Attenuation of Somatosensory Responses to Self-Produced Tactile Stimulation

Sensory stimulation resulting from one’s own behavior or the outside world is easily differentiated by healthy persons who are able to predict the sensory consequences of their own actions. This ability has been related to cortical attenuation of activation elicited by self-produced stimulation. To date, however, the neural processes underlying this modulation remain to be elucidated. We therefore recorded whole-scalp magnetoencephalographic (MEG) signals from 10 young adults either when they were touched by another person with a brush or when they touched themselves with the same device. The main MEG responses peaked at the primary somatosensory cortex at 54 ± 2 ms. Signals and source strengths were about a fifth weaker to self-produced than external touch. Importantly, attenuation was present in each subject. Control recordings indicated that the suppression was neither caused by hand movements as such nor by visual cues. The very early start of the attenuation already about 30 ms after stimulation onset is in line with the hypothesis of forward mechanisms, based on motor commands, as the basis of differentiation between self-produced and externally produced tactile sensations.

Keywords: agency, forward models, magnetoencephalography, somatosensory cortex, touch

Introduction

For a contingent percept of both the external world and the own body, it is fundamental to dissociate sensory signals resulting from one’s own actions from those that are externally generated by the environment. From an ecological perspective, the predicted and desired consequences of our own actions should not waste the limited capacities of our sensory systems but rather spare them for catching more important, unexpected events that we need to react to. Previous studies have shown weaker neuronal responses to self-produced than externally generated similar stimuli in different sensory modalities. For example, in the auditory domain, speaking primes the subject’s own auditory cortex at millisecond time accuracy, dampening and delaying reactions to self-produced and thereby expected vowels (Curio et al. 2000). Likewise, in the vestibular nuclei, some neurons that are vividly activated when the head or body is passively turned do not respond when the head is actively moved in space (Cullen and Roy 2004; Roy and Cullen 2004).

One striking example of a differential perception of self-versus externally produced stimulation in humans is tickling: it is difficult, often even impossible, to tickle oneself (Weiskrantz et al. 1971; Claxton 1975) unless a delay is introduced between the causing action and the produced tactile sensation. For example, subjects report their own movements to be significantly less ticklish than externally produced or manipulated movements, in which the tactile sensation is delayed or the trajectory of the movement is rotated (Blakemore et al. 1999, 2000). Using functional magnetic resonance (MR) imaging in a block design, Blakemore et al. (1998) showed weaker activity in the secondary somatosensory (SII) cortex and in the anterior cingulate gyrus during own relative to externally produced touch. Predictive forward models are generally assumed to underlie this attenuation: the forthcoming consequences of one’s own actions are derived from motor plans and used to alter the sensory signal online, thereby increasing the relative salience of externally caused sensations. Given that cerebellar activation levels have been shown to correlate with activity in the primary somatosensory (SI) and SII cortices (as well as in the thalamus), the cerebellum has been suggested to play a substantial role in mediating this modulation (Blakemore et al. 1998, 2000).

Having used macrostimulation (MEG) to study in an event-related manner the early cortical somatosensory evoked fields (SEFs) elicited by one’s own or somebody else’s actions leading to similar sensory stimulation. Based on previous findings, we hypothesized that responses to touch stimuli produced by one’s own actions would be weaker than externally produced touch. We furthermore wanted to be sure that these possible effects would not be affected by movements of the subject’s hand but rather by an accurate prediction of the expected sensory changes. Thus, brain signals to external touch were also recorded when the subjects performed rotatory wrist movements unrelated to the stimulation. Finally, if predictions were based on efference copies of motor output rather than, for example, visual cues of the movement trajectories, the effects should be the same whether or not the subjects use visual cues for their predictions. We therefore also compared brain responses when the subjects had their eyes open versus eyes closed.

