Activation of Primary and Secondary Somatosensory Regions Following Tactile Stimulation of the Face

Rainer Kopietz, Vehbi Sakar, Jessica Albrecht, Anna Maria Kleemann, Veronika Schöpf, Indra Yousry, Jennifer Linn, Gunther Fesl, Martin Wiesmann[1]

Abstract

Background: Since the work of Penfield & Rasmussen it is well established that the human primary somatosensory cortex is organized somatotopically. However, the order of the representation of the face is still a matter of discussion, i.e., it is yet unclear whether the face is represented upside-down or vice versa in the somatosensory cortex.

Material and Methods: In a functional magnetic resonance imaging study (n = 30), tactile stimuli to three different locations on each side of the face were applied using a pneumatic device. Locations of stimulation corresponded to the three branches of the trigeminal nerve (forehead, cheek, chin). To determine the representation of the face on primary and secondary somatosensory cortices, peak coordinates within these regions were analyzed subjectwise.

Results: Contralateral activation of the primary somatosensory cortex following tactile stimulation of the face was found, whereas the secondary somatosensory cortices were activated bilaterally. However, differences between activation coordinates of different tactile stimuli applied to one side of the face were not statistically significant.

Conclusion: Tactile stimulation of the face leads to contralateral activation of primary and bilateral activation of secondary somatosensory cortices. Using the authors' methodological approach it was not possible to detect a somatotopic organization related to different facial areas.

Key Words: Somatosensory · Mechanoception · Somatotopy · Homunculus · Trigeminal nerve

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Aktivierung primärer und sekundärer somatosensorischer Regionen nach taktiler Stimulation des Gesichts

Zusammenfassung

Hintergrund: Seit Penfield & Rasmussen ist bekannt, dass der menschliche primäre somatosensorische Kortex somatotopisch organisiert ist. Die Reihenfolge dieser Repräsentation wird jedoch immer noch diskutiert, d.h., es ist nicht klar, ob das Gesicht in kraniokaudaler oder in kaudokranialer Reihenfolge repräsentiert ist.

Material und Methodik: Mittels funktioneller Magnetresonanztomographie wurden an 30 Probanden taktile Stimuli an drei verschiedenen Orten auf jeder Seite des Gesichtes mit einem pneumatischen Gerät appliziert (Stirn, Wange, Kinn). Diese Orte korrespondierten mit den drei Ästen des N. trigeminus. Um die Repräsentation des Gesichts in primären und sekundären somatosensorischen Kortizes zu untersuchen, wurden Koordinaten lokaler Maxima probandenweise innerhalb dieser Regionen bestimmt.

Ergebnisse: Es konnte eine kontralaterale Aktivierung des primären somatosensorischen Kortex bei taktiler Stimulation des Gesichts festgestellt werden. Der sekundäre somatosensorische Kortex war bilateral aktiviert. Die Unterschiede in den Aktivierungskoordinaten der verschiedenen taktilen Stimuli auf einer Seite des Gesichts waren jedoch nicht signifikant.

Schlussfolgerung: Taktile Stimulation des Gesichts führt zu einer kontralateralen Aktivierung des primären und bilateralen Aktivierung des sekundären somatosensorischen Kortex. Mit der verwendeten Methodik konnte eine somatotopische Auflösung verschiedener Gesichtsareale nicht erreicht werden.

Schlüsselwörter: Somatosensorisch · Mechanozeption · Somatotopik · Homunkulus · Nervus trigeminus

[1] Department of Neuroradiology, University of Munich, Germany.

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Introduction

Somatosensory perception is one of the most basic functions of the nervous system. The somatosensory system is not a single sensory system but a multiple one composed of several submodalities. Major submodalities include haptics (fine touch and pressure), proprioception (body awareness), and nociception (pain and temperature).

