# Dynamic organization of the somatosensory cortex induced by motor activity

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## Summary

**Intensive and long-lasting experience of altered sensory input induces permanent changes in the functional organization of the somatosensory cortex. In addition, an increasing body of evidence suggests the existence of dynamic, short-term and task-dependent adaptation of representational maps within somatosensory cortex. It is hypothesized that somatosensory maps can, not only, be acquired within a short period of time, but might also be set up during periods of training related to specific tasks and subsequently activated dynamically upon performance of that particular task. In order to test this hypothesis we studied the functional organization of somatosensory cortex for a heavily overlearned and frequently performed task for which no new acquisition of a sensory map had to be assumed. To this end, the functional organization of somatosensory cortex for handwriting was compared with the organization during rest in healthy humans. Functional organization of the somatosensory cortex was assessed using non-invasive, neuromagnetic source imaging based on tactile stimulation of the thumb (D1) and little finger (D5) during writing and rest. In different blocks, subjects wrote with their right, dominant and their left hand, respectively. During writing, D1 and D5 of the writing hand were stimulated. To test the reliability of our results all measurements were repeated after 1 week. It was found that amplitudes of somatosensory evoked magnetic fields with latencies of 45 ms were reduced during writing compared with rest. This finding is in accordance with the sensori-motor gating effect. Using source localization we could show that cortical representations of D1 and D5 are more distant during writing with either hand compared with rest. Our data suggest that somatosensory cortical maps undergo rapid modulation depending on task-specific involvement of sensory processing in daily-life overlearned movements. As it is unlikely that a new sensory map is always acquired when a frequently used task such as writing is performed, we suggest that somatosensory cortex switches between different, concurrently pre-existing maps depending on actual requirements. Task-dependent activation of pre-existing maps might be a powerful mechanism to optimize stimulus processing.**

**Keywords**: plasticity; somatosensory cortex; gating; skilled movement; magnetoencephalography

**Abbreviations**: MEG = magnetoencephalography; D1 = thumb; D5 = little finger

## Introduction

Numerous previous experiments studying plastic changes within somatosensory cortex have shown that the functional organization of primary somatosensory cortical areas is modulated by long-lasting experience of decreased sensory input, e.g. after deafferentation (Merzenich *et al*., 1984; Flor *et al*., 1995), or due to increased input experience such as massive tactile stimulation (Jenkins *et al*., 1990; Elbert *et al*., 1995; Kaas, 1995; Bunomano and Merzenich, 1998). In contrast to these rather long-lasting modifications, recent studies suggest that the functional organization of primary sensory and motor cortex may also change dynamically according to task requirements and context (Karni *et al*., 1995; Birbaumer *et al*., 1997; Moore *et al*., 1999). In a previous experiment by our group (Braun *et al*., 2000*a*), subjects were trained in a tactile discrimination task that involved simultaneous stimulation of thumb (D1) and little finger (D5) of one hand for 4 weeks, 1 h/day. After training, segregation of the primary somatosensory cortical representation of D1 and D5 occurred when stimulus discrimination was requested. In contrast, functional integration of the two finger representations emerged during passive stimulus perception that required no discrimination. We concluded

that different task-specific maps evolve during the training period, which may then be activated selectively and dynamically on demand.

We hypothesize that task-dependent modulation of the functional organization of somatosensory cortex represents a general principle of somatosensory cortex organization that is not only relevant for the acquisition of a novel task, but may also be active when previously learned specific tasks are performed. In particular, during the execution of skilled precision movements, task-dependent adaptation of the functional organization of the somatosensory cortex may occur. During movement execution, sensory input originating not only from touch but also from proprioception of joint positions, muscle tension and skin receptors activated by folding and stretching of the skin is processed in order to continuously control and adjust motor output.

Evidence for strong somatosensory and motor interaction is provided by studies investigating sensory-motor gating. In sensory gating, the activity of somatosensory cortex is reduced during the execution of a voluntary movement (Abbruzzese *et al.*, 1981; Jones *et al.*, 1989; Rossini *et al.*, 1999). However, it is unclear if the observed changes in amplitudes are associated with topographically specific modulations indicating a task-specific activation of cortical maps.

Impairments of movement-dependent adaptation of somatosensory cortex organization may play a role in pathological conditions such as focal dystonia. In focal dystonia, as in writer's cramp for example, dystonic movements occur in a task- and context-dependent manner; handwriting may be severely impaired in a patient with writer's cramp. However, the patient may be capable of writing normally when writing on a blackboard or even when changing the grip of the pen. In accordance with our hypotheses, recent studies indicate that somatosensory representations are altered in focal dystonia patients at least when studied at rest (Bara-Jimenez *et al.*, 1998; Elbert *et al.*, 1998). However, at this point, it is not well understood how exactly task-dependent changes are implemented in the nervous system.

In the present set of experiments, we sought to characterize the effects of motor action upon the organization of somatosensory cortex in normal subjects using handwriting as a model of high precision, well-trained movement. The functional topographic organization of somatosensory cortex was assessed both during writing and at rest by means of non-invasive neuromagnetic source imaging. Source localization revealed that the pattern of activation of somatosensory cortex changes during writing, suggesting that cortical maps are modulated rapidly according to the context and the specific requirements of a particular task.

