Bilateral Cortical Representation of the Trunk Midline in Human First Somatic Sensory Area

Mara Fabri,^{1*} Gabriele Polonara,² Ugo Salvolini,² and Tullio Manzoni¹

¹Department of Neuroscience, Section of Physiology, Università Politecnica delle Marche, Ancona, Italy

²Department of Neuroradiology, Università Politecnica delle Marche, Ancona, Italy

Abstract: The cortical representation of the trunk zone in the human first somatosensory area was studied with functional magnetic resonance imaging (fMRI) to establish whether the cutaneous regions close to the midline are represented in this area of both hemispheres. Cortical activation foci evoked by unilateral tactile stimulation of ventral trunk regions were detected in the postcentral gyrus of the contralateral hemisphere slightly medial to or just behind the omega-shaped region of the central sulcus and in the anterior bank of the postcentral sulcus. These regions probably correspond to the trunk ventral midline representation zones of areas 3a–3b and 1–2, respectively. Stimulation of cutaneous regions adjacent to the midline evoked activation foci also in the ipsilateral postcentral gyrus in regions symmetrical to those activated in the contralateral hemisphere. These data demonstrate that in humans, as in nonhuman primates, the cutaneous regions adjacent to the trunk midline are represented bilaterally in the first somatic sensory cortex. Whether the ipsilateral activation depends on callosal or extracallosal inputs remains to be elucidated. *Hum Brain Mapp* 25:287–296, 2005. © 2005 Wiley-Liss, Inc.

Key words: body midline; brain imaging; fMRI; somatosensory cortex; bilateral representation

INTRODUCTION

The body midline, defined as the cutaneous region straddling the midsagittal plane, is represented in the mammalian brain in the first somatic sensory cortex (SI) of both hemispheres [Conti et al., 1986; Iwamura et al., 2001; Manzoni et al., 1980, 1989; Taoka et al., 1998]. Electrophysiologic studies of nonhuman primates [Conti et al., 1986; Mezernich et al., 1978; Killackey et al., 1983; Nelson et al., 1980; Whitsel

et al., 1971] have confirmed that neurons driven by tactile stimulation of the trunk surface are present in all four cytoarchitectonic areas of the postcentral gyrus (PCG; areas 3a, 3b, 1 and 2). Cortical neurons possessing bilateral receptive fields (RFs) straddling the ventral or dorsal midline have been recorded in these areas. Neuroanatomic studies combining electrophysiologic recording and neuronal tracing have shown a close topographic correspondence between distribution of callosal projecting elements (axon terminals and neurons) and the presence of neurons with bilateral RFs, indicating that the ipsilateral component of bilateral RFs could have a callosal origin [Conti et al., 1986; for a review see Manzoni et al., 1989; Manzoni, 1997]. These studies confirmed that the ventral and dorsal trunk midlines are represented near the cytoarchitectonic boundaries 3a–3b and 1–2, and 3b–1, respectively, and that the lateral trunk surfaces are represented in the central parts of areas 3b and 1. The finding of a callosal origin of the ipsilateral RF component was confirmed later by electrophysiologic and ablation studies [see Iwamura et al., 2001, for a review].

Human area SI lies in PCG and consists of four cytoarchitectonic areas [Brodmann, 1909; Burton, 2001; Geyer et al.,

Contract grant sponsor: MIUR (Ministero Istruzione, Università e Ricerca, Cofin 2001, 2003); Contract grant sponsor: CNR (Consiglio Nazionale delle Ricerche); Contract grant number: 99.02520.CT04.

*Correspondence to: Mara Fabri, Department of Neuroscience, Section of Physiology, Università Politecnica delle Marche, Via Tronto 10/A, 60020 Ancona-Torrette, Italy. E-mail: m.fabri@univpm.it

Received for publication 15 September 2004; Accepted 13 October 2004

DOI: 10.1002/hbm.20099

Published online 12 April 2005 in Wiley InterScience (www.interscience.wiley.com).