Afferent somatosensory fibers from the body are organized in two major pathways, one for epicritic sensibility, and one for protopathic sensibility. Epicritic sensibility includes fine touch, conscious proprioception, and vibratory sense. Protopathic sensibility includes rough pressure, pain, and temperature. Epicritic fibers ascend in the dorsal column of the myelon, protopathic fibers ascend in the anterior and lateral spinothalamic tract of the myelon. The fibers from both pathways reach the ventrobasal thalamus through the medial lemniscus. From there fibers project to the primary somatosensory cortex (SI), specifically Brodmann's areas 3-1-2 on the postcentral gyrus. In contrast to the transduction of somatosensory information from the body, somatosensory signals from the face are transmitted by the trigeminal nerve mainly through the trigeminal spinal tract to the trigeminal nuclear complex which is somatotopically organized [1]. Second-order neurons then project to contralateral thalamic nuclei [2]. From there fibers mainly project to SI. A few of the fibers project directly to the secondary somatosensory cortex (SII) which is located in the parietal operculum. Due to its reciprocal connections to SI and its connections to the motor cortex, SII is believed to be involved in sensorimotor integration [3].

Since the work of Penfield & Rasmussen [4] it is known that the primary human motor and sensory cortices are organized somatotopically. Their famous visualization of the somatotopically organized cortex has been termed homunculus. New models suggest that SI comprises four subsections. These subsections, namely areas 3a, 3b, 1, and 2, form a separate homunculus for each somatosensory modality. Although the homunculi are organized in parallel to each other, they are characterized by different granularities or overlapping representations [5].

Yet unclear within the topography of the homunculi is the orientation of the face representation. Penfield & Rasmussen [4] proposed a representation of forehead, cheek, and chin in craniocaudal order along the postcentral gyrus. Instead, newer studies showed evidence for an upside-down representation [6]. Other studies could not confirm either orientation [7].

By contrast, our knowledge about a somatotopic organization of SII is still limited. Using functional magnetic resonance imaging (fMRI), a somatotopy in SII could be demonstrated between hallux and fingers [8]. As yet, somatotopic representation of the face area has not been reported [9].

Therefore, in this study we aimed to investigate the representation of the facial skin on SI and SII using fMRI. This was accomplished by tactile stimulation of three different areas on each side of the face, corresponding to the three branches of the trigeminal nerves.

Material and Methods

Subjects

30 healthy subjects (17 females, 13 males; age 21–43 years; mean age 29 ± 6.17 years; handedness: 22 right-handed) participated in the study. All subjects gave their written informed consent. The study was approved by our local ethics committee.

Experimental Procedure

Participants were lying in the scanner with their eyes closed [10] and their heads carefully fixated using a vacuum headrest. They were advised to lie still and not to perform any action. During each of two scanning sessions per subject blocks of tactile isobaric stimuli were applied to locations corresponding to the three branches of the trigeminal nerve on each side of the face (forehead left/right, cheek left/right, and chin left/right). Each block consisted of a stimulus (e.g., forehead left) repeated 16 times with a frequency of 1 Hz resulting in a 16-s block. Five blocks per stimulus type resulting in 30 stimuli blocks were applied in randomized order intercepted by rest conditions of the same length. The first and the last block of every session were rest conditions.

Stimulus Device

For the application of isobaric tactile stimuli a pneumatic device was developed. The device consisted of six half-open pressure tubes, one for each stimulus location. On the open side, which was affixed to the skin, the tubes were coated with a rubber membrane. They were connected by plastic tubings to a single source of compressed air of approximately 1 bar (see Figure 1). The inlets of the tubes were controlled by a computer-controlled valve. When the valve was opened, the pressure

Figure 1. Positioning of subject within the head coil. Six tubings for tactile stimulation are attached to the subject's forehead, cheek, and chin.

at the rubber membrane increased effecting a moderate tactile sensation.

Data Acquisition

Functional images were acquired on a 1.5-T standard clinical scanner (Siemens Erlangen, Germany) using echo-planar imaging (EPI) with a T2*-weighted gradient-echo multislice sequence. The parameters of the sequence were: TE (echo time) = 60 ms, voxel size 3.75 × 3.75 × 6.25 mm^3, matrix size 64 × 64, interscan interval 3.2 s. 26 half-coronal slices covering the whole brain and eyes of the subject were acquired. The slices were adjusted orthogonally to the bisecting line of an angle between intercommissural line and brain stem line based on a sagittal localizer image.