## Methods

Twelve subjects, nine males and three females at ages ranging from 24 to 43 years (mean ± standard deviation, 28.8 ± 5.3 years) participated in the study after giving informed consent. The study was in accordance with the Declaration of Helsinki (1991) and was approved by the ethics committee of the medical faculty (Ethik-Kommission der Medizinischen Fakultät der Universität Tübingen). All subjects were healthy, showing no signs of neurological or psychological impairments. Subjects were right-handed as measured by the Edinburgh handedness scale (Oldfield, 1971).

During the experiments, subjects were lying on a bed inside a magnetic shielded room (Vakuumschmelze, Hanau, Germany) with their head placed in the mould of the Dewar of the 151-channel whole-head magnetoencephalography (MEG) system (CTF Inc., Vancouver, Canada). The subjects received tactile stimuli at the distal phalanges of D1 and D5 of either the left or right hand using a pneumatically driven stimulator. The stimulation device consisted of a membrane with a diameter of 10 mm that could be inflated towards the skin by a pulse of pressed air of 2 atm for 50 ms producing a distinct tactile sensation corresponding to a force of ~1.6 N. As stimulation devices were only 4 mm in height, they were easily taped to each of the four fingers in such a way that the subjects were able to hold and move a pen with almost no restrictions.

To test the reliability of the results, the experiment consisted of two identical sessions scheduled on two different days 1 week apart. During each session four blocks of stimulation were applied, with each block lasting for 10 min. Between consecutive blocks there was a break of 5 min. During individual experimental blocks, D1 and D5 of one hand were stimulated in random order, one finger at a time as source localization was based on magnetic brain responses evoked by individual fingers. Each finger received 500 stimuli resulting in 1000 stimuli for each experimental block. Stimuli were presented at interstimulus intervals ranging from 450 to 500 ms.

In one of the four blocks D1 and D5 of the left hand, and in another block both fingers of the right hand, were stimulated during rest condition during which subjects were told to relax their hand and finger muscles. In the remaining two blocks, the subjects had to write continuously a given sentence ('Das Kind spielt mit dem Ball') on a writing pad that was placed on the subjects' abdomen. In one block they had to write with their dominant right and in the other block with their left hand while D1 and D5 of the writing hand were stimulated (Fig. 1). Subjects wrote without visual feedback.

Subjects were instructed to keep their eyes open, to gaze at a fixation point and not to move their head. Furthermore, the fixation of the subjects' head was supported by small cushions placed in the gap between the head and the mould of the Dewar.

Somatosensory evoked magnetic fields were recorded using a whole head MEG system with 151 sensors. In all blocks, motor activity was recorded from finger flexors (M. flexor digitorum) and extensors (M. extensor digitorum) of the left and right arm by means of EMG. To control for eye-movement artefacts, vertical and horizontal electro-oculograms were recorded. MEG, EMG and electro-oculogram sweeps of 300 ms duration, including a pre-stimulus baseline of 50 ms,

Left hand          Right hand



**Fig. 1** Examples of handwriting of five subjects (each row corresponds to one subject) using the dominant right (*right*) and the non-dominant left hand (*left*) during tactile stimulation. Writing was performed without visual control.

were registered in response to each tactile stimulus. MEG and EMG activities were low-pass filtered at 208 Hz and digitized at a sampling rate of 625 Hz. While MEG was recorded in DC-mode, EMG responses were high-pass filtered at 16 Hz.

After discarding all trials with electro-oculogram-activity exceeding 70 V, somatosensory evoked magnetic fields of each of the two stimulation sites, i. e. D1 and D5, were averaged for the four experimental blocks (rest and writing × left and right hand) with the two sessions resulting in a total of 16 averages per subject. EMG-responses were scored by calculating the root mean square of the activity of the whole sampling epoch.

Cortical representations of the stimulated fingers were assessed by source modelling of the earliest prominent activity peak of the magnetic brain response in a time window ranging from 35 to 75 ms. In the dipole source analysis a spherical head model was used whose centre and radius were specified on the basis of a 3-dimensional headshape generated by a 3D-digitizer (Fastrack; Polhemus Inc., Colchester, Vt., USA). In all subjects a two dipole-model was used. One dipole modelled the activity contralateral to the stimulation, whereas the other dipole accounted for spurious activity. The second dipole was excluded from further analysis. Both dipoles together explained at least 90% of the variance of the magnetic field.

Changes in the functional organization of the somatosensory cortex were quantified using a distance measure between the equivalent dipole locations modelling the cortical representations of D1 and D5. Changes in cortex organization

affect either location of sensory representations or their extent or both. Using equivalent dipole models, representational shifts are expressed in changes of dipole source locations along the cortical surface. In contrast, increased cortical representations correspond to dipole positions that are located towards the centre of the head. If changes in Euclidean distances between two sensory representations are used to characterize functional reorganization, representational shifts cannot be distinguished from changes in source extension. Using polar coordinates, representational shifts along the somatosensory cortex are mainly expressed in modifications of polar angle theta ($\vartheta$), whereas changes in source extent are reflected by altered dipole eccentricity (r) (Braun *et al.*, 2000*a*) (see Fig. 2 for the definition of the polar coordinate system).