TABLE I. Summary of subjects studied and stimulation sites

Subject	Age (yr)	Gender	Handedness (Oldfield score)	Tactile stimulation						PCG activation	
				R trunk		L trunk		R hand	L hand	Medial trunk stim	Lateral trunk stimulation
				Medial	Lateral	Medial	Lateral				
LB	29	M	Right (12)	Yes	Yes	No	No	Yes	No	Bilateral	Contralateral
LA ^a	23	M	Right (26)	Yes	Yes	No	No	Yes	No	Bilateral	Contralateral
GF ^a	24	F	Right (13)	Yes	Yes	Yes	Yes	No	No	Bilateral	Bilateral
VB	23	M	Right (14)	Yes	Yes	Yes	Yes	No	No	Bilateral	Contralateral
IC	24	F	Right (22)	Yes	Yes	Yes	Yes	No	No	Bilateral	Bilateral
AN	22	M	Right (13)	Yes	Yes	Yes	Yes	No	No	Bilateral	Contralateral
IP ^{a,b}	22	F	Right (18)	No	No	Yes	Yes	No	Yes	Bilateral	Contralateral
EP ^{a,b}	24	F	Right (19)	No	No	Yes	Yes	No	Yes	Bilateral	Contralateral
FF ^b	23	F	Right (13)	No	No	Yes	No	No	Yes	Bilateral	—
EG ^{a,b}	24	F	Right (10)	No	No	Yes	No	No	Yes	Bilateral	—

^a Data analyzed with SPM2 software.^b Data analyzed with BrainVoyager software. stim, stimulation.

1997; White et al., 1997]. Based on data from magnetoencephalography (MEG) [Kagiki et al., 2000; Nakamura et al., 1998], positron emission tomography (PET) [Burton et al., 1997], and functional magnetic resonance imaging (fMRI) [Lin et al., 1996; Moore et al., 2000], each of these areas seems to contain a complete representation of the receptive periphery [Burton, 2001; see also Iwamura, 1998], although a systematic and complete study is currently not available. Most recent studies focus on the cortical representation of the hand, foot, and face. Investigations of the trunk representation in human SI are scarce [see, for example, Nakamura et al., 1998], however, and do not address the existence of bilateral responses to unilateral stimulation of skin receptors close to the trunk midline [Itomi et al., 2000]. Bilateral activation could explain the perception and mental representation of the body midline demonstrated recently in a psychophysical investigation [Spidalieri and Sgolastra, 1997] in which the trunk midline was shown to be perceived as “a straight line approximating the line orthogonal to the intermammary line and crossing its midpoint.” The authors hypothesized that somatosensory input from the trunk should have a critical role in this process.

The aim of the present study was to identify the cortical representation of the trunk region in SI and to establish whether in humans, as in nonhuman primates, the cutaneous regions close to the midline are represented bilaterally in area SI.

SUBJECTS AND METHODS

Subjects

Ten healthy volunteers (aged 22–29 years; six women, four men; Table I) gave their informed consent to participate in the study. The experimental protocol was approved by the Ethical Committee of Università Politecnica delle Marche (Ancona, Italy). All subjects were right-handed as

determined by the Edinburgh handedness inventory [Oldfield, 1971] (Table I).

Imaging Protocols

Subjects were placed in a 1.5-Tesla scanner (Signa LX NV/I; General Electric Medical System, Milwaukee, WI) equipped with 50 mT/m gradients with their head restrained within a circularly polarized head coil. They were instructed to keep their eyes closed, find a comfortable position and relax, and to avoid even minimal movement. Their ears were plugged. The experimental procedure consisted of three steps. In the first, an anatomic sagittal localizer (SPGR 2-D; repetition time [TR] 120 ms, echo time [TE] 15 ms, flip angle 70 degrees, field of view [FOV] 23 × 23 cm, slice thickness 5 mm, matrix 256 × 256, 1 NEX, and scan time 31 s) was acquired to select section levels. Ten contiguous 5-mm-thick axial sections were selected. The second step involved the acquisition of high-resolution axial anatomic images (SPGR 2-D; TR 100 ms, TE 12 ms, flip angle 70 degrees, FOV 28 × 21 cm, thickness 5 mm, matrix 256 × 256, 1 NEX, and scan time 3:17 min for 10 images) on which the functional activation was to be superimposed. A 3-D data set (IR Prep Fast SPGR 3-D; TR 14.9 ms, TE 6.7 ms, TI 500 ms, flip angle 15 degrees, FOV 25 × 25 cm, slice thickness 0.7 mm, matrix 256 × 256, 1 NEX, and scan time 12 min) was acquired from four subjects (I.P., E.P., F.F., and E.G.). The third step consisted of fMRI acquisitions during the stimulation cycle that were obtained in the same axial planes using single-shot T2*-weighted gradient-echo echo planar imaging (EPI) sequences (TR 3,000 ms, TE 60 ms, flip angle 90 degrees, FOV 28 × 21 cm, matrix 64 × 64, 1 NEX, and scan time 5:12 min), resulting in 1,000 axial functional images (100 per section, 1 image/3 s) from the 10 contiguous 5-mm-thick axial sections selected under step 1. Functional images were obtained with the blood oxygenation level-dependent (BOLD) contrast method. The axial planes were