Data Analysis

Data processing was performed using statistical parametric mapping (SPM2) [11]. The first five images of each scanning series were discarded to eliminate spin saturation effects. Motion correction was performed by realigning each volume to the first one of the scanning series [12]. A correction for field inhomogeneities was applied to the volumes [13]. Then the image volumes were spatially normalized into the standard space defined by the Montreal Neurological Institute (MNI) EPI template [12]. The resulting voxel size was 2 × 2 × 2 mm^3. Afterwards the datasets were smoothed using an 8-mm (FWHM) isotropic Gaussian kernel to compensate intersubject gyral variability and to attenuate high-frequency noise in order to improve signal-to-noise ratio. For single subject analyses statistical parametric maps were calculated using the general linear model with hemodynamic models [11]. A first-level analysis comprised of the two scanning sessions was carried out for each subject with the realignment parameters from the motion correction of each single session included as covariates. Contrasts for each of the six stimuli (e.g., forehead left, cheek left, etc.) and the combination contrast of the three stimulus conditions for each side of the face (e.g., forehead left + cheek left + chin left) were formed. A second-level analysis (one-sample t-test) was performed on the resulting contrast images.

Within the second-level analysis the combination contrasts of the three stimulus conditions for each side of the face were used to determine two search coordinates for each hemisphere corresponding to SI and SII. The search coordinates were obtained manually by selecting a local maximum within these anatomic regions at thresholds varying from $p < 0.001$ to $p < 0.05$ (uncorrected) in order to find search coordinates for weaker activations as well.

These anatomically confirmed coordinates were used to look up the activation peak coordinate for each single stimulus contrast within the first-level analysis of each subject:

We employed two methods to search the activation coordinates in the SI region on the first-level analyses of each subject. First, the anatomically confirmed search coordinates from the second-level group analysis were used to find the nearest local maximum within a search radius of 16 mm. This was done within the first-level analysis of each subject thresholded at $p < 0.001$ (uncorrected) for each stimulus condition. The resulting lists of coordinates were filtered to contain only postcentral coordinates that were confirmed by automated anatomic labeling (AAL) [14].

Second, the ten highest local maxima within a radius of 16 mm around the search coordinates were identified. This was done to avoid overlooking local maxima which did not satisfy the constraint of being the nearest one to the search coordinate, i.e., a local maximum that is even higher than the maximum next to the search coordinate. Again, the found coordinates had to satisfy the constraint to be located within the postcentral gyrus confirmed by AAL. Using this search method, local maxima which did not hold a threshold of $p < 0.05$ (uncorrected) were discarded.

