensory evoked magnetic fields (SEFs). The sources were located in the posterior bank of the central sulcus in the hemisphere contralateral to the side stimulated. The graphs show the mean and standard deviation of the ECD moments of the M20 and M35 components in the rest condition and premovement subperiods. ** $p < 0.01$; Statistical significance compared with the values in the rest condition, # $p < 0.05$, ## $p < 0.01$; Statistical significance compared with the values for the 4,000–3,000 ms subperiod before EMG onset. Two periods for the M35 showed a significant reduction as compared with the rest condition and/or the 4,000–3,000 ms subperiod before EMG onset. The M20 showed no significant change. Adapted from Wasaka et al. (2003)

5 Modulation in the SII During the Preparatory Period of Voluntary Movement

There is no consensus as to the function of the SII concerning sensorimotor integration during voluntary movement. Enhancement of SII activation was observed (Huttunen et al. 1996; Forss and Jousmaki 1998; Lin et al. 2000) and it was assumed that this phenomenon reflects tuning of the SII neurons to relevant somatosensory information from the regions of contracting muscle. On the other hand, some researchers reported an attenuation of SII activation (Avikainen et al. 2002; Inoue et al. 2002). Using a self-initiated movement task to investigate the preparatory period, whereby the centripetal effect on the SEF response can be eliminated, one can mainly examine the centrifugal effect. We showed an enhancement of SII activation in the 0 to –500 ms sub-period (Fig. 2) (Wasaka et al. 2005a).

It is generally agreed that attention to somatosensory information enhances activation of the SII cortex (Hari et al. 1990; Mauguiere et al. 1997; Fujiwara et al. 2002). Although it is hard to eliminate the attentional effect, we instructed the subjects to concentrate on self-initiated finger extension and not to pay attention to electrical stimulation. Subjects reported that they concentrated on the finger extension and did not turn their mind to the electrical stimulation throughout the recording session. Therefore, although it is possible that attention contributed in a small way to the enhancement of SII activation, the activation of motor related areas prior to voluntary movement enhances the cortical effects of the SII either by increasing synchronicity or by increasing the number of neurons active via the centrifugal process.

6 Differential Modulation in the SI and SII Preceding Voluntary Movement

In the period of 500 ms before the onset of self-initiated movement, an attenuation of activation in the SI and enhancement in the SII was found. The opposite effects of movement on SI and SII cortices indicated that the motor and higher-order brain

