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Asymmetry in the Human Motor Cortex and Handedness

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Handedness is one of the most obvious functional asymmetries, but its relation to an anatomical asymmetry of the hand representation area in the motor cortex has not been demonstrated. This would be a crucial test for the hypothesis of structure–function correlation in cortical motor organization. Using magnetic resonance morphometry, we show for the first time that the depth of the central sulcus is related to handedness. In right-handers, the left central sulcus is deeper than the right, and vice versa in left-handers. Macrostructural asymmetry is complemented by a microstructural left-larger-than-right asymmetry in neuropil volume (i.e., tissue compartment containing dendrites, axons, and synapses) in Brodmann's area 4. These asymmetries suggest that hand preference is associated with increased connectivity (demonstrated by an increased neuropil compartment in left area 4) and an increased intrasulcal surface of the precentral gyrus in the dominant hemisphere.

INTRODUCTION

Since the demonstration of lateralized language functions by Broca (1864) and Wernicke (1874) many attempts have been made to relate functional differences with structural asymmetries between the hemispheres (e.g., von Economo and Horn, 1930; Geschwind and Levitzky, 1968; Witelson and Kigar, 1992). *In vivo* morphometry revealed a correlation between the anatomical asymmetry in the planum temporale and planum parietale (the cortex covering the posterior wall of the posterior ascending Sylvian ramus) and hand dominance (Steinmetz *et al.*, 1991; Jäncke *et al.*, 1994). The correlation of handedness with structural asymmetries between the left and the right cortical motor areas has not been proven. Contradictory anatomical observations in the sensorimotor cortex of human brains of unknown handedness were recently published: White *et al.* (1994) provided evidence of left–right differences by measuring the depths of the central sulcus (CS) in a region that controls the movement of the upper extremity. The depth of the CS was interpreted to be an indicator for the size of the primary motor cortex, i.e., of Brodmann's area 4 (Brodmann, 1909). In contrast to this first publication, the same group reported in a following abstract that measurements of the central sulcus provided little evidence for structural asymmetry in the depth of CS (White *et al.*, 1995).

The aim of the present study was to reexamine the hypothesis that there is a structural difference in the motor cortex between the left and the right hemisphere. Interhemispheric differences were analyzed in a population of tested right- and left-handers by using high-resolution, *in vivo* magnetic resonance (MR) morphometry. This investigation was supplemented by an analysis of cytoarchitectonic differences between the left and the right area 4 in histological sections of postmortem brains.

SUBJECTS AND METHODS

Subjects

In vivo MR morphometry was performed on 31 male right-handers and 14 male left-handers (Table 1). Only male subjects were analyzed in order to exclude possible gender influences on brain asymmetry and handedness (Geschwind and Galaburda, 1985a,b; Jäncke *et al.*, 1994; Kertesz *et al.*, 1990; Witelson and Kigar, 1992). All subjects were without neurological or psychiatric diseases. Most of them were medical students or young faculty members in university hospitals. All subjects gave informed consent.

Handedness classification was performed by using criteria suggested by previous studies (Witelson, 1989; Steinmetz *et al.*, 1992; Jäncke, 1996). Asymmetry in hand performance was measured and defined for the MR part of this study with the Hand Dominance Test (HDT) (Steinmetz *et al.*, 1991; Steingrüber, 1971). This test divided subjects into two groups: left- and right-

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TABLE 1

Age and HDT Scores of the Subjects Included in the Observations with MR Morphometry

	n	Age range (years)	Mean age (years)	HDT range	Mean HDT
Right-handers	31	19 to 33	26.4	0.05 to 0.25	0.133
Left-handers	14	20 to 29	23.3	−0.01 to −0.21	−0.122

handers (Fig. 1, Table 1). HDT is a paper-and-pencil test which consists of three dexterity tasks (tracing lines, dotting circles, tapping on squares), each to be performed with maximal speed and precision over 15 s. Laterality coefficients were calculated according to (R − L)/(R + L) for each subtest (tracing, dotting, tapping). The total score of this test was calculated by averaging the scores of the three subtests. Negative values indicated left-handedness, and positive values, right-handedness. The total score as well as the subtest asymmetry coefficients are significantly correlated to results of other tests of asymmetric hand performance, as, for instance, tapping tests and target tests for speed and accuracy (Jäncke, 1996). A comparison of the HDT scores of the subjects in the present analysis with the results of the hand preference test (Annett, 1970) shows that all subjects with HDT scores smaller than 0 are left-handers according to Annett. All subjects with a HDT greater than 0 constitute the group of right-handers in the Annett test.