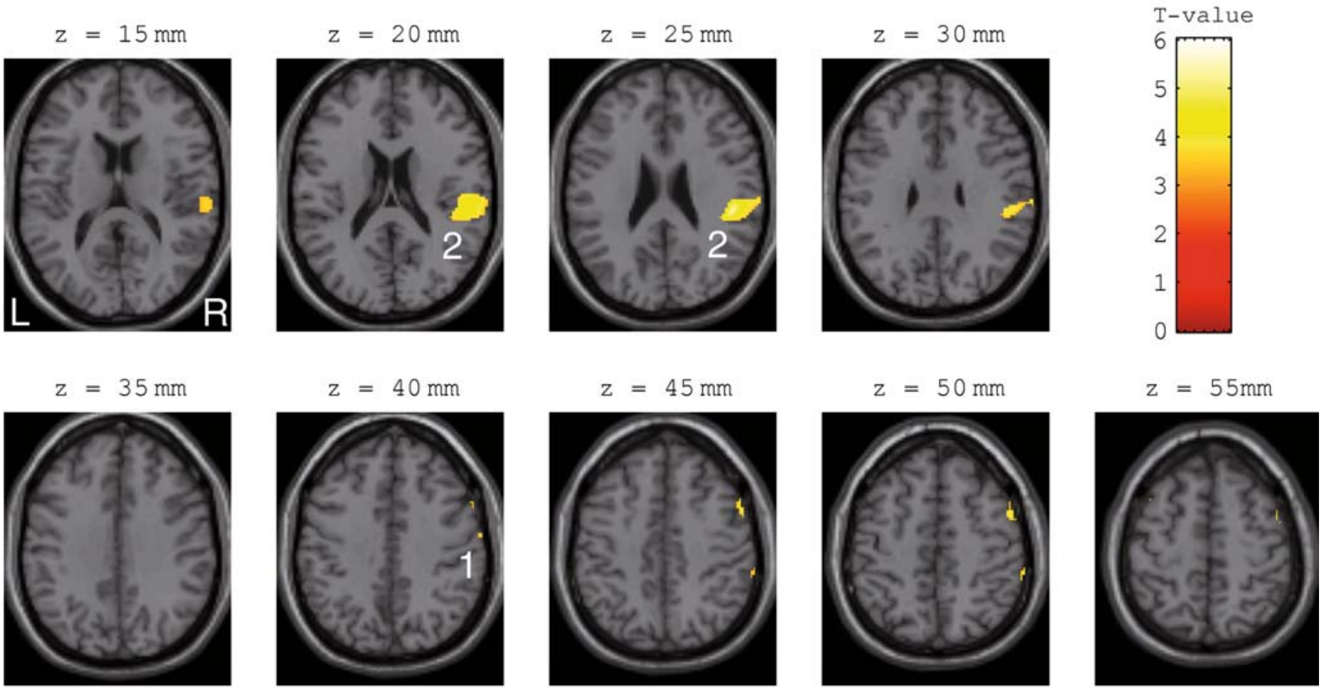

Figure 2. Results of tactile stimulation of the facial skin. The combination contrast of stimulation of left forehead, left cheek, and left chin is shown ($p < 0.001$, uncorrected, random effects analysis, n = 30). Tactile stimulation effected activation of contralateral SI (1) and SII (2) areas.

For each stimulus, the resulting coordinates of search method 1 were averaged to create a mean activation coordinate for the stimulus location. Coordinates of the highest activation peak found by method 2 were averaged accordingly.

To find activation coordinates within the SII region, only the first method was employed on the first-level analysis of each subject. Coordinates not located in the AAL regions superior temporal gyrus, supramarginal gyrus, or rolandic operculum were discarded. Again, the resulting activation coordinates of each stimulus condition were averaged.

Results

As expected, the second-level group analysis revealed contralateral activation in SI for the combination contrast of the three stimuli applied to one side of the face ($p < 0.001$, uncorrected). No ipsilateral activation in SI was noted following tactile stimulation of the face. Activation of the contralateral SII was found at $p < 0.001$ (uncorrected). Ipsilateral activation of SII was seen at a threshold of $p < 0.01$. Figures 2 and 3 show the activation loci at a threshold of $p < 0.001$ (uncorrected) for the combination contrasts of stimuli applied to one side of the face.

As mentioned above, the activations in SI and SII found in the random effects analyses for the combination of stimuli of each side of the face were used to define the coordinates for the centers of search volumes (listed in Table 1).

When performing a subjectwise search for the nearest local maximum of the search coordinate (method 1) in contralateral SI at a threshold of $p < 0.001$ (uncorrected), we found local maxima in 9/30 subjects when stimulating the right forehead, in 13/30 subjects when stimulating the right cheek, and in 11/30 subjects when stimulating the right chin. Similar numbers of local maxima were found for the contralateral SI when stimulating the left side of the face: 4/30 left forehead, 11/30 left cheek, and 12/30 left chin (Table 2). Mean values and standard deviations of the resulting coordinates are listed in Table 3 and depicted on the yz-plane in Figure 4. t-tests did not reveal a significant difference in means and therefore no somatotopic order of activation loci.

The alternative method of selecting the highest local maximum for the SI region at a lower threshold ($p < 0.05$, uncorrected) resulted in a higher number of coordinates (see also Table 2). Mean coordinates are listed in Table 3.