Materials and Methods

Subjects

Ten healthy young Japanese adults (5 females and 5 males; aged 20–31 years, mean 24.7 years; all right handed) volunteered for the recordings after informed consent. The experimental protocol was approved by the Ethics Committee of the National Rehabilitation Center for Persons with Disabilities in Tokorozawa, Japan.
Stimuli and Experimental Conditions
Tactile stimuli were produced by a novel handheld tactile stimulator (Jousmäki et al. 2007) consisting of a bundle of 650 optical fibers (Schott SpectraFlex, Mainz, Germany), each 50 μm in diameter (Fig. 1). The diameter of the whole bundle was 1.5 mm, resulting in a stimulated area of about 2 mm². The bundle was fixed at the end of an arch-shaped handle (see Fig. 1), and the device was used in a hammer-like way to tap the skin. The other end of the fiber bundle was fixed to a photoelectric sensor (Omron E3X-N41, Kyoto, Japan) that used modulated red light (680 nm). Half of the fibers emitted the light, and the others detected reflectance from the skin that turned on a photoelectric switch at the moment of skin contact; thus, a precise trigger pulse was obtained for MEG averaging.

Using this device, the lateral dorsum of the subject’s left hand between the first and the second metacarpal bones was tapped within a region of less than 4 cm² once every 2–3 s. The application of proper taps was the first and the second metacarpal bones was tapped within a region of moment of skin contact; thus, a precise trigger pulse was obtained for (680 nm). Half of the fibers emitted the light, and the others detected reflectance from the skin that turned on a photoelectric switch at the moment of skin contact; thus, a precise trigger pulse was obtained for MEG averaging.

Photograph of the device used for stimulation (modified from Jousmäki
et al. 2007).

MEG Recordings
During the MEG recordings, the subjects were sitting comfortably in a magnetically shielded room (NKP, Yokohama, Japan), with the head supported against the helmet-shaped sensor array of the neuromagnetometer (Vectorview™, Neuromag Ltd, Helsinki, Finland). This 306-channel device contains 102 identical triple sensors, each of them housing 2 orthogonal planar gradiometers and 1 magnetometer. Before each recording, the exact position of the head with respect to the sensors was found on the basis of magnetic signals produced by currents led into 4 indicator coils placed at known sites on the scalp. The sites of the coils with respect to anatomical landmarks on the scalp were determined before the recording with a 3D digitizer. Consequently, it was possible to align the MEG and MR image coordinate systems. In the applied head coordinate system, x axis passes from the left to the right preauricular point, with the positive direction toward the right; the y axis goes forward from inion to nasion, and the positive z axis goes upward orthogonal to the xy plane (for reviews of the principles of MEG data collection and analysis applied in this study, see, e.g., Hämäläinen et al. 1993; Hari and Forss 1999).

The recording passband was 0.1–176 Hz, and the signals were digitized at 601 Hz. The analysis period was 1600 ms, including a pre- and poststimulus period of 800 ms each. Responses coinciding with amplitudes exceeding 300 μV in the simultaneously recorded vertical electrooculogram were automatically rejected from the analysis. To replicate conditions within each run, every second response was averaged to a separate bin, and about 50 + 50 stimuli were delivered in each session.

For later coregistration of functional and anatomical information, structural T1-weighted MR images of the brains of all subjects were acquired with a 1.5-T Siemens Magnetom system Vision Plus™ (Siemens, Erlangen, Germany).

Data Analysis

**SEF Distribution and Waveforms**
Distinct and replicable deflections of SEFs, clearly exceeding the noise level, were first visually searched in the signals recorded by the 204 gradiometers; the signals were band-pass filtered through 3–40 Hz to eliminate premovement shifts (Fig. 2). We focused on the activity of the right SI cortex contralateral to the stimulated (left) hand. Amplitudes (in femtotesla per centimeter, fT/cm) and latencies of the first major deflection at the channel showing the maximum response above the right SI cortex were determined for each condition and in each individual subject. A baseline from -100 to 0 ms prior to each tactile stimulus was used for amplitude measurements. To determine concurrent activity in the other hemisphere, the amplitudes and latencies of signals from the ipsilateral (left) motor cortex in the self-touch condition were analyzed in the same way. For further statistical analysis, the peak amplitudes for all subjects were entered into a 3 × 2 analysis of variance (ANOVA) model with the 3 touch conditions (external touch, self-touch, and external touch + rotation) and 2 viewing conditions ("eyes open" and "eyes closed"). Post hoc Student’s paired 2-tailed t tests were performed. Bonferroni correction was applied to account for multiple comparisons.