orthogonal to both the sagittal and the coronal planes and allowed identification of the central sulcus (CS) and PCG.

Stimulation

Unilateral tactile stimulation consisted of gently rubbing skin areas of about 20×10 cm located on the ventral (medial or lateral) trunk surface between two imaginary horizontal lines crossing the umbilicus and the nipples, respectively, using a soft cotton pad (frequency 1 Hz). Stimulation of this skin area likely involves cutaneous receptors of thoracic dermatomes from Th4 to Th10. The tactile stimulus was applied to the left or the right side medially and laterally (Table I). To avoid the risk of the stimulation crossing the midline, the utmost care was exercised to rub skin areas about 2 cm away from it. Because in monkeys the RFs of cortical neurons within the trunk midline zone extend well beyond the midline [Conti et al., 1986], there is reason to believe that this may also be true in humans, and that stimulation of skin receptors at this distance from the midline should activate cortical neurons with bilateral RFs. The paradigm lasted 5 min and consisted of ten 30-s alternating periods of rest and stimulation (block-designed experiment). Subjects received two or four scans depending on whether one or both sides were being stimulated (Table I). As control for stimulus-related signal intensity changes [Yetkin et al., 1996], the experimenter made the same movements 10–15 cm above the subject's body also during the rest periods. Owing to the subjects' position in the magnet, tactile stimulation was only administered to the ventral and ventrolateral trunk surfaces.

To assess the consistency of the topographic localization of activation foci thus evoked with the known topographic organization of area SI, in subsequent experimental sessions six subjects received unilateral tactile stimulation of the hand and two subjects also of other regions (foot, leg, shoulder, and lower face).

Data Analysis

At the end of the experimental sessions, consecutive images from each section were examined in cine mode to detect possible head movements [see Kim and Urgubil, 1997, for a review], in which case images were discarded. The images were transferred to a Unix workstation (General Electric Advantage Windows 1.2) and analyzed using the general linear model [Friston et al., 1995] with custom-designed General Electric software (Functool; FT). Using a least-square algorithm, this software calculates a correlation coefficient that relates the time-course data to a reference function, which is a periodic square wave (boxcar predictor) [Xiong et al., 1996]. The correlation coefficient is related to the t parameter of Student's t test by a precise relationship and is thresholded by a confidence level (CL) selected by the operator. In our case, its value was 0.0001, indicating a 0.01% probability that the signal increase was unrelated to the reference function. For each image (obtained by superimposing the functional and the anatomic image from the same section level), the software drew a correlation map display-

ing, by way of a color scale, the degree of correlation of each pixel value with the square wave. For each activated zone, a region of interest (ROI) was defined as a cluster of at least four contiguous functional voxels in which the P value of the test was equal to or less than 0.05. For each ROI, the software displayed the signal variations that occurred during the stimulation cycle. The signal change was reported in a graph, where the x-axis is a time scale reporting the progressive number of the functional images acquired (1 image/3 s), and the y-axis reports the percent signal change from the baseline (0%), represented by the image acquired at rest. When the signal increase in the selected ROIs, which lay in regions corresponding anatomically to SI and posterior parietal (PP) cortex (in PCG), correlated temporally with the stimulation pattern, the activation was assumed to be evoked by the tactile stimulus.