Changes in the cortical representation of the fingers along the postcentral gyrus were quantified by differences in polar angle $\Delta\vartheta$ between dipole locations corresponding to the stimulation of D1 and D5 of either the left or right hand. Changes in the cortical finger representation in anterior–posterior and radial direction were expressed by either azimuth differences ($\Delta\varphi$) or by differences in eccentricity ($\Delta$r) of the different dipole positions. Instead of analysing absolute dipole positions, distances between dipole positions corresponding to stimulation of D1 and D5 were investigated, because this measurement is more robust with respect to systematic localization errors. Changes in the amount of cortical activity due to different stimulation conditions were assessed by comparing the dipole moments corresponding to the stimulation of D1 and D5 of both hands under both conditions.

In order to verify whether the motor activity truly differed between the handwriting and resting conditions, EMG-parameters were analysed using a four-way ANOVA (analysis of variance) with the within-factors 'session' (levels: first and second), 'hand' (levels: left and right), 'condition' (levels: writing and rest) and the factor 'EMG-recording site' (levels: stimulated and unstimulated hand in the rest and writing condition, which, in the writing condition, is also the writing or non-writing hand, respectively).

In order to analyse the effects of writing on the amplitudes of the somatosensory magnetic responses, the global field activity

$$a_i = \sqrt{\frac{\sum_{k=1}^{n} b_{ik}^2}{n}}$$

was defined with $b_{ik}$ representing the magnetic activity of sample $i$ at sensor $k$, and $n$ being the total number of sensors. Two four-way ANOVAs with repeated measurements comprising the factors 'session', 'hand', 'condition' and 'finger' with the levels D1 and D5 were computed for the maximum of the global field activity and the dipole moment in the time window ranging from 35 to 75 ms relative to stimulus onset to test for statistical significance.
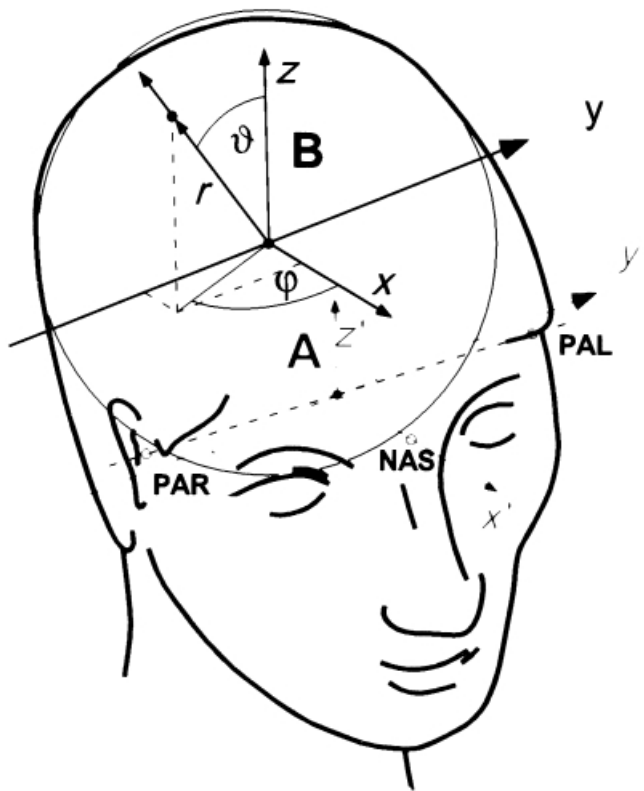
**Fig. 2** The location of the cortical representations of D1 and D5 was determined by dipole analysis. Polar coordinates were used to define distances between the locations. In a first step a coordinate system (A) with an origin between the left (PAL) and right pre-auricular points (PAR) was defined. The *x*-axis pointed towards the nasion (NAS). The *y*′-axis lying in the plane defined by PAR, PAL and NAS was orthogonal to the *x*′-axis pointing to the left hemisphere. The *z*′-axis was orthogonal to both the *x*′- and *y*′-axes. In a second step, a sphere was fitted to markers on the head surface that had been defined before by MRI-scans or 3D-digitization of the head. On the MRIs, markers were placed on the scalp all over the head whereby the central area was sampled more densely. The location parameters and their differences were defined in a second coordinate system (B) whose origin was set to the centre of the sphere and whose axes *x*, *y* and *z* were parallel to the axes *x*′, *y*′ and *z*′ of system (A). The cortical representations of individual fingers were described by the polar coordinates *r*, $\vartheta$, and $\varphi$ of the corresponding dipole position. (*r* = length of the location vector; $\varphi$ = angle between the z-axis and the location vector; $\varphi$ = angle between the *x*-axis and the projection of the location vector onto the *x*–*y* plane).

