

## Cortical asymmetries of the human somatosensory hand representation in right- and left-handers

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### Abstract

Hemispheric asymmetry is known for higher brain functions like language and attention. We tested whether such an asymmetry also exists in the representation of elementary sensory functions. Magnetic source imaging was used to compare the cortical somatosensory hand representation in seven right- and five left-handed individuals. In all right-handers the representation of the dominant hand was larger than the contralateral one in the corresponding hemispheres. In contrast, only two out of five left-handers revealed a larger representation of the dominant left hand compared to the right one. In agreement with previous findings on the lateralization of language and attention, there is a strong correlation between handedness and the extent of the cortical hand representation in right-, but not in left-handers. We conclude that a profound functional hemispheric asymmetry also exists in primary sensory cortices. © 1999 Elsevier Science Ireland Ltd. All rights reserved.

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Asymmetries of the cortical organization have been demonstrated in several higher brain functions like language and attention [17]. For example, lesions of the left frontal or temporal cortex can cause aphasia while disorders of the right parietal cortex can cause neglect.

It remains unclear, however, whether an asymmetrical organization can be found in primary sensory cortices as well. A previous study showed hemispherical differences in the amplitudes of somatosensory evoked potentials in right-handed individuals with a higher amplitude in the dominant hemisphere [3]. However, because of methodological limitations, this study did not allow to identify the mechanism underlying this difference.

In the present study we tested the hypothesis that the primary somatosensory cortex (S1) is asymmetrical and that this asymmetry is correlated to the individual's hand dominance. We used magnetic source imaging (MSI) to assess the somatosensory hand representation of right- and left-handed volunteers. MSI is a reliable and valid method

for noninvasive mapping of the human brain with a spatial resolution high enough to demonstrate the somatotopic organization of the somatosensory homunculus [6,14].

MSI was performed in 12 healthy volunteers aged 26–30 years. Seven subjects (four male, three female) were right handed with handedness scores between 25 and 91 as indicated by the Edinburgh Handedness Inventory [15]. Five subjects (three male, two female) were left-handed with handedness scores between –23 and –100. Two of the left-handed individuals had left-handed first-degree relatives, while in two no familial sinistrality was known. In one left-handed subject this information was not available.

Cortical magnetic fields were detected using a 37-channel biomagnetic system equipped with first-order axial gradiometers (Magnes I, Bti, San Diego, CA). The dewar covers a circular concave area of 14.4 cm in diameter, and it was positioned over C3 or C4 contralateral to the stimulated hand. The surface of the dewar was moved to the skull as close as possible to account for individual head geometry and to maximize the detectable magnetic signal. After a short initial test measurement the dewar was repositioned if needed to focus the phase reversal of the magnetic waveforms in the center of the sensor array. All measurements

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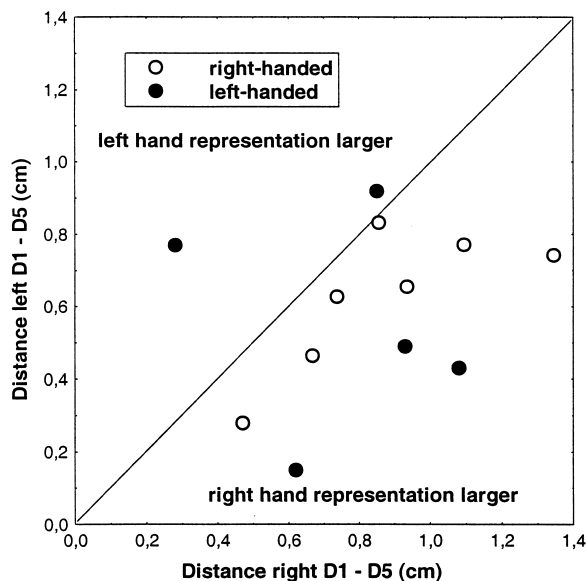