Handedness of the subjects included in the postmortem study was not determined. Considering an incidence of left-handedness of 10% in the general population (Annett, 1973), we assume that probably not more than 1 to 2 (of 12) subjects were left-handers.

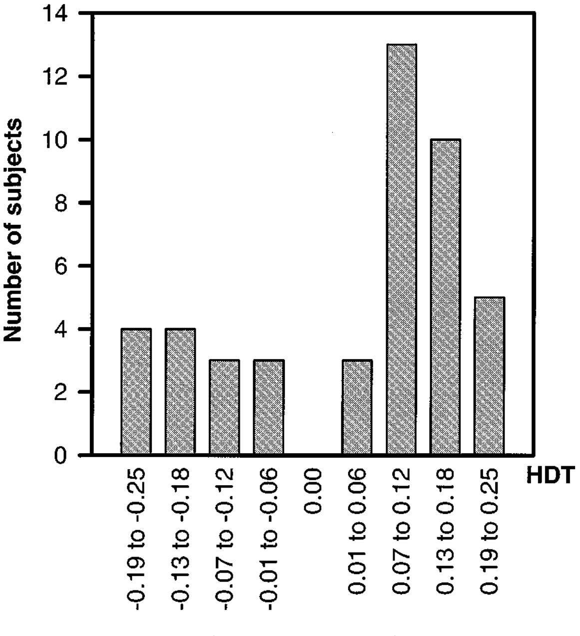

FIG. 1. Distribution of HDT scores in left-handers ($n = 14$) and right-handers ($n = 31$). All left-handers had HDT scores lower than 0, all right-handers—greater than 0.

MR Imaging

A Siemens 1.5 T magnet and a 22-min fast low-angle shot magnetic resonance sequence (3-D Flash) covering the entire brain, and yielding 1.00 × 1.00 × 1.17-mm image voxel size, were used. Each dataset consisted of 128 contiguous, 1.17-mm-thick sagittal slices. Parts of the image not corresponding to telencephalic gray or white matter were removed by an interactively controlled segmentation procedure. Total brain volumes were determined by counting all voxels within the segmented images (resolution 1.0 × 1.0 × 1.17 mm).

The brains were 3-D reconstructed from the MR sequences and were spatially aligned in the standard anatomical format of the computerized human brain atlas (Roland and Zilles, 1994). This procedure includes normalization of all brains to the same volume and, thus, excludes blurring of left–right differences by intersubject variability in absolute brain size. The images of the brains were spatially oriented according to the Talairach system (Talairach and Tournoux, 1988). Horizontal sections were parallel to the anterior–posterior commissure plane. For morphometry, all datasets were coded and images of hemispheres randomly mirrored, so that neither subject nor side of hemisphere under investigation could be identified by the observer during measurements. Measurements of the depth of the CS on the horizontal sections were performed interactively on a digitizer. Intraobserver reliability (Bartko and Carpenter, 1976) was calculated using a subset of 15 brains. The intraobserver correlation was $R = 0.95$ ($P < 0.0001$).

The intrasulcal length of the posterior contour of the precentral gyrus (= depth of CS) was measured as an indicator of the size of the primary motor cortex (White *et al.,* 1994) in the hand representation area in 35 horizontal sections (Fig. 2). The sections extended from Talairach coordinates $z = 69$ to 35. In selecting this region, we relied on data from positron emission tomography (Colebatch *et al.,* 1991; Grafton *et al.,* 1991; Kawashima *et al.,* 1994) and MR imaging (Karni *et al.,* 1995; Kim *et al.,* 1993; Sanes *et al.,* 1995). In some of the latter reports, changes in activity in the primary motor cortex in response to single digit movements were found to span up to 40 mm in dorsoventral direction. These findings are the basis of demarcation used for MR morphometry of CS.