The statistical significance of differences of cortical D1–D5 distance across the stimulation conditions was analysed using an ANOVA with repeated measurement factors 'session' (levels: first and second session), 'hand' (levels: left and right hand) and 'condition' comprising the levels rest and writing.

## Results
### EMG
As expected, EMG activities were significantly larger [$F(1,11) = 57.68$, $P < 0.0001$] during writing (mean ± standard error $31.63 ± 3.12$ µV) compared with the resting condition ($4.21 ± 0.30$ µV). Furthermore, EMG activity in the writing hand was larger than the activity in the contralateral resting hand [$F(1,11) = 46.54$, $P < 0.0001$]. Significant interactions between 'condition' × 'EMG-recording site' [$F(1,11) = 61.17$, $P < 0.0001$] indicated that EMG at the stimulated hand was only increased during writing condition in which the stimulation was applied to the writing hand. All effects were more pronounced during the first session than during the second [$F(1,11) = 14.96$, $P = 0.0026$].

### Amplitudes of MEG-activity
The effects of writing on somatosensory evoked magnetic fields revealed a significant reduction of global field activity of the somatosensory evoked field during writing [$39.73 ± 1.23$ fT (femto-tesla)] compared with rest ($59.25 ± 2.26$) [$F(1,11) = 46.09$, $P < 0.0001$] (Fig. 3).

The reduction was more prominent for stimulation of D1 (37.7 %) than D5 (27.2 %) as indicated by significant interactions between 'condition' × 'finger' [$F(1,11) = 8.734$, $P = 0.013$].

A single equivalent dipole contralateral to the side of the tactile stimulation could be identified in all subjects. In accordance with the reduction of the magnetic global field activity during writing, a reduction in dipole moment was also observed [rest $30.56 ± 1.65$ nAm, writing $17.08 ± 0.73$ nAm, $F(1,11) = 28.61$, $P = 0.0002$]. As revealed by significant interactions between 'condition' × 'finger' [$F(1,11) = 11.67$, $P = 0.006$] and 'condition' × 'finger' × 'side' [$F(1,11) = 5.90$, $P = 0.034$] the strongest activities were evoked by stimulating the right thumb during the rest.

### Topographical changes of MEG-activity
A statistical test for representational changes revealed significant main effects for condition. Polar angle $\Delta\vartheta$ between the representation of D1 and D5, serving as a distance measure of the cortical hand representation, was larger during writing ($8.37 ± 0.55°$) compared with rest ($5.31 ± 0.61°$), irrespective of the side of writing [$F(1,11) = 8.113$, $P = 0.016$]. Additional contrast analysis revealed a stronger condition effect for left hand stimulation and movement ($F(1,11) = 21.40$, $P = 0.0007$) than for right hand ($F(1,11) = 5.549$, $P = 0.038$) (Figs 4 and 5).

The distance in anterior–posterior direction ($\Delta\varphi$) between the dipole location corresponding to D1 and D5 stimulation was larger during writing ($4.57 ± 1.10°$) than at rest ($0.92 ± 0.94°$), yet the difference was only significant at borderline [$F(1,11) = 4.95$, $P = 0.048$]. No significant differences in eccentricity ($\Delta r$) between the dipole sources of D1 and D5 were found. No significant differences between the two sessions were obtained for all dipole parameters.