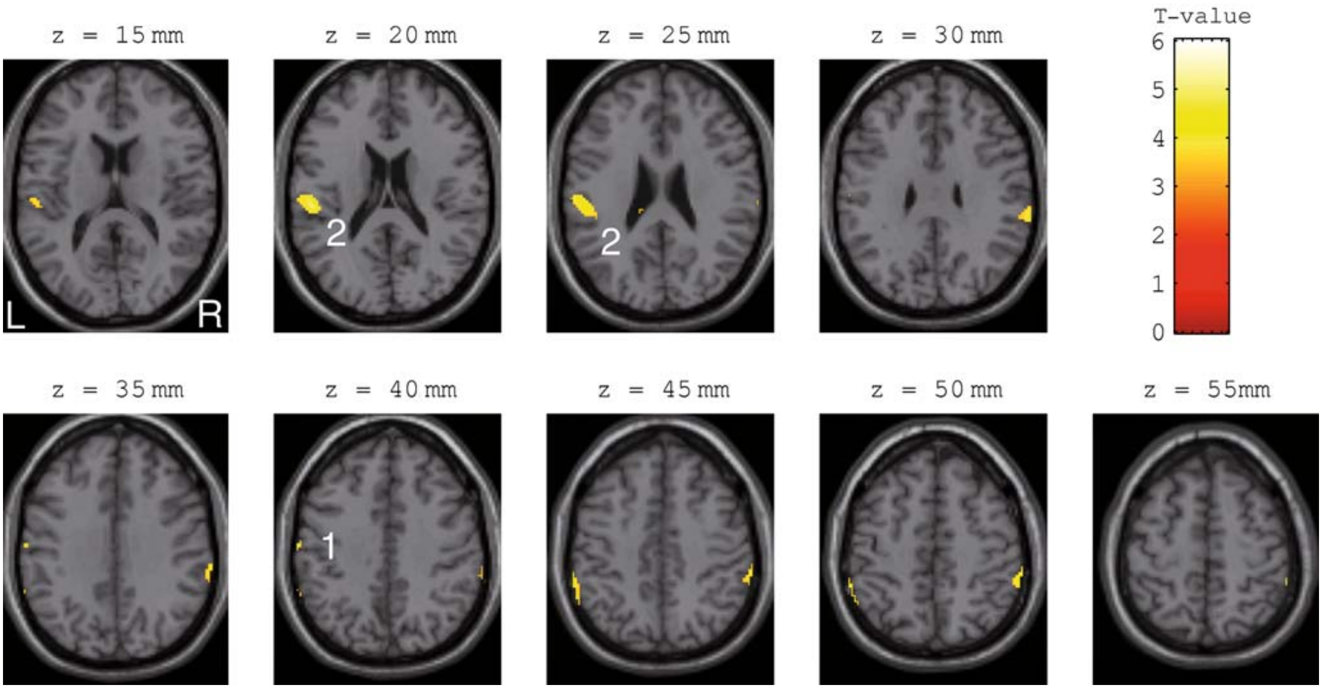

Figure 3. Results of tactile stimulation of the facial skin. The combination contrast of stimulation of right forehead, right cheek, and right chin is shown ($p < 0.001$, uncorrected, random effects analysis, $n = 30$). Tactile stimulation effected activation of contralateral SI (1) and SII (2) areas.

More robust activations could be found for the search volume around the contralateral SII coordinate. For stimulation of the left side of the face we found local maxima in contralateral SII in 17/30 subjects (stimulation of forehead), 13/30 (cheek), and 15/30 (chin); for stimulation of the right side we found local maxima in contralateral SII in 15/30 subjects (forehead), 20/30 (cheek), and 15/30 (chin). Ipsilateral local maxima for stimulation of the left side were found in 9/30 subjects (forehead), 10/30 (cheek), and 11/30 (chin); for stimulation of the right side: 12/30 (forehead), 15/30 (cheek), and 11/30 (chin).

Mean values and standard deviations of the coordinates can be found in Table 4. Figures 5 and 6 show these coordinates on the xy-plane. Again, t-tests did not show any significant difference in means and therefore did not yield evidence for a somatotopic organization.

Discussion

This study aimed to investigate the activation of SI and SII in humans following tactile stimulation of the facial skin. We compared the effects of isobaric stimulation of three different facial locations per side. Tactile stimulation led to unilateral activation of the contralateral SI, whereas SII was activated bilaterally. However, we were not able to provide statistical evidence for a somatotopic representation of the different facial locations in SI or SII.

Stimulation Paradigm

We decided to use a paradigm of pneumatic tactile stimulation applying isobaric stimuli to the forehead, cheek, and chin, corresponding to the three divisions of the trigeminal nerve. To facilitate discrimination between anatomic locations, we aimed to induce activation in small areas of the cortex only. Therefore, we chose stimuli of moderate intensity to effect a monomodal tactile stimulation only. Although all stimuli were isobaric, our subjects reported that they perceived them as weaker on the forehead than on the cheek or chin. This finding may be due to differences in the density of skin receptors and may have influenced our results regarding SI activation (see below).

Methodical Considerations on the Data Analysis

Obviously, the algorithm to identify activations has a strong implication on the results. We decided to search for local activation maxima in individual subjects for the following reasons: we assumed that the representation

Table 1. Search coordinates in MNI space revealed by second-level analysis. MNI: Montreal Neurological Institute; SI: primary somatosensory cortex; SII: secondary somatosensory cortex.