Asymmetry coefficients (AC, in %) were calculated as differences between the depths of left (L) and right (R) CS according to 100 × (L − R)/[(L + R)/2] for each section of each dorsoventral sequence. Thus, an AC curve for each brain was defined (Fig. 3). We then

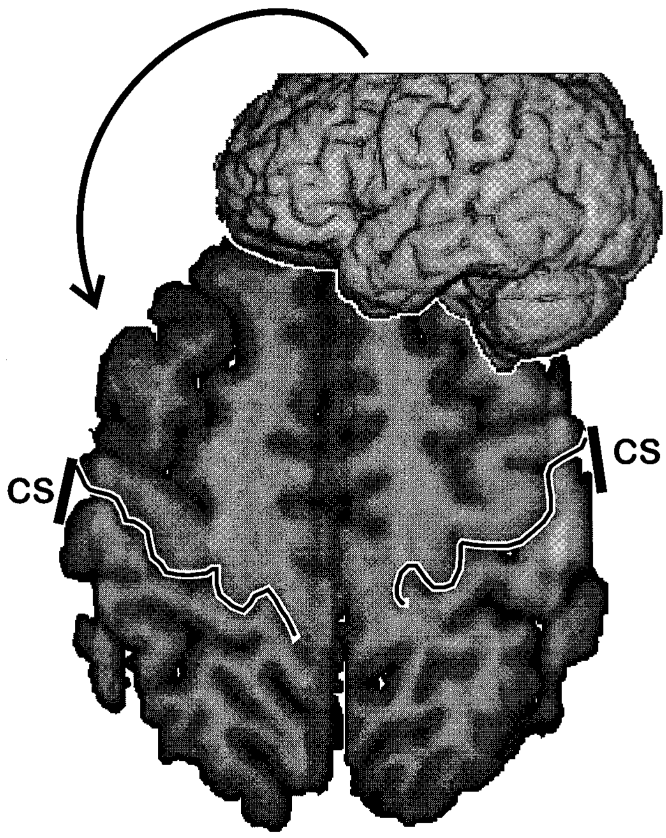

FIG. 2. Horizontal section with prominent central sulci (CS). At upper right, lateral view of a 3-D reconstructed brain showing the position of this section. In each horizontal section, the intrasulcal contours of the posterior banks of the left and right precentral gyri (thick black line) were traced with a digitizer from the deepest point of the CS to the tangent connecting the free surfaces of the pre- and postcentral gyri (=depth of CS). Left–right differences in depth were calculated for each horizontal section as directional asymmetry coefficients.

compared AC curves of left- and right-handers (Fig. 4). Ten features were extracted from each AC curve: the mean AC coefficient and the first four moments, as well as the analogous parameters for the differential quotient. All features were z-transformed. The Hotelling's T^2 statistic was used as a multivariate test for differences between the AC curves of the two groups (left- and right-handers). We applied a multivariate test procedure because this test does not require independent variables. A stepwise discriminant analysis was applied to reveal those features which best discriminate the groups. This procedure also defines the degree of overlap or separation of the two groups by calculating the percentage of correct classifications, when each AC curve has been reclassified into one of the two groups using the discriminant function. In order to visualize differences between AC curves for left- and right-handers, cumulative AC curves were calculated for both groups and drawn in comparison to a cumulative AC curve with randomly occurring left–right differences (see Fig. 5).