## Discussion
Until now, it has been widely held that changes of the functional organization of the somatosensory cortex following
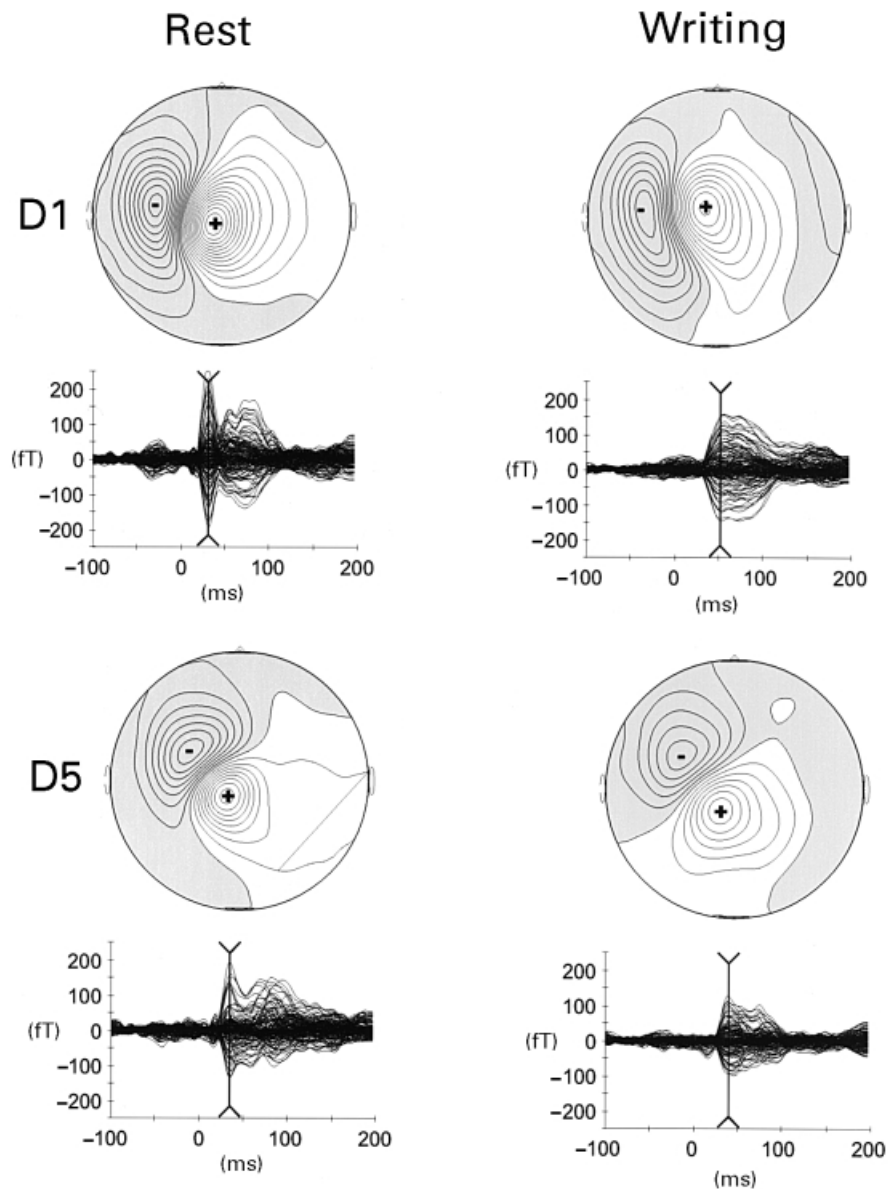
**Fig. 3** Waveforms and topographic maps of magnetic responses evoked by stimulation of D1 (*top*) and D5 (*bottom*) of the right hand during either rest (*left column*) or writing (*right column*). Waveforms of single MEG channels are superimposed. The time point to which the map corresponds in the wave plot is indicated by the vertical line. In the maps, shaded areas indicate negative polarity corresponding to in-going magnetic fields. Single subject results of one session are displayed.

long-term experience of altered stimulus input are rather static and require subsequent long-term training to undergo further modulation. However, a few studies suggest rapid task-specific dynamic changes of cortical organization of such pre-stabilized maps (Birbaumer *et al.*, 1997; Karni *et al.*, 1998; Moore *et al.*, 1999; Braun *et al.*, 2000a).

In most of the experiments that addressed short-term reorganization, stimuli and tasks previously not known to the subjects were applied. Therefore, it is not clear if the observed map changes are acquired gradually, similar to long-term reorganization but on a shorter time-scale, or whether, as opposed to long-term reorganization, the appearance of altered