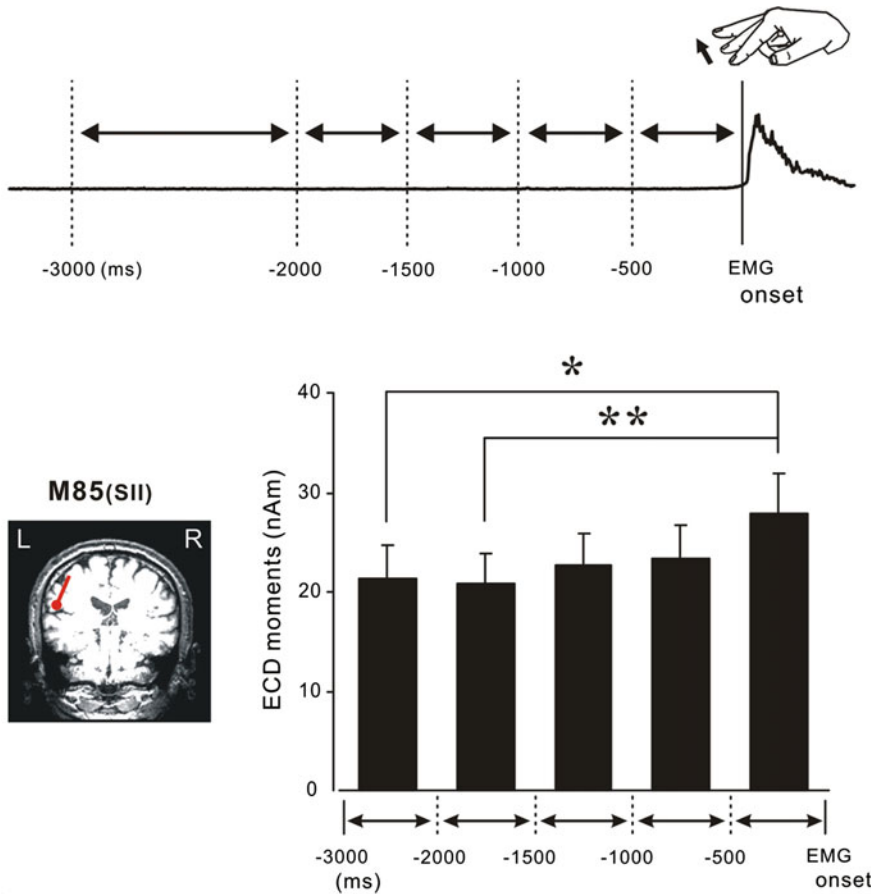


Fig. 2 The premovement subperiods and the onset of the rectified EMG. The preparatory period was divided into five subperiods from the onset of EMG to 3000 ms before movement. The time scale is expressed in minus values before the onset of movement. The dipole for the 80 ms response was identified in the temporal region, corresponding to the SII cortices. The graph shows the mean and standard error of the dipole moment of the SII contralateral to electrical stimulation in the premovement subperiods. * $p < 0.05$, ** $p < 0.01$; Statistical significance within two pairs. The dipole moment for the SII was significantly larger in the 0–500 ms subperiod than the 1500–2000 ms or 2000–3000 ms subperiod before EMG onset. Adapted from Wasaka et al. (2005a)

systems regulate sensory information at several processing stages by the centrifugal process. Motor commands can facilitate or suppress sensory responsiveness and, thus, probably perception, depending on temporal and behavioral constraints.

Removal of the SI area seriously impaired the processing of tactile information in the SII in macaques (Pons et al. 1987). However, deactivation of the SI did not have clear effects on the responsiveness of the SII (Zhang et al. 1996). In addition, tactile information could be directly conveyed to both SI and SII cortices from overlapping

regions within the ventral posterior nucleus of the thalamus (Zhang et al. 2001). In humans, MEG responses from SII increased with active attention, while little effect of attention was observed in the SI (Mima et al. 1998; Fujiwara et al. 2002). Moreover, the responses in the SI and SII are modulated differently depending on the intensity of the electrical stimulation (Torquati et al. 2002; Lin et al. 2003). From these results, it appears that somatosensory information processing, concerning sensorimotor integration in SII, may be independent of that in SI.

Our sensory systems are constantly bombarded by numerous sensory stimuli, from which we must extract the few stimuli important to the control of our movement. One can therefore recognize that an attenuation of SI activation is involved in filtering information. Although much attention has been given to sensorimotor integration in the SI, there is little evidence of such a phenomenon in the SII and the role of the SII in motor execution has not been fully elucidated in humans. Compared with the SI, SII is speculated to serve a higher level of cognitive function in somatosensory information processing, such as attention, decision-making, object recognition, and the integration of nociceptive and non-nociceptive inputs (Mima et al. 1998; Steinmetz et al. 2000; Romo et al. 2002; Inui et al. 2003; Qiu et al. 2004). Our results showed that these cortical areas play a different functional role in sensorimotor integration. When we are moving, the sensory threshold is attenuated. By contrast, exploration using fingertips is sensitive during movement execution (active touch). This neural mechanism can be explained by an enhancement of SII activation. To clarify the function of SII concerning sensorimotor integration, we conducted further research.

7 Crossmodal Interaction Between Somatosensory and Visual Information

Crossmodal interaction occurs when neural activity from one sensory modality modulates activity in another (Macaluso et al. 2000; Kida et al. 2007). Crossmodal links between visual and somatosensory information have shown the critical role of vision in determining limb position and localizing tactile sensations (vanBeers et al. 1996; Botvinick and Cohen 1998; Graziano 1999). For example, viewing a body part improves tactile perception and facilitates the amplitude of long-latency components of event-related potentials (Taylor-Clarke et al. 2002; Cardini et al. 2011). In addition, there is evidence that vision of the body is crucial for localization of tactile stimuli (Eimer et al. 2004; Sambo et al. 2009).

Although less attention has been devoted to the effect of observation of movement on information processing in somatosensory areas, some studies have reported neural modulation in SI and SII. Previous studies showed that viewing another person's gestures modulates the excitability of somatosensory areas (Avikainen et al. 2002; Rossi et al. 2002; Mottonen et al. 2005; Pihko et al. 2010). These results indicate that the somatosensory areas are involved in the mirroring of actions.

8 Somatosensory and Visual Interaction During the Execution of Voluntary Movement

Recognizing one's own movement is essential to the control of voluntary movement. Movement causes changes to sensory inflow as well as changes in the position of body parts. The movement of one's body parts is perceived not only by visual information but also by somatosensory feedback from muscles, skin and tendons which provide information on the status of each part being moved in a moment. Under normal conditions, the visual estimate of limb position is congruent with the somatosensory estimate and motor command, and movement is usually achieved automatically without awareness of the component processes. By contrast, in novel motor tasks or situations which produce conflict or incongruence between intentions and sensorimotor consequences, the mismatch between the actual sensory feedback and predicted movement of the body part disrupts motor execution. A crucial issue is elucidating the brain mechanisms that integrate the multi-sensory information and motor commands for motor control.