Quantitative Cytoarchitecture

Quantitative cytoarchitectonic analysis was performed on histological sections through the region of hand representation in Brodmann's area 4 of 12 postmortem brains. The age of the subjects ranged from 39 to 79 years (mean 52.8 years). None of them had any records of neurological problems. The brains were fixed in 4% buffered formalin. One tissue block was dissected from the lateral surface of each hemisphere in the region of the hand representation area. To determine this region in autopsy material, we projected Talairach coordinates $z = 69–35$ onto the lateral surface of each 3-D reconstruction of the brains used for MR morphometry. We found that these coordinates define a region extending approximately from the level of the superior frontal sulcus to the level of the inferior frontal sulcus. Each block for histology contained this portion of the precentral gyrus. Tissue blocks were embedded in paraffin and serially sectioned (20 μm). Each 60th section was stained according to Gallyas (1979). Only cell bodies, no dendrites or axons, are stained. The sequence of sections from each block was then divided into four equal parts. The first section of each part was collected, and from these four sections, three were selected randomly for further analysis. If the section was not suitable for image analysis due to artifacts (scatter, ruptures, folds, etc.), the neighboring section was used.

We estimated the fraction of cortical volume occupied by nerve cell bodies by measuring the gray level index (*GLI;* Schleicher and Zilles, 1990; Wree *et al.*, 1980) with an image analyzer (KS400, Kontron). Profile curves were obtained which described the laminar distribution of the volume density of nerve cell bodies from the border between layers I/II to the border between cortex and white matter (as an example: Fig. 6A). AC values were calculated from the profile curves of the left and right hemispheres for each point according to $100 \times [\mathrm{GLI(left)} - \mathrm{GLI(right)}]/[(\mathrm{GLI(left)}) + \mathrm{GLI(right)}/2]$. As an example see Fig. 6B.

RESULTS

In vivo MR morphometry of the CS yielded significant differences between left- and right-handers in the shape of the AC curves (Hotelling's $T^2 = 50.09$; $df = 10, 34$; $F = 3.96$; $P < 0.01$; Fig. 4). The shape was defined by 10 features extracted from each AC curve (see Subjects and Methods). Discriminant analysis showed a correct classification of the AC curves into those of either right- or left-handers in 82% of the cases, i.e., 37 of 45 (12 of the 14 left- and 25 of the 31 right-handers) were assigned to their original group. This high amount