maps is the consequence of switching between stable maps established earlier. The neural mechanism causing activation of different maps may be related to sub-threshold synaptic activity (Moor and Nelson, 1998; Fregnac and Shulz, 1999). If the assumption of rapid acquisition of new cortical representations were true, highly over-learned and frequently applied tasks should not cause any map changes, because the functional organization could have been adapted already over a long period of time. In contrast, if specific representational maps were activated by switching, each time a certain task is executed a similar map should appear. In order to discern between both alternatives, handwriting was
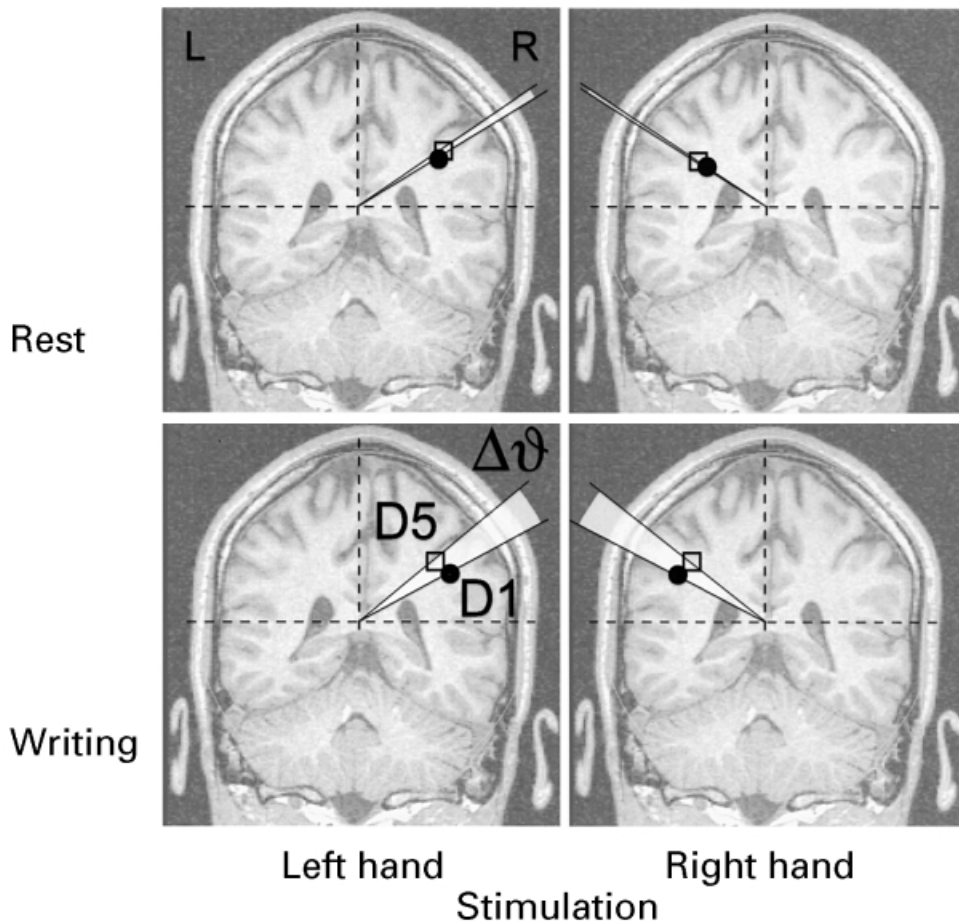
**Fig. 4** Source localization results for a single subject for the first session of the experiment. Stimulation of the left hand yielded right-hemispheric and stimulation of the right hand left-hemispheric activity. The distance between the representation of D1 (filled circles) and D5 (open squares) is marked for the resting (*top*) and writing condition (*bottom*). Differences between writing and rest are clearly visible in this particular subject, independent of the rather small distance between cortical representations of D1 and D5 during rest.
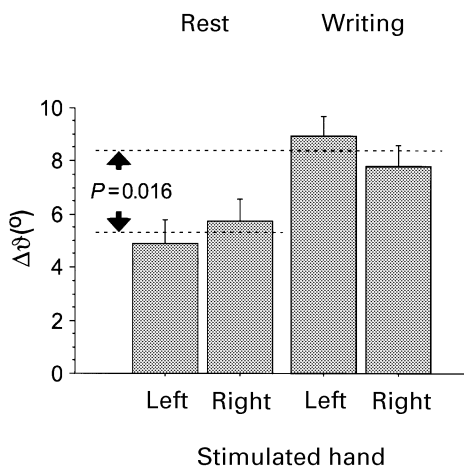


**Fig. 5** Group means and standard error for the cortical distance between the representation of D1 and D5 of the left and right hand during rest and writing averaged over both sessions. The cortical distance is expressed by polar angle difference. The level of significance of the difference between rest and writing is indicated by the error probability *P*.

chosen as a long-trained, frequently used task that was compared with rest.

As indicated by the differences in electromyographic activity, both writing and rest conditions appear to be well defined and clearly different with respect to motor action. Previous studies on the effects of motor activity on somatosensory cortex have focused exclusively on changes in the amplitudes of somatosensory cortex activity (Jones *et al.*, 1989; Rossini *et al.*, 1999). The majority of these studies coincide in that motor action reduces the amplitudes of evoked somatosensory responses within latencies of up to 100 ms (Abbruzzese, 1981; Kakigi *et al.*, 1997). In an MEG study by Hoshiyama and Kakigi, handwriting caused a reduction in amplitude of somatosensory evoked potentials following median nerve stimulation for the components P25, N30 and N33 (Hoshiyama and Kakigi, 1999). It was concluded from these experiments that motor activity exerts a gating effect upon the processing of somatosensory input. Our experiment confirms these earlier findings as both the global field activity and the dipole moment of the somatosensory evoked responses around 50 ms following

finger stimulation were reduced when writing. The consistency of our results with previous studies concerning sensorimotor gating provides a necessary basis for the interpretation of topographic changes of somatosensory evoked fields.

Somatosensory evoked magnetic responses up to 60 ms are generated in the primary somatosensory area mainly in area 3b (Mauguière *et al.*, 1997). As a first order approximation, locations of dipole sources derived from magnetic field topography model the centre of the cortical representation of the stimulated body part (Scherg, 1990). Since dipole sources are assumed to represent point-like cortical activity, it has to be taken into account that the equivalent dipole of an extended representational area might be located deeper in the brain, inferior to the cortical surface. The precision with which neural generators can be located depends on the signal-to-noise ratio of the evoked activity and on the localization of the source inside the brain. Signal-to-noise ratios of >6.7 as in our study and superfical sources, e.g. short latency somatosensory evoked magnetic responses, yield a resolution in the range of 1–2 mm (Hari *et al.*, 1988). Decreased signal-to-noise ratio, as introduced by reduced somatosensory evoked field amplitudes during handwriting, leads to increased confidence volumes of individual dipole localizations (Braun *et al.*, 1997) and thus to increased errors in dipole distance that are accounted for by statistical analysis.

Dipole location accuracy is also affected by systematic localization errors that might be introduced by head movements during data acquisition, by wrongly specified head-models or by errors in coregistration of anatomical images. Therefore, changes in functional organization of somatosensory cortex were assessed by calculating the distance changes between representations of D1 and D5. Since both fingers were stimulated within the same block, both dipole sources were similarly affected by this type of errors. Calculating the difference between dipole coordinates eliminates the impact of systematic errors and hence improves data quality.