**Source Modeling**
To rule out the possibility that any coinciding movement-related activity in the left Rolandic region would have affected the amplitude measurements of the right-hemisphere SEFs, amplitude measurements were repeated in source space. Equivalent current dipoles (ECDs) that best explained the field patterns during the signals were found by a least-squares search using a subset of 30 planar gradiometers over the area of the maximum response (for a review of the method, see

Figure 1. Photograph of the device used for stimulation (modified from Jousmäki et al. 2007).
Hämäläinen et al. 1993). For modeling of the SI sources, the selected gradiometers covered the right SI cortex, including the channels of the maximum response. As the first step, ECDs were determined for each condition individually to check for reproducibility. In addition, for the 2 self-touch conditions (with eyes open and eyes closed), a second source was found in the left primary motor (MI) cortex using the same procedure and a subset of 30 gradiometers above the left motor cortex. The 3D locations, orientations, and strengths of the ECDs were obtained in a spherical volume conductor, the dimensions of which were found from the individual MR images. Goodness of fit (obtained in a spherical volume conductor, the dimensions of which were found from the individual MR images. Goodness of fit (obtained in a spherical volume conductor, the dimensions of which were found from the individual MR images. Goodness of fit (g) of the model was computed to quantify how much the dipole accounted for the measured field variance; only ECDs with g > 85% at selected periods of time in the subset of channels were accepted. The adequacy of the model was also examined by comparing the measured signals with those predicted by the ECDs. The ECDs were superimposed onto individual MR images to show source locations with respect to brain structures. In addition, the coordinates were transformed into Talairach space using linear transformations within Matlab 6.5 on the basis of the locations of the anterior and posterior commissure, the midline, as well as the extensions of the brain in all directions.

We next extended the analysis to the whole signal duration, and all channels were taken into account in computing a time-varying 2-dipole model that was kept identical for all conditions. The 2 dipoles of the model, 1 located in the right SI and the other in the left MI, were derived from the self-touch condition where both sources were active with excellent signal-to-noise ratios. It should be noted that the SI locations did not differ between the external touch and self-touch conditions. To determine the adequacy of the 2-dipole model, the goodness of fit (g) was computed across all channels. The model was only accepted if accounting for more than 75% of the measured field variance of the whole scalp at the selected periods of time.

The time courses of SI sources were determined with respect to a baseline from -100 to 0 ms. The maximum strength of each source was determined as the mean value within a 5-ms window centered on the peak response, separately for each condition. Based on the above 3 × 2 ANOVA model, post hoc Student’s paired r-tests were performed, and Bonferroni correction was applied.

Results

Somatosensory Evoked Fields

Figure 2 shows responses of subject 2 to external touch (solid lines) and to self-touch (dashed lines). The insets show enlarged signals from the left and right rolandic regions. The 2 averages collected during the same session illustrate the reproducibility of signals.

Prominent responses are seen above the right SI cortex in both conditions. In this subject, the response peaks 3 ms later (54 vs. 51 ms) and the peak amplitude is 23% lower (86 vs. 112 fT/cm) in the self-touch than the external touch condition.

During the self-touch condition, strong movement-related signals were seen in the left rolandic region both before and after the touch. Across subjects, these movement-related signals were less consistent than the somatosensory responses; a slow shift peaked at -8 ± 3 ms (range from -40 to +20 ms) and was followed by a transient deflection of opposite polarity at 101 ± 4 ms (range from 72 to 138 ms, 94 ms in subject 2 shown in Fig. 2).

For further analysis, the signals were band-pass filtered through 3–40 Hz (see lower panels of the insets in Fig. 2) to remove the slow readiness fields prior to and during one’s own movements. The high-pass filter did not have much effect on the signal above right SI, as is evident from Figure 2 (right inset).