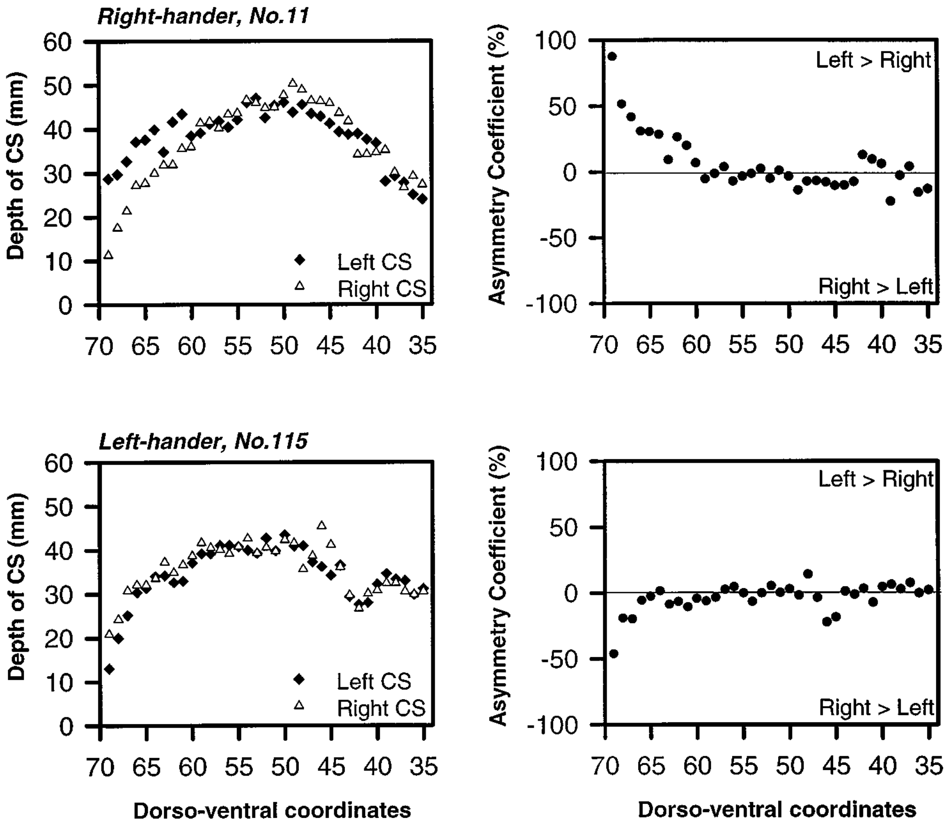

FIG. 3. Depth of the right and left CS with corresponding asymmetry coefficients in two representative subjects: right-hander, No. 11, 26 years, HDT = 0.1; and left-hander, No. 115, 23 years, HDT = −0.21.

of correct classification demonstrates, first, the existence of differences in asymmetry of CS depth and second, the sensitivity of the selected set of features to capture these differences; i.e., the selected parametrization of the shape of the curves is an adequate tool for the analysis of the shape of the curves.

The analysis of the features describing the shape of the AC curves revealed that the following features have the highest contribution for discriminating the curves of right- and left-handers: the first moment (*x* coordinate of the center of gravity of the AC curve: right-handers, −0.270, SD = 0.913 vs left-handers, 0.393, SD = 1.199), the second moment (standard deviation of the AC-curve: right-handers, 0.171, SD = 1.046 vs left-handers, −0.199, SD = 1.061), the fourth moment (kurtosis of the AC curve: right-handers, −0.142, SD = 1.009

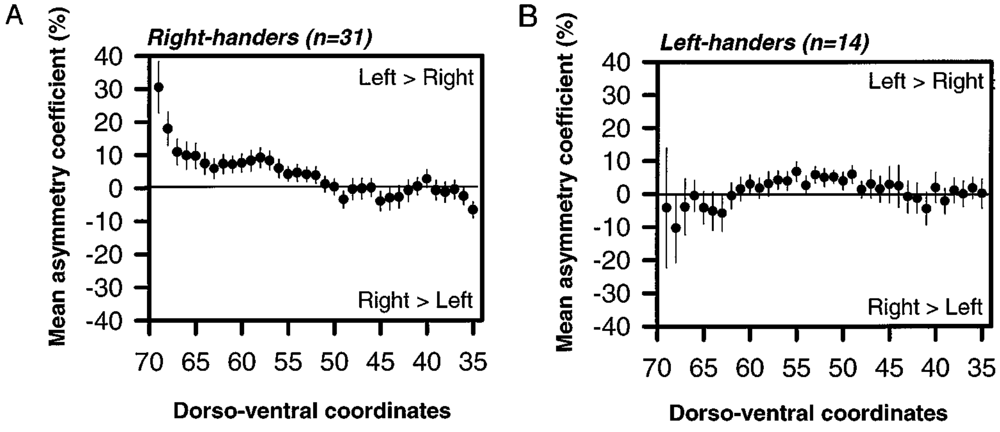

FIG. 4. (A) Mean asymmetry coefficients (±SE) for 35 consecutive horizontal sections in 31 right-handers. A leftward asymmetry was more pronounced at dorsal levels, corresponding to sites of cortical motor hand representation. (B) Data as in (A) but for 14 left-handers. Shapes of AC curves differed significantly between left- and right-handers (Hotelling's T^2 test, $P < 0.01$).