It has been suggested that a copy of the motor signal, known as an efference copy, is created so that sensory signals generated from external stimuli can be distinguished from reafferent signals from body movement (von Holst and Mittelstaedt 1950; Wolpert et al. 1998). Corollary discharges are produced only if the motor commands interact with unpredicted sensory inputs and inhibit the neural response to self-generated sensory signals (Sperry 1950). More activity in somatosensory areas was found when an unpredicted stimulus was externally delivered (Hesse et al. 2010). Since crossmodal interaction between somatosensory and visual inputs exists in the somatosensory areas, there is considerable validity to the notion that the prediction of visual feedback of movement modulates the somatosensory areas.

We investigated whether activation in somatosensory areas was affected by discordance between an intended and executed action. A mirror box creates unintended visual feedback of body movement (Fig. 3). Subjects inserted their hands into the mirror box with the forearm supine (Mirror condition). The position of the right hand was adjusted so that the mirror image precisely overlapped the view of the masked left hand. Since the actual visual information on the left hand was masked by the mirror, a mirror image of the right hand was provided. In the Normal and Mirror conditions, subjects experienced the appropriate somatosensory feedback, but in the Mirror condition, what they watched was incongruent with the expected visual feedback which produced a state of cognitive conflict. The motor task was a self-paced thumb movement of the left hand. Electrical stimulation for the recording of somatosensory responses was delivered to the median nerve at the left wrist. Subjects watched the stationary image of the hand while they performed the self-paced movement of the left thumb. In this situation, subjects felt that the movement was not controlled by themselves or the moving body part did not belong to them. The cortical response showed that neural activation in the SII and parietal cortex was strongly affected by the unexpected visual

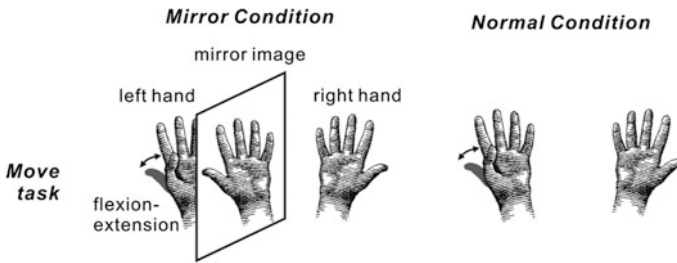
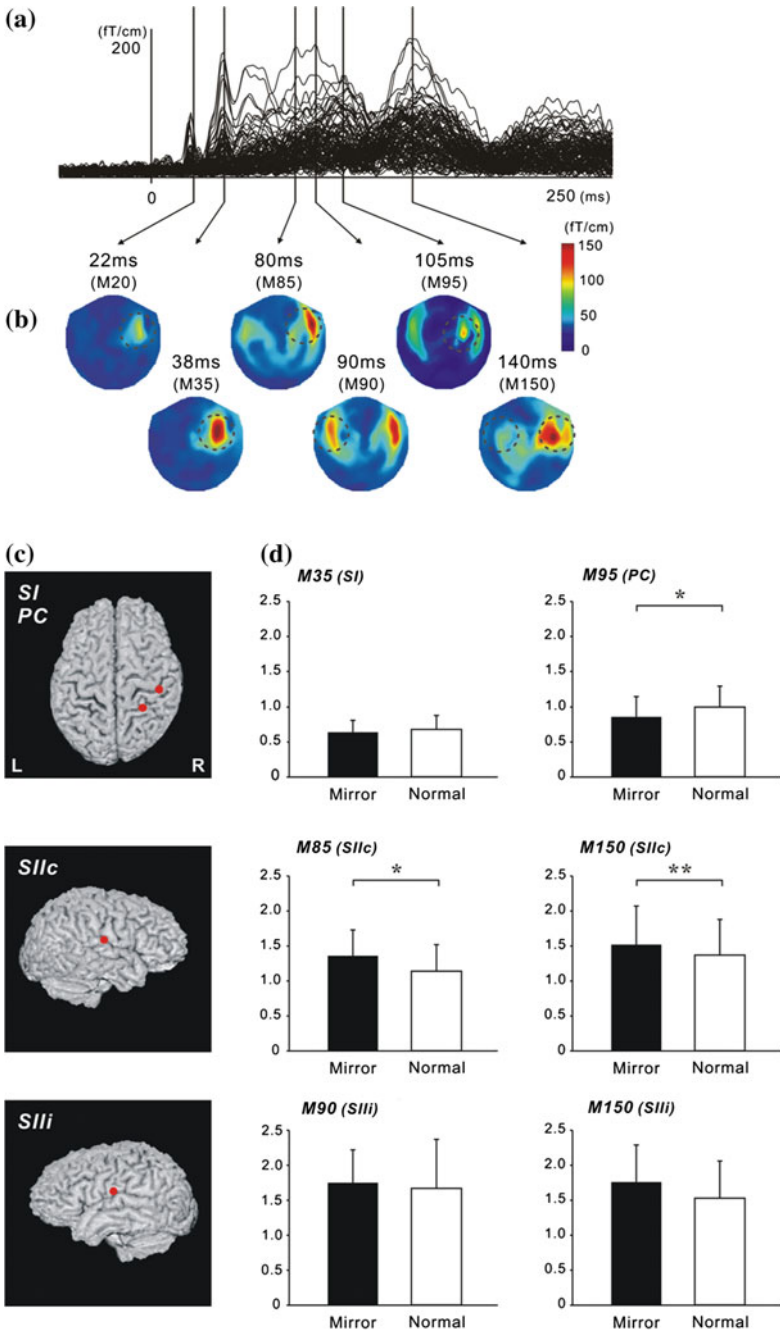