For further validation of results, data that were in a format compatible with such tools were also analyzed using the BrainVoyager (BV) software package (R. Goebel, Brain Innovation, Maastricht, The Netherlands) on data from subjects I.P., E.P., F.F., and E.G., and statistical parametric mapping software (SPM2; developed by members and collaborators of The Wellcome Department of Imaging Neuroscience, Institute of Neurology, University College London, UK) on data from subjects L.A., G.F., I.P., E.P., and E.G. A multisubject analysis was also carried out on subjects G.F., I.P., E.P., and E.G. using the SPM2 package. In brief, the first two images of each functional series were discarded. In BV analysis, the functional images were superimposed on 2-D anatomic images and incorporated into 3-D data sets through trilinear interpolation. Data were then transformed into Talairach space [Talairach and Tournoux, 1988]. Preprocessing of functional scans included 3-D motion correction. Before analysis with SPM2, the fMRI data were preprocessed as follows: (1) spatial realignment of the images to remove movement artifacts; (2) coregistering of coplanar and EPIs to the high-resolution image; and (3) normalization, to translate brain images into common 3-D brain space. With multisubject analysis, smoothing was the preprocessing step.

The somatic sensory areas were identified by analyzing their anatomic localization as defined by standard anatomic landmarks (e.g., the omega-shaped central sulcus in the axial views) and by a reference atlas [Mai et al., 1997]. To identify the position of activation foci, the individual scans were adjusted to the Talairach coordinate system [Talairach and Tournoux, 1988]. The Talairach coordinates (x , y , z) of the significant voxels were produced manually for data processed with FT and automatically for data analyzed with BV and SPM2. A maximum intensity projection (MIP) was displayed on a glass brain in three orthogonal planes.

Statistical analysis was carried out separately on data processed with FT (from 10 subjects), BV (from 4 subjects), and SPM2 (from 5 subjects). In subjects in whom both trunk and hand regions were stimulated, the paired t test was applied to the mean x (mediolateral) Talairach coordinates of activation foci evoked in the contralateral hemisphere by the two cutaneous regions (hand and medial trunk), taking

Figure 1.

Cortical activation evoked in PCG by tactile stimulation of the left medial trunk surface (**A–D**) and left hand (**E, F**). Left hemisphere on the right. **A**: Axial image (subject I.P.) obtained from an SPGR T1-weighted sequence on which the regions activated during stimulation (obtained from a GE T2* single-shot EPI sequence [3,000/60/1]) have been superimposed. Activated regions are present in PCG of the contralateral (1) and ipsilateral (2) hemisphere. In both hemispheres, activation foci are likely in the anterior part of the gyrus, on the 3a–3b border. **B, C**: Signal increase in the ROIs shown in **A**. In the five 30-s stimulation periods, the signal was about 2% above baseline. Graph 1 (**B**) and 2 (**C**) represent the signal time course in foci 1 and 2, respectively, shown in (**A**). The five red bars indicate the stimulation periods. **D**: Axial image from

the same subject, more ventral than the one shown in (**A**): activation in the posterior part of PCG. Foci likely correspond to the posterior representation of the ventral midline in SI, on the 1–2 border. **E**: Axial image from the same subject during a different scan, showing the focus evoked in right PCG by unilateral stimulation of the left hand. Activation was detected in the contralateral hemisphere. Activation evoked by tactile stimulation of the trunk lies in a PCG region more medial than the one evoked by tactile stimulation of the hand. **F**: Graph illustrating the signal increase in the ROI shown in (**E**). In the five 30-s stimulation periods, the signal was about 3% above baseline. Graph 3 represents the signal time course in focus 3 shown in (**E**). CS, central sulcus.

their absolute values. Because we found no evidence of interhemispheric differences between the two areas SI, the values of the left and right hemisphere (relating to right- and left-side stimulation, respectively) were pooled (negative and positive x Talairach values, respectively). One-way analysis of variance (ANOVA) was applied to the more significant Talairach coordinates (obtained from SPM2 analysis of data from L.A., I.P., E.P., and E.G.) of each area according to the expected localization of the activation to test whether the areas of activation evoked by trunk midline and hand stimulation actually had similar coordinates. A P value of 0.05 was considered significant.

RESULTS

Stimulation of the Ventromedial Trunk Surface

Data were obtained from 10 subjects (Table I). Unilateral tactile stimulation of the trunk ventral surface close to the midline elicited an increase in blood flow in both contralateral and ipsilateral PCG (Fig. 1 and 2A,B; Table I). In the contralateral hemisphere, activation was detected in the pos-

terior part of PCG of eight subjects (mean Talairach coordinates x, y, z : 32.87, –33.38, 53.75; Fig. 1 and 2A,B; Table II). In six subjects (four of whom also presented a posterior focus), a more anterior focus was observed (mean Talairach coordinates x, y, z : 34, –25, 53.33; Fig. 1A, and 2A; Table II). In all ten subjects, activation was also present in the ipsilateral hemisphere: in six subjects a posterior focus was observed (mean Talairach coordinates x, y, z : 32.5, –34.17, 54.17; Table II), in two of them and in the remaining four an anterior activation focus was present (x, y, z : 21.17, –27, 55.83; Table II). In all subjects, the signal increase during stimulation was about 2% above baseline, and the contralateral foci seemed to occupy a larger cortical area than did those elicited in the corresponding regions of the ipsilateral hemisphere (Fig. 1).