Combination contrast	Search area	Left hemisphere (x/y/z; mm)	Uncorrected p-value	Right hemisphere (x/y/z; mm)	Uncorrected p-value
Left forehead + left cheek + left chin	SI			(64/–8/40)	0.001
Right forehead + right cheek + right chin	SI	(–62/–14/40)	0.001		
Left forehead + left cheek + left chin	SII	(–48/–30/24)	0.05	(48/–30/26)	0.001
Right forehead + right cheek + right chin	SII	(–52/–26/22)	0.001	(56/–22/24)	0.01

of neurologic function, e.g., tactile sensation of the face, is located where the cortical surface displays the highest neuronal excitation. In general, this corresponds to the coordinate with the strongest blood oxygenation level-dependent (BOLD) signal change, i.e., a local maximum in the statistical t-value landscape. We excluded coordinates located outside the cortex or in other regions by anatomic masking.

To be able to identify local maxima, we first needed to restrict the search area. While it was well justified by neuroanatomic evidence to limit the search area to the postcentral gyrus, we still needed to define the area of interest in the craniocaudal direction. To do so, we performed a random effects group analysis based on a combination contrast of all stimulations of each side of the face versus baseline. We assumed that the resulting coordinates were well within the face area of the somatosensory cortices. It is a possible limitation of our study, however, that stimulation of the forehead was perceived as being weaker than stimulation of the cheek or chin. In consequence, not all local stimulations may have contributed equally to the combination contrast and thus the resulting coordinates may be biased. To overcome this, we performed a second analysis: we did not only identify the nearest local maximum to the search coordinates, but also identified the strongest local maximum on the postcentral gyrus within a radius of 16 mm around the search coordinates. We decided for a radius of 16 mm based on evidence from other neuroimaging studies: the face area in SI is located between the representations of the thumb and the tongue. In z-direction these representations differ by roughly 20 mm (see below) [15–17]. Dimensions of SII are smaller than those of SI. A search area with a total diameter of 32 mm could therefore well be expected to suffice.

Table 2. Number of activations in contralateral SI (n = 30). NA: no search performed within this region; SI: primary somatosensory cortex.

Stimulation	Nearest local maximum ($p < 0.001$, uncorrected) Left SI	Right SI	Highest local maximum ($p < 0.05$, uncorrected) Left SI	Right SI
Right forehead	9	NA	13	NA
Right cheek	13	NA	19	NA
Right chin	11	NA	17	NA
Left forehead	NA	4	NA	15
Left cheek	NA	11	NA	17
Left chin	NA	12	NA	17

Activation of SI Following Tactile Stimulation

In line with the neuroanatomic literature we observed unilateral activation of the contralateral SI following tactile stimulation of the face. Our results regarding the precise location of the representation of the face were

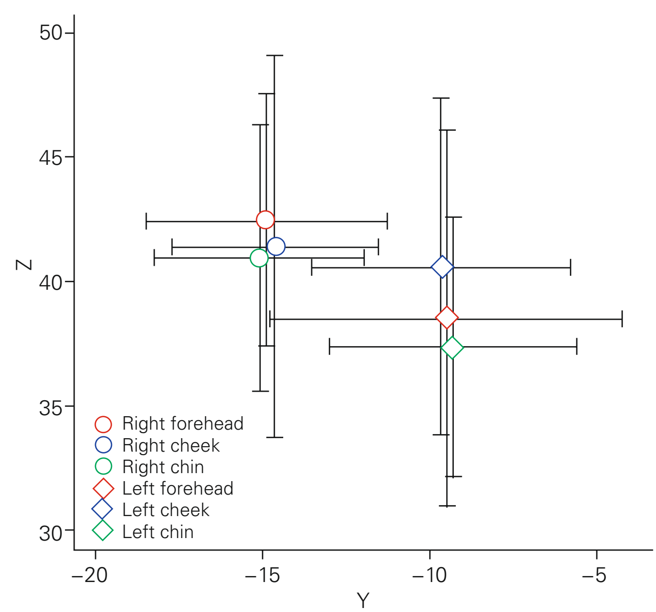

Figure 4. Mean coordinates of SI activation of different contralateral stimuli (whiskers indicate the standard deviation of the mean). Shown are only y- and z-coordinates. The coordinates were found by selecting the nearest local maximum within a search radius of 16 mm at a threshold of $p < 0.001$ (uncorrected). This was done for all stimulus conditions within each volunteer's first-level analysis.