In our study, source localizations resulting from the evoked activity following stimulation of D1 and D5 revealed an average polar angle difference of 5.31° corresponding to 8.63 ± 0.5 mm Euclidean distance between the representation of both fingers in the rest condition. This distance is somewhat smaller than distances reported in the literature, 12.8 ± 2.9 (Biermann *et al.*, 1998) and 12.5 ± 2.8 (Nakamura *et al.*, 1998). Possibly, stimulation of both fingers in a randomized series within one block, in contrast to stimulation of D1 or D5 in separate blocks, might be the reason for a reduced distance between the representations of D1 and D5 (Braun *et al.*, 2000*b*). Furthermore, our results indicate that the distance between the centres of cortical activation of the two fingers grew larger when writing, and immediately became smaller when resting. Due to the curvature of the postcentral gyrus, larger distances between the representations of D1 and D5 during writing are indicated both by changes in polar angles ($\Delta\vartheta$) and azimuth differences ($\Delta\varphi$). As motor action

during writing is performed constantly and is not temporally related to the tactile stimulation, the observed changes cannot be attributed to additional activities in motor cortex during the movement condition. Instead, from our results one may conclude that writing causes segregated representations for D1 and D5 with less overlap compared with rest. Taking the results of an earlier study (Braun *et al.*, 2000*a*) into account, where the increased distance between the cortical representations of D1 and D5 was associated with improved stimulus discrimination, one may also speculate that during execution of fine motor tasks such as handwriting, inputs from various sources have to be processed separately by minimizing any cross-talk between the different representational sites.

From our data, we cannot distinguish whether changes in the functional organization of somatosensory cortex during movements represent the consequence (i) of altered reafferent input from joints, muscles and skin during the execution of the motor task, (ii) of a supervising effect of motor and premotor areas upon the organization of somatosensory cortex, or (iii) of descending fibres changing the connectivity, and hence the functional organization, of the somatosensory cortex. However, our findings indicate that the functional organization of somatosensory cortex dynamically adapts to the requirements of a given task. Since handwriting is a task that has been trained for several years, it is unlikely that a new sensory map is always acquired whenever a frequently used task such as writing is performed. Instead, we suggest that somatosensory cortex switches between different, concurrently pre-existing maps depending on actual requirements. The replication of our results 1 week later is also in favour of this interpretation, as no significant adaptation to the writing task could be observed.

The source localization results for the non-dominant left hand were similar to the results for the right hand. Whether differences between writing and rest of left finger representations are also due to switching of representational maps remains unclear, as subjects had not experienced any specific training in left hand writing. However, evidence exists that motor sequence learning is at least partially effector independent (Bapi *et al.*, 2000).

From our results, it may be speculated that dynamic switching of somatosensory maps does not exclusively occur during writing, but may accompany other types of movements that are trained as intensively as handwriting. In contrast, it is expected that complicated motor sequences that are learned from the beginning require gradual development of new sensory maps.

Equivalent task-specific activations of different cortical maps within a certain representational zone have also been found in the motor cortex. Performing different finger movements, movement-specific representational changes are found in primary motor cortex (Karni *et al.*, 1995, 1998). Attentional changes in the functional organization of the somatosensory cortex reported by Noppeney and colleagues might also fit into the concept of task-specific cortical maps

(Noppeney *et al.*, 1999). From the results of these studies, and from our own results, it can be concluded that task-specific activation of cortical connectivity patterns might represent a general principle of how the cortical networks support optimal performance.

## Acknowledgements

### References

Abbruzzese G, Ratto S, Favale E, Abbruzzese M. Proprioceptive modulation of somatosensory evoked potentials during active or passive finger movements in man. J Neurol Neurosurg Psychiatry 1981; 44: 942–9.

Bapi RS, Doya K, Harner AM. Evidence for effector independent and dependent representations and their differential time course of acquisition during motor sequence learning. Exp Brain Res 2000; 132: 149–62.

Bara-Jimenez W, Catalan MJ, Hallett M, Gerloff C. Abnormal somatosensory homunculus in dystonia of the hand. Ann Neurol 1998; 44: 828–31.

Biermann K, Schmitz F, Witte OW, Konczak J, Freund HJ, Schnitzler A. Interaction of finger representation in the human first somatosensory cortex: a neuromagnetic study. Neurosci Lett 1998; 251: 13–16.

Birbaumer N, Lutzenberger W, Montoya P, Larbig W, Unertl K, Töpfner S, et al. Effects of regional anesthesia on phantom limb pain are mirrored in changes in cortical reorganization. J Neurosci 1997; 17: 5503–8.

Braun C, Kaiser S, Kincses WE, Elbert T. Confidence interval of single dipole locations based on EEG data. Brain Topogr 1997; 10: 31–9.

Braun C, Schweizer R, Elbert T, Birbaumer N, Taub E. Differential activation in somatosensory cortex for different discrimination tasks. J Neurosci 2000a; 20: 446–50.