Fig. 3 Schema of the experimental paradigm. In the Mirror condition, subjects inserted their hands into a mirror box with the forearm supine. The position of the *right hand* was adjusted so that the mirror image precisely overlapped the view of the masked *left hand*. A mirror image of the *right hand* was presented instead of the *left hand*. Subjects performed self-paced continuous and repetitive flexion-extension of the *left thumb* in the normal visual feedback (*Normal condition*) and the incongruent non-veridical visual feedback condition (*Mirror condition*). Electrical stimulation for the recording of somatosensory responses was delivered to the median nerve at the *left wrist*. Adapted from Wasaka et al. (2012a)

feedback (Fig. 4) (Wasaka and Kakigi 2012a; Wasaka and Kakigi 2012b). The SII showed significantly higher activation with unpredicted visual feedback of movement, whereas the opposite was true of the parietal activation. These results provide evidence that the visual information modulates activation in somatosensory areas during voluntary movement.

The parietal cortex has been implicated in mediating multisensory integration in different modalities (Andersen et al. 1997) while a fronto-parietal network has been shown to be involved in selecting behaviorally relevant stimuli (Posner and Petersen 1990; Corbetta et al. 1998; Burton et al. 1999). The parietal area integrates the predicted proprioceptive and visual feedback to calculate how the commands affected the state of the body (Shadmehr and Krakauer 2008). The new finding was that the SII had crossmodal functions in the somatosensory and visual modalities during motor execution, and the visual information plays a crucial role in sensorimotor integration of the SII during motor execution. Modulation in the SII during conflicting visual feedback might be involved in computing the motor errors by comparing the actual hand location to the estimated location for controlling movement.

The forward model of the motor system predicts the behavior of a body segment in response to a motor command. In this model, a motor plan is updated continuously by internal feedback loops, and the parietal cortex and cerebellum appear to play a crucial role. In the Mirror condition, subjects faced the surprise of seeing their hand not responding as expected, and our results showed a modulation of activation in the parietal area. We assume that this modulation during conflicting visual feedback might be involved in computing the motor errors by comparing the actual hand location to the estimated location for controlling movement.



◀ **Fig. 4** Superimposed MEG waveforms and topographical maps. **a** Superimposed root sum square (RSS) waveforms from 102 sensors. **b** Map of the topography of the RSS at the peak components. The first cortical activation was identified around the central area contralateral to the hemisphere of the side stimulus (M20 and M35). Then, bilateral activations were identified in temporal areas at around 80–100 ms (SII). PC activity was identified in the centro-parietal area located posterior to the SI activity. **c** The location of equivalent current dipoles in each component superimposed on 3D images. **d** The modulation of RSS components with voluntary movement in the Mirror and Normal conditions. A significant difference was observed in the components in the SIIc (M85 and M150) and PC (M95). The ratios of the M85 and M150 in the SIIc were significantly larger in the Mirror than Normal Condition. By contrast, the ratio of the M95 was significantly smaller in the Mirror condition than Normal condition. * $p < 0.05$, ** $p < 0.01$; Statistical significance within two pairs. Adapted from Wasaka et al. (2012a)