Fig. 1. Euclidean distances between the cortical representations of the thumb (D1) and the little finger (D5) of the right and left hand in seven right-handers (open circles) and in five left-handers (filled circles). Localizations were obtained by recordings of somatosensory evoked magnetic fields. Light superficial pressure was used as stimulus on the tip of each finger (average of 1000 stimuli, interstimulus interval  $500 \pm 50$  ms). The oblique line divides individuals with a larger representation of the right hand (all seven right-handers and three left-handers) and a larger representation of the left hand (two left-handers).

were recorded in a magnetically shielded room (Vacuumschmelze, Hanau, Germany).

The first and the fifth finger of both hands were stimulated successively by light superficial pressure via a pneumatic stimulator (1000 stimuli, interstimulus interval  $500 \pm 50$  ms). Since the pneumatic stimulus used for this study selectively activates cutaneous mechanoreceptors, only sensory fibers projecting into area 3b are innervated [14]. All data was corrected for the delay of 40 ms between stimulus onset and peak tactile pressure.

Magnetoencephalographic recordings were sampled at a rate of 520.8 Hz, digitally filtered using a high-pass filter of 0.1 Hz and a band-pass filter of 1–20 Hz, baseline corrected and averaged. Epochs containing an amplitude of more than 2 pT in any of the 37 channels were rejected as artifacts before averaging.

To localize the neuronal sources of the magnetic field distribution, the model of a single equivalent current dipole in a spherical volume conductor was applied [7]. The dipole with the best goodness of fit during the 20 ms before the peak latency of the M1 component, defined as the maximal root mean square of amplitudes, was selected. The latency of the M1 peak varied between 40.3 and 67.2 ms, corresponding to the N20 component after electrical median nerve stimulation. The selected dipole was characterized by its location in 3D space, its orientation and its dipole moment  $Q$ . The Euclidean distance between the dipoles obtained for the first and the fifth finger served as a measure for the size of the cortical hand representation. A laterality index was calculated for the hand representations:  $((r - l) / (r + l)) \times 100$ ;  $r$  denotes distance between the right D1 and D5,  $l$  denotes distance between the left D1 and D5. To assess statistical significance the Wilcoxon test was employed and Spearman correlation coefficients were calculated.  $P$ -values  $< 0.05$  were regarded as indicating statistical significance. Data is presented as mean  $\pm$  SEM.

In all seven right-handers included in this study, the cortical representation of the right hand was larger than the one of the left hand ( $0.87 \pm 0.11$  vs.  $0.62 \pm 0.07$  cm;  $P = 0.018$ ). In three left-handers, the right hand, and in two left-handers, the left hand had a more extended cortical representation. For individual data see Fig. 1.

No significant correlation was seen between the laterality index and the handedness quotient according to Oldfield, neither in right- nor in left-handers. One left-handed female with familial sinistrality had a larger representation of the right than of the left hand (1.08 vs. 0.43 cm, laterality index +43). In one left-handed male, also with familial sinistrality, the representation of the left hand was larger than that of the right hand (0.77 vs. 0.28 cm, laterality index -47).

No significant correlation was seen between the dipole moment of single fingers, representing the number of the cortical neurons active during stimulation [12], and the extension of the cortical hand representation. All five left-handers had a larger dipole moment of the left than of the right little finger. The dipole moments of D1 in left-handers, as well as of D1 and D5 in right-handers, were not related to the degree of handedness. No significant difference was seen between the dipole moments of D1 and D5 in any of the groups (Table 1).