The anatomic localization of the foci evoked by trunk stimulation was analyzed and compared to that evoked in the same subjects by hand stimulation (Fig. 1). Trunk foci, especially the posterior one, were located in significantly more medial PCG zones (Fig. 1A,D; Table III) than were those evoked by hand stimulation (x, y, z : 41.67, –25.17, 54.17; Fig. 1E; Table II) [Polonara et al., 1999].

Figure 2.

Cortical activation in PCG during stimulation of left medial trunk (**A,B**) and left lateral trunk (**C,D**). Left hemisphere on the right. **A:** Axial image from subject A.N. (as in Fig. 3) showing foci in contralateral (1 and 1') and ipsilateral PCG (2) evoked by unilateral stimulation of the left medial trunk. **B:** Axial image from

subject I.C. showing foci in contralateral (1) and ipsilateral PCG (2). Axial image from subject A.N. (**C**) and from subject I.P. (**D**) showing only contralateral foci (1) evoked by unilateral stimulation of the left lateral trunk. CS, central sulcus.

Data analysis yielded similar results with BV and SPM2. Both methods, which could not be applied to all data due to format inhomogeneity of part of the data, evidenced an increase in blood flow in contralateral as well as ipsilateral PCG in all cases. Whereas with these two tools a first-level data analysis, comparable to that carried out with FT, showed in some cases an anterior and a posterior focus in PCG (as described by FT analysis), further processing reduced activation areas and in most cases revealed a single focus. The description that follows is based on the latter data. Activation foci evoked by unilateral trunk and hand stimulation were found in similar locations to those described above, as expected considering the mean Talairach coordinates calculated using BV and SPM2 (Table III), respectively. Figure 3 shows data from subject E.G. (BV analysis). As mentioned above, the contralateral focus seemed larger than the one elicited in the ipsilateral hemisphere; on the 3-D brain reconstruction, the activation focus was seen in both hemispheres in the cortex buried in the CS (Fig. 3C,D). Consistent results were obtained with multisubject analysis

(Fig. 4). Multisubject response to unilateral tactile stimulation of the trunk midline showed activation foci in PCG of both hemispheres in a consistent anatomic location. Similarly, unilateral tactile stimulation of the hand produced cortical activation in a consistent site. The significantly different location of foci evoked by hand and medial trunk stimulation was also confirmed, as shown by the results of the *t* test (Table IV and V). In addition, significant differences were also demonstrated by ANOVA analysis ($P_x = 0.0053$; $P_y = 0.0120$) between the mediolateral (*x*) and anteroposterior (*y*) coordinates of trunk and hand foci, and weaker although significant ($P_z = 0.0565$), differences in the dorsoventral (*z*) coordinates.

Stimulation of the Ventrolateral Trunk Surface

Unilateral tactile stimulation of the trunk ventrolateral surface away from the midline evoked activation in contralateral PCG (Fig. 2C,D) and in two subjects (Table I), also in ipsilateral PCG. Activation was present in the middle part of PCG in a mediolateral location similar to the foci evoked by

TABLE II. Talairach coordinates of activation foci evoked in first somatosensory cortex by tactile stimulation of midline trunk, lateral trunk, and hand