9 Sensorimotor Integration Related to the Feeling of Agency

There is evidence that humans are normally not consciously aware of sensory feedback from movement (Fournieret and Jeannerod 1998), and are aware that their arms and legs belong to them through somatosensory and visual inputs. This feeling of self-attribution is impaired when the predicted sensory information estimated from motor intention does not match the actual sensory information. In our study, the Mirror condition corresponded to this situation. Some subjects reported feeling that movement was not controlled by themselves or the body did not belong to them in the Mirror condition. We showed a significant enhancement of a SII component at around 150 ms and reduction of parietal activation in the non-veridical visual feedback of movement (Wasaka and Kakigi 2012a). Our group reported simultaneous activation in the SII and insula peaking at 90 to 160 ms after electrical stimulation. We assumed that the late component peaking at 150 ms in the SII may involve the activity of the neighboring insula (Inui et al. 2003). Studies in patients and recent neuroimaging results in healthy subjects suggest a prominent role for the posterior parietal cortex (Farrer et al. 2008) and insula (Farrer et al. 2003; Karnath et al. 2005) in the sense of limb ownership as well as the self-awareness of limb actions, the sense of agency. Further study will be needed to clarify the functional role of these areas in sensorimotor integration.

10 Conclusions

The sensory information for movement is provided by visual and somatosensory feedback. It has been postulated that the integration between motor commands and sensory information plays an important role in motor control. Efferent neural signals created by central motor networks in parallel with the motor commands are used to predict the sensory consequences of own motor acts. In this process, this signal modulates information processing in sensory areas. Preceding and during voluntary movement, it has been reported that information processing in

somatosensory areas is modulated by the effect of efferent signals. Activities in the SI show a reduction with voluntary movement, whereas those in the SII are enhanced. The functional role for this difference in modulation in somatosensory areas may be the regulation of motor control by facilitating the appropriate information and/or suppressing inappropriate information. Compared with SI, SII is speculated to serve a higher level of somatosensory information processing, such as decision-making, objective recognition and integration of nociceptive and non-nociceptive inputs. Our research showed that neural responses in SII was strongly affected by the unexpected visual feedback during movement execution. This result provides evidence that the visual information plays a crucial role in sensorimotor integration in the SII.

References

- Allison T, McCarthy G, Wood CC, Jones SJ (1991) Potentials evoked in human and monkey cerebral cortex by stimulation of the median nerve. a review of scalp and intracranial recordings. *Brain* 114:2465–2503
- Andersen RA, Snyder LH, Bradley DC, Xing J (1997) Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annu Rev Neurosci* 20:303–330
- Avikainen S, Forss N, Hari R (2002) Modulated activation of the human SI and SII cortices during observation of hand actions. *Neuroimage* 15(3):640–646
- Blakemore SJ, Goodbody SJ, Wolpert DM (1998) Predicting the consequences of our own actions: the role of sensorimotor context estimation. *J Neurosci* 18(18):7511–7518
- Bocker KB, Forget R, Brunia CH (1993) The modulation of somatosensory evoked potentials during the foreperiod of a forewarned reaction time task. *Electroencephalogr Clin Neurophysiol* 88(2):105–117
- Botvinick M, Cohen J (1998) Rubber hands ‘feel’ touch that eyes see. *Nature* 391(6669):756
- Burton H, Abend NS, MacLeod AM, Sinclair RJ, Snyder AZ, Raichle ME (1999) Tactile attention tasks enhance activation in somatosensory regions of parietal cortex: a positron emission tomography study. *Cereb Cortex* 9(7):662–674
- Cardini F, Longo MR, Haggard P (2011) Vision of the body modulates somatosensory intracortical inhibition. *Cereb Cortex* 21(9):2014–2022
- Cohen LG, Starr A (1987) Localization, timing and specificity of gating of somatosensory evoked potentials during active movement in man. *Brain* 110:451–467
- Corbetta M, Akbudak E, Conturo TE, Snyder AZ, Ollinger JM, Drury HA, Linenweber MR, Petersen SE, Raichle ME, Van Essen DC, Shulman G (1998) A common network of functional areas for attention and eye movements. *Neuron* 21(4):761–773
- Crapse TB, Sommer MA (2008) Corollary discharge circuits in the primate brain. *Curr Opin Neurobiol* 18(6):552–557
- Desmedt JE, Nguyen TH, Bourguet M (1987) Bit-mapped color imaging of human evoked potentials with reference to the N20, P22, P27 and N30 somatosensory responses. *Electroencephalogr Clin Neurophysiol* 68(1):1–19
- Desmedt JE, Tomberg C (1989) Mapping early somatosensory evoked potentials in selective attention: critical evaluation of control conditions used for titrating by difference the cognitive P30, P40, P100 and N140. *Electroencephalogr Clin Neurophysiol* 74(5):321–346
- Eimer M, Forster B, Fieger A, Harbich S (2004) Effects of hand posture on preparatory control processes and sensory modulations in tactile-spatial attention. *Clin Neurophysiol* 115(3):596–608