Buchner et al. [3] recorded somatosensory evoked poten-

Table 1  
Dipole moment  $Q$  of the thumb and the little finger in right- and left-handers<sup>a</sup>

	Right-handers ( $n = 7$ ) Dipole moment (nAm)	Left-handers ( $n = 5$ ) Dipole moment (nAm)
Right thumb	$7.4 \pm 0.8$	$8.3 \pm 1.3$
Right small finger	$6.9 \pm 0.4$	$7.3 \pm 0.5$
Left thumb	$8.9 \pm 2.0$	$8.2 \pm 1.1$
Left small finger	$7.5 \pm 0.8$	$9.2 \pm 1.2$

<sup>a</sup> Recording of somatosensory evoked magnetic fields (light superficial pressure, 1000 stimuli, interstimulus interval  $500 \pm 50$  ms).

tials after electrical stimulation of the right and left median nerve in right-handers. The authors found higher amplitudes of the N20 component after right-sided than after left-sided stimulation, but they could not identify the underlying functional differences in S1. These findings are, nevertheless, in line with our results. The electrical stimulation of the median nerve activates afferent fibers from the first to the third finger and from the thenar, resulting in a widespread activation of S1. Assuming that higher amplitudes in somatosensory evoked potentials correspond to a larger cortical representation, a larger N20 component after median nerve stimulation reflects a larger hand representation.

In contrast to somatosensory evoked potentials after median nerve stimulation, our method can localize the cortical representation of single fingers and assess the number of neurons corresponding to their representation. The number of cortical neurons representing a single finger corresponds to the magnetic dipole moment [12]. Our results do not show differences between the dipole moments of the dominant and the non-dominant hand, neither in right- nor in left-handers (Table 1). Based on the estimates by Lü and Williamson [12], the mean dipole moment of one finger found in our volunteers represents an activated cortical area of approximately 80 mm<sup>2</sup>, corresponding to a circle of 5 mm radius. Given the mean extent of the hand representation in our data (6–9 mm, Fig. 1), which is well comparable with previous reports [8,13,14,18], these calculations demonstrate a substantial overlap of cortical neurons activated by the stimulation of single fingers. A similar overlap of afferent input was seen in the somatosensory cortex of monkeys after electrical stimulation of the median, ulnar, and radial nerves [16] and in the somatosensory cortex of humans after pneumatic stimulation of fingers [2].

While MSI measurements failed to show a somatotopic representation of hand and finger movements in the primary motor cortex [19], a somatotopic organization of the primary somatosensory cortex was clearly demonstrated [8,14]. Thus, the distances between D1 and D5, as used in this study, are reasonable estimators of the extent of the somatosensory hand representation.

Previous studies on the motor system have revealed functional [10] and anatomical [1] asymmetries and a correlation between handedness and the extent of the cortical hand motor representation [1,19]. Magnetic resonance morphometry demonstrated that the left central sulcus, serving as a marker for the size of the hand motor representation, is deeper than the right one in right-handers, and vice-versa in left-handers [1]. These results were confirmed by Volkman et al. [19] who used MSI to show larger cortical representations of hand and finger movements of the dominant vs. the non-dominant hand, both in right- and left-handers.

While we found a close correlation between hand preference and cortical somatosensory representation in right handers, no association was seen in left-handers. Morphometrical and cytoarchitectonical measurements did not

demonstrate a lateral asymmetry of the somatosensory system, including S1 [20]. Thus, our results on the larger cortical representation of the preferred hand in right-handers indicate that functional, e.g. synaptic, rather than gross morphological differences influence the neuronal organization within S1. This interpretation is supported by recent studies demonstrating the reorganization of the somatosensory system after both, upper limb amputation [5,11] and increased practice of single fingers [4].

The data obtained in this study do not provide a clear explanation for the larger individual differences in left-compared to right-handers, since familial sinistrality does not seem to influence the cortical hand representation. Left-handers have a less pronounced functional [9] and anatomical asymmetry [17] in the language system. Our results suggest that sinistrals in general might be characterized by a less determined cerebral asymmetry, allowing a greater variability of individual hemispheric specialization. Future research has to clarify to what extent genetic and developmental factors account for the individual asymmetries of the primary somatosensory cortex seen in this investigation.

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