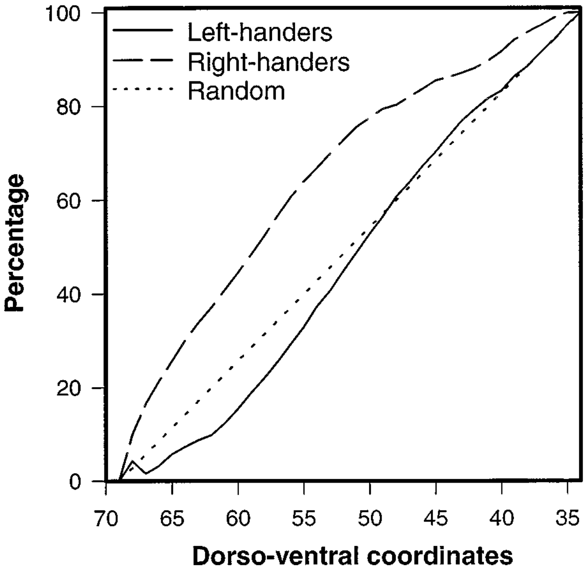

FIG. 5. Cumulative AC curves in dependence on dorsoventral coordinates for right- and left-handers in comparison to a cumulative AC curve of randomly occurring left–right differences.

vs left-handers, 0.406, SD = 1.111), and the mean of the differential quotient (right-handers, 0.306, SD = 0.973 vs left-handers, −0.479, SD = 0.832).

Right-handers were more asymmetrical in CS depths than left-handers (median AC 3.92; mean AC 4.84, SE = 1.31 for right-handers vs median AC −2.10; mean AC 1.57, SE = 1.81 for left-handers; Mann–Whitney Rank Sum Test, $P < 0.05$). The AC curve of right-handers was characterized by high AC in more dorsal horizontal sections and lower values in more ventral sections. The AC values of the total analyzed region showed a significant side difference in right-handers (One-Sample Test, $P < 0.05$). Thus, right-handers had a deeper CS in the left than in the right hemisphere (Fig. 4A). By contrast, the CS of left-handers was deeper in the right hemisphere at more dorsal levels (Fig. 4B). The small right-larger-than-left asymmetry in left-handers was expressed by absolutely smaller, negative AC values and was even more restricted to the most dorsal horizontal sections. The AC values of the total analyzed region did not reveal any significant side differences in left-handers.

The differences in degree (mean AC values) and direction (either left-larger-than right or right-larger-than-left asymmetry) asymmetry between right- and left-handers can also be demonstrated by cumulative AC curves (Fig. 5). The cumulate of right-handers lies above a cumulate of a random distribution of left–right differences. The cumulate of left-handers is below the random distribution. Thus, left-handers as well as right-handers revealed asymmetry between right and left CS in the dorsal part of the hand representation area, but the asymmetry in left-handers was *opposite* to that of right-handers and less prominent than in right-handers.

Side differences were also discovered at the microstructural level. The volume densities of cells were compared between left and right area 4 of each brain. Profile curves of the GLI revealed that area 4 had a smaller volume density in the left than the right hemisphere (Fig. 6). Thus, area 4 on the left had relatively more neuropil, i.e., more volume between cell bodies occupied by dendrites, axons, and synapses. The mean asymmetry coefficient of laminar profiles (Fig. 7) was significantly lower than 0 and corroborated this finding (mean −4.05%, SE = 0.23, One-Sample Test; $P < 0.05$). Side differences were not restricted to single cortical layers.

DISCUSSION

The present study describes asymmetry in the intrasulcal length of the posterior bank of the precentral