Braun C, Wilms A, Schweizer R, Godde B, Preissl H, Birbaumer N. Activity patterns of human somatosensory cortex adapt dynamically to stimulus properties. Neuroreport 2000b; 11: 2977–80.

Buonomano DV, Merzenich MM. Cortical plasticity: from synapses to maps. [Review]. Annu Rev Neurosci 1998; 21: 149–86.

Elbert T, Pantev C, Wienbruch C, Rockstroh B, Taub E. Increased cortical representation of the fingers of the left hand in string players. Science 1995; 270: 305–7.

Elbert T, Candia V, Altenmuller E, Rau H, Sterr A, Rockstroh B, et al. Alteration of digital representations in somatosensory cortex in focal hand dystonia. Neuroreport 1998; 9: 3571–5.

Flor H, Elbert T, Knecht S, Wienbruch C, Pantev C, Birbaumer N, et al. Phantom-limb pain as a perceptual correlate of cortical reorganization following arm amputation. Nature 1995; 375: 482–4.

Fregnac Y, Shulz DE. Activity-dependent regulation of receptive field properties of cat area 17 by supervised Hebbian learning. J Neurobiol 1999; 41: 69–82.

Hari R, Joutsiniemi SL, Sarvas J. Spatial resolution of neuromagnetic records: theoretical calculations in a spherical model. Electroencephalogr Clin Neurophysiol 1988; 71: 64–72.

Hoshiyama M, Kakigi R. Changes of somatosensory evoked potentials during writing with the dominant and non-dominant hands. Brain Res 1999; 833: 10–19.

International Committee of Medical Journal Editors. Statements from the Vancouver Group. BMJ 1991; 302: 1194.

Jenkins WM, Merzenich MM, Ochs MT, Allard T, Guic-Robles E. Functional reorganization of primary somatosensory cortex in adult owl monkeys after behaviorally controlled tactile stimulation. J Neurophysiol 1990; 63: 82–104.

Jones SJ, Halonen JP, Shawkat F. Centrifugal and centripetal mechanisms involved in the 'gating' of cortical SEPs during movement. Electroencephalogr Clin Neurophysiol 1989; 74: 36–45.

Kaas JH. The reorganization of sensory and motor maps in adult mammals. In: Gazzaniga MS, editor. The cognitive neurosciences. Cambridge (MA): MIT Press; 1995. p. 51–71.

Kakigi R, Shimojo M, Hoshiyama M, Koyama S, Watanabe S, Naka D. Effects of movement and movement imagery on somatosensory evoked magnetic fields following posterior tibial nerve stimulation. Brain Res Cogn Brain Res 1997; 5: 241–53.

Karni A, Meyer G, Jezzard P, Adams MM, Turner R, Ungerleider LG. Functional MRI evidence for adult motor cortex plasticity during motor skill learning. Nature 1995; 377: 155–8.

Karni A, Meyer G, Rey-Hipolito C, Jezzard P, Adams MM, Turner R, et al. The acquisition of skilled motor performance: fast and slow experience-driven changes in primary motor cortex. [Review]. Proc Natl Acad Sci USA 1998; 95: 861–8.

Mauguière F, Merlet I, Forss N, Vanni S, Jousmaki V, Adeleine P, et al. Activation of a distributed somatosensory cortical network in the human brain. A dipole modelling study of magnetic fields evoked by median nerve stimulation. Part I: location and activation timing of SEF sources. Electroencephalogr Clin Neurophysiol 1997; 104: 281–9.

Merzenich MM, Nelson RJ, Stryker MP, Cynader MS, Schoppmann A, Zook JM. Somatosensory cortical map changes following digit amputation in adult monkeys. J Comp Neurol 1984; 224: 591–605.

Moore CI, Nelson SB. Spatio-temporal subthreshold receptive fields in the vibrissa representation of rat primary somatosensory cortex. J Neurophysiol 1998; 80: 2882–92.

Moore CI, Nelson SB, Sur M. Dynamics of neuronal processing in rat somatosensory cortex. [Review]. Trends Neurosci 1999; 22: 513–20.

Nakamura A, Yamada T, Goto A, Kato T, Ito K, Abe Y, et al. Somatosensory homunculus as drawn by MEG. Neuroimage 1998; 7: 377–86.

Noppeney U, Waberski TD, Gobbelé R, Buchner H. Spatial attention modulates the cortical somatosensory representation of the digits in humans. Neuroreport 1999; 10: 3137–41.

Oldfield RC. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 1971; 9: 97–113.

Rossini PM, Babiloni C, Babiloni F, Ambrosini A, Onorati P, Carducci F, et al. 'Gating' of human short-latency somatosensory evoked cortical responses during execution of movement. A high resolution electroencephalography study. Brain Res 1999; 843: 161–70.

Scherg M. Fundamentals of dipole source potential analysis. In: Grandori F, Hoke M, Romani GL, editors. Auditory evoked magnetic fields and electric potentials. Basel: Karger; 1990. p. 40–69.