Table 1 presents the mean ± standard error of the mean (SEM) of peak latencies and amplitudes of the right and left rolandic responses across all 10 subjects for all conditions. The tactile responses in the right rolandic region peaked at 54 ± 2 ms, with no difference between conditions; in individual subjects, the peaks occurred at 47–63 ms. A second deflection of the same polarity was found in 5 of the 10 subjects, with

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<th>Table 1</th>
<th>Mean ± SEM latencies and peak amplitudes of the main MEG deflection at the channel showing the maximum response above the right SI cortex</th>
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<tr>
<td>Latencies [ms]</td>
<td>Amplitudes [fT/cm]</td>
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<tr>
<td>Eyes open</td>
<td>Eyes closed</td>
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<tr>
<td>External touch</td>
<td>53 ± 2</td>
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<tr>
<td>Self-touch</td>
<td>52 ± 1</td>
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<tr>
<td>External touch + rotation</td>
<td>53 ± 2</td>
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a mean latency at 73 ± 3 ms. It was smaller than the first one in 4 of the 5 subjects, and it was not analyzed further.

The 2 × 3 ANOVA analysis of the peak amplitudes above the right SI cortex (including factors “touch” [self-touch/external touch + rotation] and “viewing” [eyes open/eyes closed]) showed a statistically significant main effect of touch only, that is, independent of whether the subject’s eyes were closed or not ($F_{1.91,13.376} = 4.924$, SEM = 3.092, $P = 0.026$, Greenhouse-Geisser corrected). Post hoc t-tests revealed a statistically significant difference between self-touch and external touch ($P = 0.021$, 2-tailed t-test, Bonferroni corrected for multiple comparisons) and between self-touch and external touch + rotation ($P = 0.002$), irrespective of whether the subjects were able to see the stimulation or not. During the self-touch condition, the responses above the right SI were about 18% weaker than during external touch and about 28% weaker than during external touch + rotation.

**Source Analysis**

In all subjects, clear dipolar field patterns were observed above the right SI cortex at the time of the response peak. Figure 3 (left) shows such field patterns of subject 2 for external touch and self-touch, with a backward pointing current dipole in the right central region, in agreement with intracellular net current from the surface to the depth of the SI cortex in the posterior wall of the central sulcus. In the self-touch condition, dipolar field patterns were observed also in the left hemisphere just prior to the touch (in this subject from -25 to 8 ms), that is, during the end part of the readiness field, as well as with opposite polarity at 75–126 ms.

To account for any putative contamination from the left-hemisphere motor fields to the right-hemisphere SEFs, we explained all data with the resulting 2-dipole model, with 1 source in the right and the other in the left central region. The adequacy of the model was determined comparing the measured signals with those predicted by the ECDs, which showed a goodness of fit above 75% in all subjects across all channels at the respective response peak. Visual inspection of response patterns did not indicate SII activation in all except 1 subject.

The identified sources were superimposed onto individual MR images to show source locations with respect to anatomical structures. In agreement with previous publications (e.g., Forss et al. 1994; Schnitzler et al. 1995, 1999), these sources were in the region of the central sulcus, contralateral to the touched and moving hand, respectively (Fig. 3 right). The mean ± SEM Talairach coordinates were $x = 41 ± 2$, $y = 12 ± 3$, and $z = 88 ± 2$ (goodness of fit $94 ± 1.1\%$) for the right SI source and $x = -40 ± 2$, $y = 11 ± 2$, and $z = 91 ± 2$ (goodness of fit $98 ± 0.4\%$) for the left MI source.

Along the anteroposterior ($y$) direction, the right-hemisphere source was located at 0 ± 2 mm with respect to the individually defined right central sulcus and the left-hemisphere source was located at 2 ± 3 mm (anterior) with respect to the left central sulcus. Mean $y$ coordinates of the central sulcus (at the same $x$ and $z$ coordinates as dipoles) were $y = 12 ± 2$ mm in the right hemisphere and $y = 9 ± 3$ mm in the left hemisphere. This is consistent with generation of these signals in the right SI and the left MI cortices, respectively, as assumed above.