- Farrer C, Franck N, Georgieff N, Frith CD, Decety J, Jeannerod M (2003) Modulating the experience of agency: a positron emission tomography study. *Neuroimage* 18(2):324–333
- Farrer C, Frey SH, Van Horn JD, Turk E, Turk D, Inati S, Grafton ST (2008) The angular gyrus computes action awareness representations. *Cereb Cortex* 18(2):254–261
- Forss N, Jousmaki V (1998) Sensorimotor integration in human primary and secondary somatosensory cortices. *Brain Res* 781(1–2):259–267
- Fourneret P, Jeannerod M (1998) Limited conscious monitoring of motor performance in normal subjects. *Neuropsychologia* 36(11):1133–1140
- Fujiwara N, Imai M, Nagamine T, Mima T, Oga T, Takeshita K, Toma K, Shibasaki H (2002) Second somatosensory area (SII) plays a significant role in selective somatosensory attention. *Brain Res Cogn Brain Res* 14(3):389–397
- Garcia-Larrea L, Lukaszewicz AC, Mauguire F (1995) Somatosensory responses during selective spatial attention: the N120-to-N140 transition. *Psychophysiology* 32(6):526–537
- Graziano MSA (1999) Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. *Proc Nat Acad Sci USA* 96(18):10418–10421
- Hari R, Hamalainen H, Hamalainen M, Kekoni J, Sams M, Tiihonen J (1990) Separate finger representations at the human second somatosensory cortex. *Neuroscience* 37(1):245–249
- Hesse MD, Nishitani N, Fink GR, Jousmaki V, Hari R (2010) Attenuation of somatosensory responses to self-produced tactile stimulation. *Cereb Cortex* 20(2):425–432
- Hoshiyama M, Sheean G (1998) Changes of somatosensory evoked potentials preceding rapid voluntary movement in Go/No-go choice reaction time task. *Brain Res Cogn Brain Res* 7(2):137–142
- Huttunen J, Wikstrom H, Korvenoja A, Seppalainen AM, Aronen H, Ilmoniemi RJ (1996) Significance of the second somatosensory cortex in sensorimotor integration: enhancement of sensory responses during finger movements. *NeuroReport* 7(5):1009–1012
- Hyvarinen J, Poranen A, Jokinen Y (1980) Influence of attentive behavior on neuronal responses to vibration in primary somatosensory cortex of the monkey. *J Neurophysiol* 43(4):870–882
- Ikeda A, Luders HO, Burgess RC, Shibasaki H (1992) Movement-related potentials recorded from supplementary motor area and primary motor area. Role of supplementary motor area in voluntary movements. *Brain* 115:1017–1043
- Inoue K, Yamashita T, Harada T, Nakamura S (2002) Role of human SII cortices in sensorimotor integration. *Clin Neurophysiol* 113(10):1573–1578
- Inui K, Wang X, Qiu Y, Nguyen BT, Ojima S, Tamura Y, Nakata H, Wasaka T, Tran TD, Kakigi R (2003) Pain processing within the primary somatosensory cortex in humans. *Eur J Neurosci* 18(10):2859–2866
- Inui K, Wang X, Tamura Y, Kaneoke Y, Kakigi R (2004) Serial processing in the human somatosensory system. *Cereb Cortex* 14(8):851–857
- Iriki A, Tanaka M, Iwamura Y (1996) Attention-induced neuronal activity in the monkey somatosensory cortex revealed by pupillometrics. *Neurosci Res* 25(2):173–181
- Jiang W, Chapman CE, Lamarre Y (1990) Modulation of somatosensory evoked responses in the primary somatosensory cortex produced by intracortical microstimulation of the motor cortex in the monkey. *Exp Brain Res* 80(2):333–344
- Johansen-Berg H, Christensen V, Woolrich M, Matthews PM (2000) Attention to touch modulates activity in both primary and secondary somatosensory areas. *NeuroReport* 11(6):1237–1241
- Jones EG, Coulter JD, Hendry SH (1978) Intracortical connectivity of architectonic fields in the somatic sensory, motor and parietal cortex of monkeys. *J Compative Neurol* 181(2):291–347
- Jones SJ, Halonen JP, Shawkat F (1989) Centrifugal and centripetal mechanisms involved in the ‘gating’ of cortical SEPs during movement. *Electroencephalogr Clin Neurophysiol* 74(1):36–45
- Kakigi R, Koyama S, Hoshiyama M, Watanabe S, Shimojo M, Kitamura Y (1995) Gating of somatosensory evoked responses during active finger movements magnetoencephalographic studies. *J Neurol Sci* 128(2):195–204
- Karnath HO, Baier B, Nagele T (2005) Awareness of the functioning of one’s own limbs mediated by the insular cortex? *J Neurosci* 25(31):7134–7138