Table 3. Mean coordinates of contralateral SI activation (standard deviations in parentheses). The coordinates were found either by selecting the nearest (upper section) or the highest local maximum (lower section) within the search radius of 16 mm at a given threshold. SI: primary somatosensory cortex.

Stimulation	Mean coordinate of nearest local maximum to search coordinate ($p < 0.001$, uncorrected) x	y	z
Right forehead	–57.11 (3.02)	–14.89 (3.62)	42.44 (5.08)
Right cheek	–57.85 (3.51)	–14.62 (3.1)	41.38 (7.72)
Right chin	–56.91 (2.26)	–15.09 (3.14)	40.91 (5.39)
Left forehead	65.0 (2.58)	–9.5 (5.26)	38.5 (7.55)
Left cheek	61.82 (3.52)	–9.64 (3.88)	40.55 (6.76)
Left chin	63.33 (3.34)	–9.33 (3.66)	37.33 (5.21)
Stimulation	**Mean coordinate of highest local maximum within search radius ($p < 0.05$, uncorrected) x**	**y**	**z**
Right forehead	–56.92 (3.43)	–14.92 (3.97)	41.08 (9.11)
Right cheek	–57.37 (3.53)	–14.21 (4.57)	39.89 (7.84)
Right chin	–58.24 (3.73)	–15.41 (2.98)	38 (8.15)
Left forehead	61.73 (5.23)	–10.8 (4.83)	36.53 (7.07)
Left cheek	61.65 (3.95)	–10.59 (3.73)	36.94 (8.4)
Left chin	61.18 (4.07)	–10.47 (4.77)	36.71 (6.52)

Table 4. Mean coordinates of contra- and ipsilateral SII activations (standard deviations in parentheses). The coordinates were found by selecting the nearest local maximum within the search radius at a threshold of $p < 0.001$ (uncorrected). SII: secondary somatosensory cortex.

Stimulation	Contralateral coordinate (mm) x	y	z
Right forehead	–49.87 (3.50)	–29.73 (4.83)	19.6 (4.91)
Right cheek	–50.80 (4.42)	–28.10 (6.03)	18.20 (3.61)
Right chin	–48.67 (5.22)	–28.8 (4.83)	19.07 (3.37)
Left forehead	49.18 (4.07)	–30.94 (4.31)	23.29 (5.14)
Left cheek	49.85 (5.91)	–30.31 (4.23)	20.46 (2.85)
Left chin	48.8 (5.39)	–31.07 (4.46)	22.27 (3.2)
Stimulation	**Ipsilateral coordinate (mm) x**	**y**	**z**
Right forehead	56.83 (4.22)	–27.83 (5.87)	19.33 (5.14)
Right cheek	53.87 (5.04)	–26.53 (6.82)	22.27 (4.83)
Right chin	55.45 (8.25)	–27.09 (7.50)	23.64 (4.27)
Left forehead	–51.78 (4.94)	–31.33 (4.24)	20.67 (5.57)
Left cheek	–50.6 (4.33)	–29 (2.87)	20.6 (3.27)
Left chin	–47.09 (4.23)	–31.64 (6.12)	21.64 (3.88)

consistent with the classic "somatosensory homunculus" proposed by Penfield & Rasmussen [4]. On the somatosensory map of Penfield & Rasmussen [4] the facial skin is represented on the postcentral gyrus beneath the thumb and superior of the tongue. Van Westen et al. [15] detected the thumb at a coordinate of z = 53. We found the contralateral face area (combination contrast of all three stimulation conditions) to be located in the postcentral gyrus at z = 40. Pardo et al. [16] found the tactile representation of the tongue in SI at z = 29 and z = 27 (left: x, y, z = –51, –15, 27; right: x, y, z = 55, –10, 29). Fesl et al. [17] investigated the effects of tongue movement and found activations in both precentral and postcentral gyri between z = 30 and z = 34 (left: x, y, z = –62, –6, 34; right: x, y, z = 66, –6, 30).