**Self-Touch versus External Touch**

Figure 4 shows the individual SI source strengths for self-touch and external touch as a function of time. In all 10 individuals (S1–S10), the responses are smaller during self-touch than external touch ($P < 0.001$, binomial test). The bottom graph...
shows the superimposed left MI source strengths in all individuals, indicating time courses that are clearly distinct from the SI source. The mean ± SEM source strength across subjects was at the peak of the SI response 23.3 ± 1.1 nAm during the external touch condition and 18.6 ± 0.8 nAm during the self-touch condition, corresponding to a reduction of the amplitude by 20.1 ± 3.6%. The source strengths in these 2 conditions differed significantly (meaning that their difference was larger than twice the root-mean-square value of the baseline period from –100 to 0 ms, corresponding to \( P < 0.05 \)) in the time interval between 32.3 ± 7 ms and 85.5 ± 6 ms following stimulus onset; the maximum difference occurred at 66.5 ± 14 ms.

**Effect of Movement-Related Activity**
The external touch + rotation condition was introduced to rule out the possibility that the observed attenuation of the SI source was related to movements of the right hand as such. When subjects performed continuous rotating movements of the right hand during external touch to the left hand (external touch + rotation), the SI source strengths were 26.4 ± 0.8 nAm (Fig. 5), that is 13.2 ± 3.3\% (\( P_{\text{corr}} = 0.027 \)) stronger than during external touch (23.3 ± 1.1 nAm) and 41.7 ± 4\% (\( P_{\text{corr}} = 0.001 \)) stronger than during self-touch, irrespective of the viewing condition.

Concurrent MI sources were present only in the self-touch condition and in the hemisphere opposite to the source of the tactile response. Their strengths were 4.6 ± 1.1 nAm in the eyes-open and 3.1 ± 1.0 nAm in the eyes-closed condition at the time of the SI peak, corresponding to an average 15\% and 25\% of the SI source strength, respectively. In the external touch + rotation condition, the movements were by no means related to the touch, and consequently, no M1 activation was detected in the averaged signals.

**Effect of Visual Stimulus Predictability**
To test whether visual cues that improved the predictability of the stimuli interacted with the SI responses, all conditions were replicated with the subjects’ eyes closed. We hypothesized that if visual cues contribute to the prediction of the sensory consequences of the stimulation as a relevant factor, responses would be even stronger to a touch that is not seen versus one that is seen. As stated above, the 2 × 3 ANOVA analysis of the peak amplitudes showed no significant main effect nor interaction as to whether the stimulus was seen or not. Although this approach prevents further statistical analysis, it seems noteworthy that at the descriptive level regarding the individual mean values of external touch and external touch + rotation conditions actually differed for the eyes-open (\( P = 0.04 \)) but not for the eyes-closed (\( P = 0.10 \)) condition (Fig. 5).

**Discussion**

**Self-Produced versus External Touch**
To assess the neural processes underlying the previously described reduction in perception as well as hemodynamic

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**Figure 4.** Source strengths as a function of time for the right SI source for each individual for external touch (solid lines) and self-touch (dashed lines). The bottom figure shows superimposed MI source waveforms for all 10 subjects.
attenuation at the cortical level would even be stronger than perceived them as equal. If this were the case, the effect of by hitting themselves "harder" than the experimenter to subject tried to compensate for the perceived attenuation to ensure identical stimulation in all subjects was unfortunately impossible in the current setup. If stimulus parameters were movement, as constant as possible. A more objective measure of stimulus parameters, that is, amplitude, frequency, and velocity of the experimenter inside the shielded room to keep the stimulation were perceived as weaker than external touch stimuli suggest to one's own touch as opposed to external touch (Blakemore et al. 1998, 2000; Bays et al. 2006), we recorded time-sensitive MEG responses to self-produced and external touch. The applied tactile device elicited clear and replicable cortical SEFs, as was previously demonstrated (Joussäväki et al. 2007). In agreement with previous findings on natural tactile stimulation in humans (Forss et al. 1994; Huttunen et al. 1999; Kakigi et al. 2000), the responses peaked at 54 ± 2 ms, with sources located in the right SI cortex contralateral to the touched left hand. Peak latencies and source locations did not differ between self-touch and external touch conditions, suggesting that up to this processing level in the SI cortex, both types of tactile stimuli activated similar neuronal structures.