Foci	Contralateral			Ipsilateral		
	<i>x</i> (ML)*	<i>y</i> (AP)	<i>z</i> (DV)	<i>x</i> (ML)*	<i>y</i> (AP)	<i>z</i> (DV)
Midline trunk						
Posterior						
LB ^a	17	−34	60	25	−35	60
LA ^a	36	−32	50	40	−30	55
GF	—	—	—	—	—	—
VB	35	−30	55	40	−35	55
IC	45	−30	50	40	−30	50
AN	40	−35	50	—	—	—
IP	33	−30	50	30	−35	50
EP	35	−40	55	20	−40	55
FF	22	−36	60	—	—	—
EG	—	—	—	—	—	—
Mean ± SD	32.88 ± 9.16	−33.38 ± 3.58	53.75 ± 4.43	32.50 ± 8.80	−34.17 ± 3.76	54.17 ± 3.76
Anterior						
LB ^a	40	−23	50	—	—	—
LA ^a	32	−35	60	10	−35	60
GF	47	−17	45	45	−20	45
VB	—	—	—	—	—	—
IC	—	—	—	—	—	—
AN	40	−15	50	20	−15	55
IP	20	−30	60	17	−35	60
EP	—	—	—	—	—	—
FF	—	—	—	15	−30	60
EG	25	−30	55	20	−27	55
Mean ± SD	34.00 ± 10.22	−25.00 ± 7.98	53.33 ± 6.06	21.17 ± 12.25	−27.00 ± 8.12	55.83 ± 5.85
Lateral trunk						
LB ^a	36	−28	55	—	—	—
LA ^a	32	−33	55	—	—	—
GF	—	—	—	—	—	—
VB	—	—	—	—	—	—
IC	35	−35	55	—	—	—
AN	25	−35	55	—	—	—
IP	28	−35	55	—	—	—
EP	25	−35	55	—	—	—
FF	—	—	—	—	—	—
EG	—	—	—	—	—	—
Mean ± SD	30.17 ± 4.88	−33.50 ± 2.81	55.00 ± 0	—	—	—
Hand						
LB ^a	40	−30	55	—	—	—
LA ^a	45	−20	55	—	—	—
GF	—	—	—	—	—	—
VB	—	—	—	—	—	—
IC	—	—	—	—	—	—
AN	—	—	—	—	—	—
IP	45	−25	55	—	—	—
EP	40	−20	55	—	—	—
FF	35	−33	55	—	—	—
EG	45	−23	50	—	—	—
Mean ± SD	41.67 ± 4.08	−25.17 ± 5.34	54.17 ± 2.04	—	—	—

Data from Functool.

* Absolute values. Means of *x*-coordinates calculated on absolute values.^a These subjects received tactile stimulation on the right side only

TABLE III. Mean Talairach coordinates of activation foci evoked in first somatosensory cortex by unilateral tactile stimulation of midline trunk, lateral trunk, and hand using Brain Voyager and SPM2 for analysis

Foci	Brain Voyager			SPM2		
	x (ML)*	y (AP)	z (DV)	x (ML)*	y (AP)	z (DV)
Midline trunk						
Contralateral	34.25 ± 0.96	-34.25 ± 4.03	43.75 ± 4.57	31.2 ± 8.32	-54 ± 7.75	60.4 ± 7.4
Ipsilateral	34.5 ± 5.80	-31.25 ± 4.35	46.5 ± 8.27	42 ± 5.29	-50.67 ± 11.015	53.33 ± 6.11
Contralateral lateral trunk	26.5 ± 2.12	-42.5 ± 10.61	53.5 ± 2.12	25.25 ± 13.2	27.5 ± 38.41	57 ± 6.63
Contralateral hand	42.5 ± 2.89	-31 ± 4.08	47.75 ± 6.95	45.2 ± 5.40	-36.4 ± 6.07	59.6 ± 3.58

* Absolute values. Means of x -coordinates calculated on absolute values.

the stimulation of skin regions close to the midline (mean Talairach coordinates x , y , z : 30.17, -33.5 , 55). The signal increase was 1.5–2% above baseline. Activation was clear

in PCG, which contains area 1 [Geyer et al., 1997], but uncertain in the posterior bank of CS, containing area 3b [Geyer et al., 1997].

Figure 3.

Cortical activation in PCG during left medial trunk unilateral stimulation (subject E.G.). Left hemisphere on the right. **A:** Axial image (as in Fig. 3) showing foci in contralateral (1) and ipsilateral (2) PCG. The horizontal red line shows the level of the coronal image depicted in B. Vertical red and green lines show the levels of parasagittal sections represented in (C) and (D), respectively. **B:** Coronal image from the same subject showing the foci in contralateral (1) and ipsilateral (2) PCG. The horizontal red line shows

the level of the axial section depicted in (A). Vertical red and green lines show the levels of the parasagittal sections represented in (C) and (D), respectively. **C,D:** Parasagittal images from the same subject showing contralateral (1 in C) and ipsilateral (2 in D) activation foci, respectively, in PCG. Horizontal lines (red in C, green in D) show the level of the image shown in (A), and vertical lines that of the image shown in (B). CS, central sulcus.