- Kawamura T, Nakasato N, Seki K, Kanno A, Fujita S, Fujiwara S, Yoshimoto T (1996) Neuromagnetic evidence of pre- and post-central cortical sources of somatosensory evoked responses. *Electroencephalogr Clin Neurophysiol* 100(1):44–50
- Kida T, Inui K, Wasaka T, Akatsuka K, Tanaka E, Kakigi R (2007) Time-varying cortical activations related to visual-tactile cross-modal links in spatial selective attention. *J Neurophysiol* 97(5):3585–3596
- Kida T, Nishihira Y, Wasaka T, Sakajiri Y, Tazoe T (2004) Differential modulation of the short- and long-latency somatosensory evoked potentials in a forewarned reaction time task. *Clin Neurophysiol* 115(10):2223–2230
- Kida T, Wasaka T, Inui K, Akatsuka K, Nakata H, Kakigi R (2006) Centrifugal regulation of human cortical responses to a task-relevant somatosensory signal triggering voluntary movement. *Neuroimage* 32(3):1355–1364
- Lin YY, Shih YH, Chen JT, Hsieh JC, Yeh TC, Liao KK, Kao CD, Lin KP, Wu ZA, Ho LT (2003) Differential effects of stimulus intensity on peripheral and neuromagnetic cortical responses to median nerve stimulation. *Neuroimage* 20(2):909–917
- Lin YY, Simoes C, Forss N, Hari R (2000) Differential effects of muscle contraction from various body parts on neuromagnetic somatosensory responses. *Neuroimage* 11(4):334–340
- Macaluso E, Frith CD, Driver J (2000) Modulation of human visual cortex by crossmodal spatial attention. *Science* 289(5482):1206–1208
- Mauguiere F, Merlet I, Forss N, Vanni S, Jousmaki V, Adeleine P, Hari R (1997) Activation of a distributed somatosensory cortical network in the human brain: a dipole modelling study of magnetic fields evoked by median nerve stimulation. Part II: effects of stimulus rate, attention and stimulus detection. *Electroencephalogr Clin Neurophysiol* 104(4):290–295
- Mima T, Nagamine T, Nakamura K, Shibasaki H (1998) Attention modulates both primary and second somatosensory cortical activities in humans: a magnetoencephalographic study. *J Neurophysiol* 80(4):2215–2221
- Mottronen R, Jarvelainen J, Sams M, Hari R (2005) Viewing speech modulates activity in the left SI mouth cortex. *Neuroimage* 24(3):731–737
- Murase N, Kaji R, Shimazu H, Katayama-Hirota M, Ikeda A, Kohara N, Kimura J, Shibasaki H, Rothwell JC (2000) Abnormal premovement gating of somatosensory input in writer's cramp. *Brain* 123:1813–1829
- Nakajima T, Wasaka T, Kida T, Nishimura Y, Fumoto M, Sakamoto M, Takashi E (2006) Changes in somatosensory evoked potentials and Hoffmann reflexes during fast isometric contraction of foot plantarflexor in humans. *Percept Mot Skills* 103(3):847–860
- Nakata H, Inui K, Wasaka T, Nishihira Y, Kakigi R (2003) Mechanisms of differences in gating effects on short- and long-latency somatosensory evoked potentials relating to movement. *Brain Topogr* 15(4):211–222
- Pihko E, Nangini C, Jousmaki V, Hari R (2010) Observing touch activates human primary somatosensory cortex. *Eur J Neurosci* 31(10):1836–1843
- Pons TP, Garraghty PE, Friedman DP, Mishkin M (1987) Physiological evidence for serial processing in somatosensory cortex. *Science* 237(4813):417–420
- Posner MI, Petersen SE (1990) The attention system of the human brain. *Annu Rev Neurosci* 13:25–42
- Qiu Y, Inui K, Wang X, Nguyen BT, Tran TD, Kakigi R (2004) Effects of distraction on magnetoencephalographic responses ascending through C-fibers in humans. *Clin Neurophysiol* 115(3):636–646
- Romo R, Hernandez A, Zainos A, Lemus L, Brody CD (2002) Neuronal correlates of decision-making in secondary somatosensory cortex. *Nat Neurosci* 5(11):1217–1225
- Rossi S, Tecchio F, Pasqualetti P, Olivelli M, Pizzella V, Romani GL, Passero S, Battistini N, Rossini PM (2002) Somatosensory processing during movement observation in humans. *Clin Neurophysiol* 113(1):16–24
- Rushton DN, Rothwell JC, Craggs MD (1981) Gating of somatosensory evoked potentials during different kinds of movement in man. *Brain* 104(3):465–491