In contrast, the maximum SI source strengths were reduced by approximately one-fifth to self-applied stimuli compared with stimuli produced externally (self-touch vs. external touch condition). This finding is well in line with previous behavioral studies showing reduced ticklishness to self-produced somatosensory stimuli compared with externally produced but otherwise comparable stimulation (Weiskrantz et al. 1971; Claxton 1975; Bays et al. 2006).

In the present study, subjects did not report any differences between perception of external or self-produced touches. We paid extra attention by continuous observation by the experimenter inside the shielded room to keep the stimulation parameters, that is, amplitude, frequency, and velocity of the movement, as constant as possible. A more objective measure to ensure identical stimulation in all subjects was unfortunately impossible in the current setup. If stimulus parameters were not identical, then previous accounts showing that self-touches were perceived as weaker than external touch stimuli suggest that subjects tried to compensate for the perceived attenuation by hitting themselves "harder" than the experimenter to perceive them as equal. If this were the case, the effect of attenuation at the cortical level would even be stronger than the results currently suggest.

Figure 5. Source strengths (mean ± SEM) for SI and MI sources for external touch, self-touch, and external touch + rotation, shown separately for the eyes-open and eyes-closed conditions. Statistical significances from post hoc t-tests are indicated by asterisks. Source strengths of the left MI source at the time of the SEF peak indicate only weak concurrent activity in the left motor cortex. Negative values correspond to opposite direction of the current.

Too little is known so far about the relationship between the responses of neurons in SI and the perceived intensity (Bensmaia 2008) to allow for any further conclusions on whether subjects should have noticed the attenuation demonstrated at the cortical level. A correlation between current intensity and SI responses was previously shown during electric stimulation (Joussäväki and Forss 1998; Torquati et al. 2002). Whether SI responses similarly correlate with intensity of touch stimulation and in particular with touch percept remains to be elucidated. In addition, attenuation may differentially affect those correlations depending on touch modality, that is, self- and external touch. Other somatosensory areas (e.g., SII, association cortex) are involved in the creation of the somatosensory percept, allowing for further modulation not captured by studying SEFs in SI. These aspects need to be addressed in future studies.

Somatosensory gating, referring to reduced cortical somatosensory responses when the hand receiving the stimuli is moved (Abbruzzese et al. 1981; Rushton et al. 1981; Kakigi et al. 1995; Schnitzler et al. 1995; Avikainen et al. 2002), cannot account for the observed attenuation because the movements were restricted to the right hand while the left hand was touched.

A previous imaging study showed decreased blood oxygen level–dependent signals in the SII cortex during self-produced touch (Blakemore et al. 1998). Consistent with Joussäväki et al. (2007), our signal patterns did not indicate systematic SII activity (in all except 1 subject). Due to the novel mode of tactile stimulation, we may currently only speculate on the cause thereof: according to previous findings (e.g., Hari et al. 1993), SII responses peaking 100–140 ms after median nerve stimuli are fully recovered only at interstimulus intervals of about 10 s. Detection of reliable SII signals might therefore have required longer interstimulus intervals than the 2–3 s applied. Alternatively, our tactile stimulus might activate the SII cortex less strongly than electric stimulation of the median nerve, to which, at 2–3 s intervals, SII responses are detectable in most subjects (e.g., Forss et al. 1994); why, however, SII activity was previously still found to short-ISI airpuff stimuli remains open. Consequently, we restricted our analysis to the rolandic regions using a 2-dipole model including SI and MI sources only.

Note that the attenuation described in the current study refers to the modulation of averaged responses to tactile stimuli, and thus, nothing can be said about possible changes in brain activity at time instants when no responses exceeded the noise level. Based on the evoked responses, we noted the earliest attenuation about 30 ms after application of the tactile stimuli. However, measurements of the whole time course of attenuation by means of MEG would require additional sensory stimuli applied at variable intervals before or after the skin contact; this issue remains to be investigated in future studies.

**Touch-Related versus Unrelated Movement**

The attenuation of cortical responses to self-produced sensations is likely to be an ecologically beneficial mechanism in everyday life: apart from allowing attributing a given sensory feedback to subject’s own actions, attenuation makes it possible to ignore expected, hence less relevant consequences of own actions and to enhance unanticipated, unintended consequences as well as unexpected, unrelated external events. This enhanced differentiation may help to detect errors that need to
be corrected, as well as external perturbations that necessitate a reaction.