Figure 4.

SPM2 graphic output for multisubject analysis reporting maximum intensity projections (MIP) on a glass brain. **A:** Contralateral focus (red arrow) after trunk midline stimulation (subjects G.F., E.P., I.P., and E.G.) shown in lateral (1), coronal (2), and axial (3) views. **B:** Ipsilateral focus (red arrow) after trunk midline stimulation (subjects G.F., E.P., I.P., and E.G.) shown in lateral (1), coronal (2), and axial (3) views. **C:** Contralateral focus (red arrow) after hand stimulation (subjects E.P., I.P., and E.G.) shown in lateral (1), coronal (2), and axial (3) views. Talairach coordinates of the significant voxels reported on the top of each figurine set. **D:** Activation foci shown superimposed on standard high-resolution brain images. Contralateral and ipsilateral foci elicited by trunk midline stimulation are shown in frames 1 and 2, respectively; focus elicited by hand stimulation is shown in frame 3.

Analysis of data with BV and SPM2 showed similar results: an increase in blood flow solely in contralateral PCG in all cases. Activation foci occupied similar locations, as expected considering the mean Talairach coordinates calculated with both BV and SPM2 (Table III).

DISCUSSION

The present fMRI study addresses the cortical representation of the trunk midline in the human brain. Data from healthy volunteers show for the first time that in humans, as in nonhuman primates, unilateral stimulation of trunk skin

TABLE IV. Comparison of mediolateral Talairach x-coordinates of midline trunk and hand activation foci in first somatosensory cortex using Functool

Subjects	Posterior midline trunk	Hand	Anterior midline trunk	Hand
LB ^a	17	40	40	40
LA ^a	36	45	32	45
IP	33	45	20	45
EP	35	40	—	—
FF	22	35	—	—
EG	—	—	25	45
Mean	28.6	41	29.25	43.75
P	0.01		0.05	

Paired *t* test of mean Talairach x-coordinates of trunk midline foci vs. hand focus.

^a These subjects received tactile stimulation on the right side only.

receptors adjacent to the ventral midline evokes cortical SI activation in both hemispheres. In most subjects, two activation foci were detected in the PCG: one anterior, in the depth of the CS; the other posterior, at the crown of the postcentral sulcus (PCS). These findings are consistent with the known ventral trunk midline representations in nonhuman primate SI on the borders between areas 1 and 2 and areas 3a and 3b [Conti et al., 1986], and with the anatomic location of these borders in human SI [Geyer et al., 1997]. In addition, the location of the focus evoked by the ventrolateral trunk surface stimulation, in the central portion of cytoarchitectonic areas 3b and 1, agrees with previously recorded trunk maps [Conti et al., 1986].

TABLE V. Comparison of mediolateral Talairach x-coordinates of midline trunk and hand activation foci in first somatosensory cortex using BrainVoyager and SPM2

Subjects	Midline trunk	Hand
BrainVoyager		
IP	33	45
EP	35	40
FF	34	40
EG	35	45
Mean	34.25	42.5
P	0.02	
SPM2		
LA ^a	28	42
IP	24	46
EP	24	54
EG	38	44
Mean	28.5	46.5
P	0.03	

Paired *t* test of mean Talairach x-coordinates of midline trunk focus vs. hand focus.

^a These subjects received tactile stimulation on the right side only.

The detection of two activation foci in anterior and posterior PCG, likely corresponding to the ventral midline representations on the architectonic borders 3a–3b and 1–2, lends further support to recent evidence obtained after stimulation of other human body regions (i.e., hand), showing that in humans, as in nonhuman primates, the PCG contains multiple body maps, one for each architectonic field constituting SI [Burton, 2001]. Moreover, the mediolateral topographic organization reported here, according to which the PCG foci evoked by trunk stimulation lie more medial and superior than do those evoked by hand stimulation, is in line with the known topographic organization of SI in nonhuman primates [Kaas, 1983; Nelson et al., 1980] and with previous functional human studies [Burton, 2001; Nakamura et al., 1998].