- Sambo CF, Gillmeister H, Forster B (2009) Viewing the body modulates neural mechanisms underlying sustained spatial attention in touch. *Eur J Neurosci* 30(1):143–150
- Schmidt RF, Schady WJ, Torebjork HE (1990) Gating of tactile input from the hand. I. Effects of finger movement. *Exp Brain Res* 79(1):97–102
- Shadmehr R, Krakauer JW (2008) A computational neuroanatomy for motor control. *Exp Brain Res* 185(3):359–381
- Sperry RW (1950) Neural basis of the spontaneous optokinetic response produced by visual inversion. *J Compar Physiol Psychol* 43(6):482–489
- Staines WR, Graham SJ, Black SE, McIlroy WE (2002) Task-relevant modulation of contralateral and ipsilateral primary somatosensory cortex and the role of a prefrontal-cortical sensory gating system. *Neuroimage* 15(1):190–199
- Starr A, Cohen LG (1985) ‘Gating’ of somatosensory evoked potentials begins before the onset of voluntary movement in man. *Brain Res* 348(1):183–186
- Steinmetz PN, Roy A, Fitzgerald PJ, Hsiao SS, Johnson KO, Niebur E (2000) Attention modulates synchronized neuronal firing in primate somatosensory cortex. *Nature* 404(6774):187–190
- Taylor-Clarke M, Kennett S, Haggard P (2002) Vision modulates somatosensory cortical processing. *Curr Biol* 12(3):233–236
- Torquati K, Pizzella V, Della Penna S, Franciotti R, Babiloni C, Rossini PM, Romani GL (2002) Comparison between SI and SII responses as a function of stimulus intensity. *NeuroReport* 13(6):813–819
- vanBeers RJ, Sittig AC, vanderGon JJD (1996) How humans combine simultaneous proprioceptive and visual position information. *Exp Brain Res* 111(2):253–261
- von Holst E, Mittelstaedt H (1950) Das Reafferenzprinzip: Wechselwirkungen Zwischen Zentralnervensystem und Peripherie. *Naturwissenschaften* 37:464–476
- Wasaka T, Hoshiyama M, Nakata H, Nishihira Y, Kakigi R (2003) Gating of somatosensory evoked magnetic fields during the preparatory period of self-initiated finger movement. *Neuroimage* 20(3):1830–1838
- Wasaka T, Kakigi R (2012a) Conflict caused by visual feedback modulates activation in somatosensory areas during movement execution. *Neuroimage* 59(2):1501–1507
- Wasaka T, Kakigi R (2012b) The effect of unpredicted visual feedback on activation in the secondary somatosensory cortex during movement execution. *BMC Neurosci* 13(1):138
- Wasaka T, Nakata H, Akatsuka K, Kida T, Inui K, Kakigi R (2005a) Differential modulation in human primary and secondary somatosensory cortices during the preparatory period of self-initiated finger movement. *Eur J Neurosci* 22(5):1239–1247
- Wasaka T, Nakata H, Kida T, Kakigi R (2005b) Changes in the centrifugal gating effect on somatosensory evoked potentials depending on the level of contractile force. *Exp Brain Res* 166(1):118–125
- Wikstrom H, Huttunen J, Korvenoja A, Virtanen J, Salonen O, Aronen H, Ilmoniemi RJ (1996) Effects of interstimulus interval on somatosensory evoked magnetic fields (SEFs): a hypothesis concerning SEF generation at the primary sensorimotor cortex. *Electroencephalogr Clin Neurophysiol* 100(6):479–487
- Wolpert DM, Miall RC, Kawato M (1998) Internal models in the cerebellum. *Trends Cogn Sci* 2(9):338–347
- Zhang HQ, Murray GM, Coleman GT, Turman AB, Zhang SP, Rowe MJ (2001) Functional characteristics of the parallel SI- and SII-projecting neurons of the thalamic ventral posterior nucleus in the marmoset. *J Neurophysiol* 85(5):1805–1822
- Zhang HQ, Murray GM, Turman AB, Mackie PD, Coleman GT, Rowe MJ (1996) Parallel processing in cerebral cortex of the marmoset monkey: effect of reversible SI inactivation on tactile responses in SII. *J Neurophysiol* 76(6):3633–3655