Concurrent but touch-unrelated rotatory movements of the hand contralateral to the one being touched did not lead to an attenuation of the tactile responses although the rather demanding rotatory movements certainly distracted the subject’s attention from the stimuli. Instead, the responses increased statistically significantly: by over 10% compared with the external touch condition and by over 40% compared with the self-touch condition (irrespective of the factor viewing). Apparently, on top of the selective attenuation of sensory events related to one’s own actions, unrelated sensory events occurring concurrently can be even enhanced compared with their encounters at rest. This finding suggests that some form of “contrast enhancement” might be used to distinguish sensory signals related to own actions from concurrent, unrelated sensory events. Note that the absence of MI activity during external touch + rotation was expected because the signals were averaged with respect to tactile stimuli that were by no means time locked to the rotatory movements.

**Internal Forward Models and Effects of Action Observation**

Finally, the attenuation of SI responses to self-touch was independent of visual cues as the effect occurred similarly when the subject had the eyes open or closed. Because the stimuli were not accompanied by any auditory cues (Jousmäki et al. 2007), the attenuation most likely relies on efference copies related to motor commands. The theory of internal forward models proposes that motor commands are used to predict the sensory consequences of an action. When these predictions are congruent with the actual sensory consequences, the brain activity and the percept will be attenuated (Wolpert 1997; Wolpert et al. 1998; Blakemore et al. 1998, 1999). Generation of the efference copies of the movement plan likely involves the cerebellum (Miall et al. 1993; Wolpert 1997; Wolpert et al. 1998; Ito 2008). Previous behavioral results further substantiate predictive internal forward models rather than postdictive processes as the basis of attenuation: sensation of touch was attenuated—and only attenuated—when the subject expected contact between his moving and passive fingers (Bays et al. 2006). Even if the moving finger did not establish a contact, but an apparatus mediated a timed touch, attenuation of the sensation similarly took place. However, if the moving finger never contacted the passive finger, thus a direct contact was not expected and not predicted, a timed mechanical touch did not lead to attenuation. If, however, the moving finger never contacted the passive finger, a timed mechanical touch did not lead to attenuation. How sensory attenuation is implemented neurally and whether it takes place already at the earliest processing stages, for example, in the thalamus or in the spinal cord, remains to be further investigated.

Although the ANOVA showed no interaction between factors touch and viewing condition, at the descriptive level, the mean values of external touch and external touch + rotation conditions differed only when the eyes were open. One may thus speculate that visual cues contributed to attenuation in the external touch condition when the subject’s eyes were open: observing the experimenter performing the touch could have activated the subject’s mirror-neuron system (for review, see Rizzolatti and Craighero 2004). Previous studies suggest that during observation, we predict rather than follow the other person’s actions (Flanagan et al. 2003; Kilner et al. 2004; Caetano et al. 2007). Therefore, observation of the experimenter’s movement might allow the subjects to predict the movement parameters, possibly by employing the mirroring mechanisms and by using these parameters to predict the sensory consequences resulting in a partial dampening of SI responses. Such predictions, however, are likely to be less precise than those based upon active movements, and therefore, the attenuation of the SI responses is likely to be weaker. Performing a different movement during observation, however, might interfere with the mirror-neuron system and thus with any prediction based upon observation: Observing a different movement than what one is performing deteriorates the performance (Kilner et al. 2003). In reverse, performing an action during action observation might interfere with the mirroring and thereby impair prediction as well as signal attenuation. Further investigations, however, are needed to support this proposition.

In summary, using MEG, we showed that in healthy humans, somatosensory input is modulated at the level of the SI cortex depending on whether the stimuli are delivered by the subject or by the experimenter. In this setup, both the SI responses and the attenuation started at about 30 ms and peaked at about 50 ms after the touch. The attenuation was not related to the movements as such, and it also occurred without visual cues. The results provide further support for feed-forward models in which motor commands generate sensory expectations that are compared with the actual sensory feedback to allow for distinction between internal and external events, to facilitate detection of external stimuli, and to subserve error detection and learning.

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### Notes

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