Methodologic Considerations

Reflex muscle contraction (sometime bilateral) evoked by the tactile stimulus used here could be responsible for the ipsilateral cortical activation. This possibility can be ruled out, however, because this contraction, observed in our subjects sometimes also bilaterally, was confined temporally to the initial 4–5 seconds of the first 30-s stimulation period, and analysis of cortical activation takes into account the signal change that occurred over all five 30-s stimulation periods, thus abolishing any event not related temporally to the stimulation protocol.

Consistent results were obtained with two different methods of analysis (BV and SPM2) and with multisubject analysis. The main difference was the presence of a single activation focus (detected with BV and SPM2) compared to two (one anterior and one posterior) often evidenced by FT analysis. Indeed, inspecting the results of a first-level data analysis, two foci were evident also with BV and SPM2. A further level of processing with these two software programs, which required realignment and coregistration of data to a standard Talairach space, may have eliminated less consistent signals.

Comparison With Other Studies

Only two studies, both using MEG, have so far addressed the cortical representation of trunk cutaneous receptors [Itomi et al., 2000; Nakamura et al., 1998]. The first obtained somatosensory responses to gentle, superficial pressure on a contact area about 1 cm in diameter. SI activation was unclear in both the contralateral and the ipsilateral hemisphere. In the second study [Itomi et al., 2000], individual transcutaneous electrical stimulation of dermatomes Th4, Th6, Th8, Th10, and Th12 carried out randomly in different sessions elicited responses in the trunk region of contralateral SI in most subjects, but no ipsilateral activation. One explanation for the unclear activation reported in the former study and for the lack of ipsilateral activation reported in the latter might reside in the extension of the skin regions stimulated in the two investigations. Receptive fields in the trunk region are far larger than 1 cm², and the stimulus likely needs to encompass them entirely to obtain an appreciable re-

sponse. In both studies, the area stimulated thus might have been too small or the activation evoked in the contralateral hemisphere too weak to be transmitted ipsilaterally.

The stimulus used in the present study involved a large area likely encompassing dermatomes Th4 to Th10 that, at variance with the study of Itomi et al. [2000], therefore received simultaneous stimulation. In addition, moving stimuli could be more effective in eliciting a cortical response. This probably produced activation strong enough to be detected in both hemispheres.

In nonhuman primates, the ipsilateral component of the bilateral RFs recorded in the anterior and posterior parietal cortical neurons is mediated by the contralateral hemisphere through the corpus callosum [Conti et al., 1986; Iwamura et al., 1994; see Manzoni, 1997 for a review], although an extracallosal contribution cannot be excluded. In other mammals, bilateral RFs on the trunk surface have been recorded at subcortical sites. Neurons with bilateral RFs in the trunk representation zone have been found in the cat thalamic ventrobasal nucleus [Barbaresi et al., 1984] and in the rat spinal cord [Smith, 1986], thus evidencing a subcortical contribution to the ipsilateral component of bilateral receptive fields, at least in these species.

Bilateral cortical activation of PCG and parietal operculum (PO) by unilateral skin stimulation of the hand has also been reported in humans [see data and literature in Fabri et al., 1999, 2001; Polonara et al., 1999]. Recent functional studies of callosotomized patients have shown the absence of cortical activation of ipsilateral PO upon unilateral tactile stimulation of the hand in patients in whom the callosal fibres running in the posterior third of the body of the commissure are interrupted [Fabri et al., 1999, 2001], demonstrating that the activation evoked in the ipsilateral hemisphere in control subjects by unilateral tactile stimulation of the hand is of callosal origin. By analogy, the ipsilateral activation evoked by tactile stimulation of trunk regions close to the midline might thus also be of callosal origin. Alternatively, the bilateral cortical representation of cutaneous inputs from proximal (e.g., trunk midline) and distal (e.g., hand) body regions might in principle be subserved by different mechanisms, *subcortical* in the former case and *callosal* in the latter. Because block-designed fMRI experiments, such as those used in the present study, do not allow time analysis to be carried out, it is impossible to know whether ipsilateral SI is activated after or simultaneously to contralateral SI. Further research is needed to establish whether the ipsilateral activation depends upon callosal or extracallosal inputs.

ACKNOWLEDGMENTS

We thank Dr. G. Mascioli for carrying out SPM2 analysis and Ms. S. Modena for language revision.

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