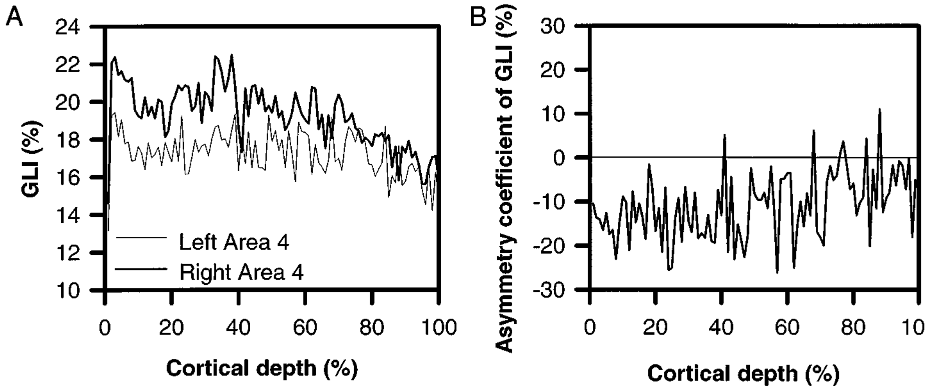

FIG. 6. (A) Representative profiles for volume density of nerve cells (GLI) in left and right cortical regions of hand representation in area 4 of one brain. The profiles extend from the layer I/II border (position 0) to the cortex/white matter border (position 100). Since the maximal GLI equals 100%, the proportion of neuropil volume (pV_{np}) can be calculated according to $pV_{np} = 100\% - \text{GLI}$. (B) Corresponding AC curve for this brain.

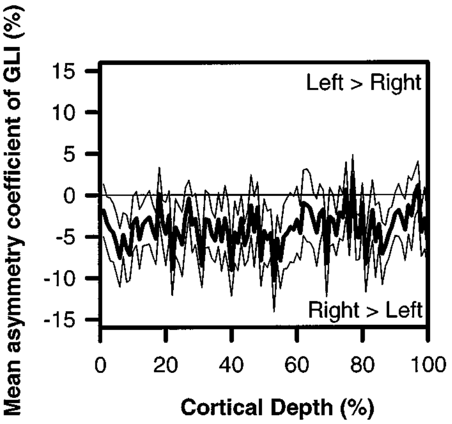

FIG. 7. Mean asymmetry coefficients AC (mean ± SE, in %) for volume density (GLI) for the cortical region of hand representation in area 4 of 12 brains. Side differences in the amount of neuropil were significant ($P < 0.05$) within the sample studied.

gyrus (i.e., depth of CS) as a marker for the size of the cortical motor hand representation area. Right-handers had a deeper CS on the left than on the right side. Left-handers had a deeper right than left CS on dorsal sections through the precentral gyrus. The asymmetry was more pronounced in right- than in left-handers and it was associated with handedness: The direction of structural lateralization in right-handers was inverse to that of left-handers. Differences in the amount of neuropil in Brodmann's area 4 supported the data on the depth of the CS of right-handers.

It can be assumed that a greater amount of neuropil in the left motor cortex reflects the presence of more larger dendritic and axonal surfaces and, thus, of an increased volume compartment for intracortical connections in the hemisphere contralateral to the preferred hand. Several lines of evidence support this conclusion. (1) Extensive intracortical, horizontally oriented connections have been found within the representation area for digit movement in monkeys (Huntley, and Jones, 1991). (2) Gould *et al.* (1986) argued that callosal connections, potentially promoting bilaterally synergistic movements, are not necessary in the finger representation area, and could even be a hindrance for independent movements of the distal parts of the upper extremity. (3) There is evidence that the number of callosal terminals in sensorimotor areas covaries with their architectonic symmetry (Rosen *et al.*, 1989). Thus, a proportionately larger amount of neuropil in the motor hand representation area of the dominant hemisphere might be indicative of more numerous intracortical, ipsilateral associative connections.

The finding of a higher degree of asymmetry in right-handers than in left-handers is in parallel to data on the planum temporale (Steinmetz *et al.*, 1991). These authors provided evidence that the asymmetry of the area of the planum temporale was greater in right- than in left-handers. However, in contrast to that study, which revealed a left-larger-than-right asymmetry in both groups, the anatomical asymmetry related to handedness is the first example of an inverse asymmetry which is obviously limited to the dorsal part of the analyzed region.

Our study does not explain the mechanism underlying this asymmetry. In particular, it is not yet known whether asymmetry between the hemispheres is determined pre- or postnatally and whether it remains modifiable during postnatal development, e.g., in response to specific stimulation. Functional imaging revealed that the area of cortical activation becomes enlarged during motor learning (Karni *et al.*, 1995; Mano *et al.*, 1995; Pascual-Leone *et al.*, 1995), but it remains unknown whether this can lead to permanent modifications of the anatomical structure. The present observations have shown that anatomical asymmetries in the region of the motor cortex covary with asymmetries in motor performance.

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