We were surprised by the generally weak activation we observed in SI following tactile stimulation. The level of activation in SI was also weaker than that observed in SII. Moreover, our results show that tactile stimulation of the chin and the cheek clearly leads to a higher number of detectable activations in SI than stimulation of the forehead. Several reasons may combine to explain these findings. (1) As outlined in the introduction, SI is anatomically comprised of Brodmann's areas 3a, 3b, 1, and 2 in anterior to posterior order with increasing complexity with respect to receptive fields [5, 18]. Each area receives input from certain receptor types. In the somatosensory cortex model described in the work of Iwamura [5] and Kolb & Wishaw [19], area 3b receives input from the slowly adapting skin receptors. Since the type of stimulus we used in the experimental setup was designed to stimulate this kind of receptor only, it is likely that only area 3b was activated. This should lead to a rather small area of activation which will be harder to detect in fMRI. (2) Other researchers have also reported that the activation of SI was generally weaker than that of SII [20, 21]. SII by itself projects back to superficial layers of SI [5]. A modulation of neuronal activity in SI by SII has been shown by Burton et al. [20]. It has been proposed that this effect involves attention [5]. Thus, to obtain robust levels of activation in SI, it might be necessary to control the attention of the subjects toward the stimuli. We decided against that and chose a paradigm of passive perception instead because we did not want activations in SI to be modulated by any directed response to the stimuli. (3) The density of somatosensory receptors varies greatly from one place to another on the body surface and somatotopic maps

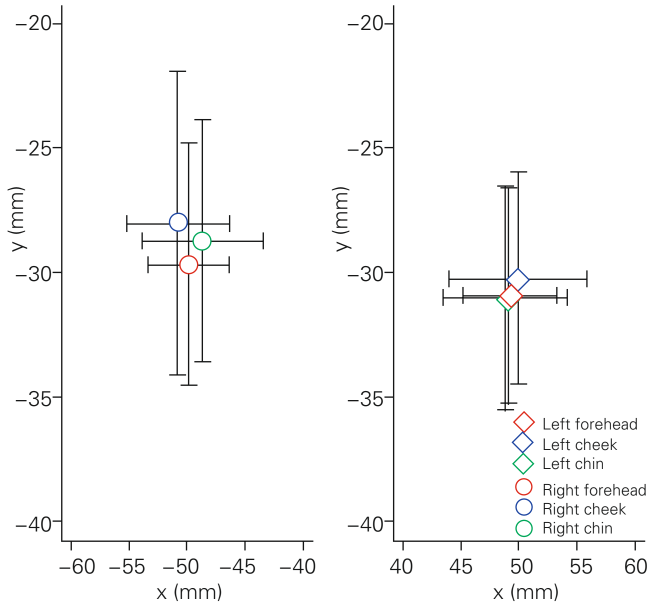

Figure 5. Mean coordinates of contralateral SII activation (whiskers indicate the standard deviation of the mean). Shown is only the xy-plane. The coordinates were found by selecting the nearest local maximum within a search radius of 16 mm at a threshold of $p < 0.001$ (uncorrected). This was done for all stimulus conditions within each volunteer's first-level analysis.

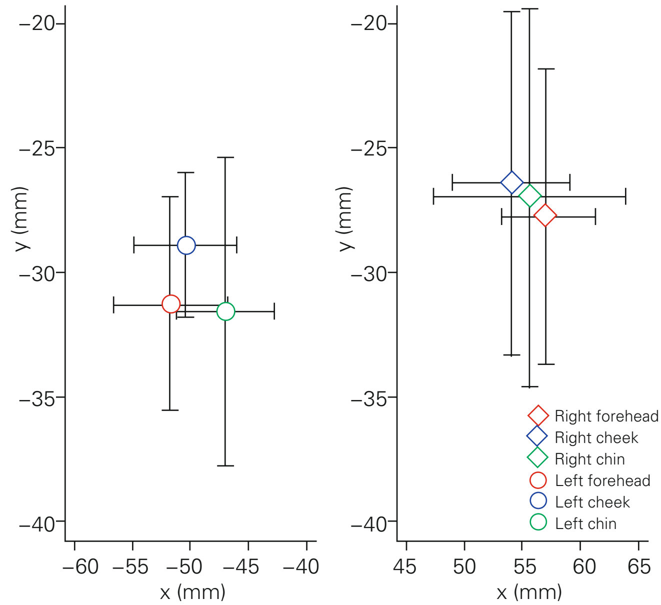

Figure 6. Mean coordinates of ipsilateral SII activation (whiskers indicate the standard deviation of the mean). Shown is only the xy-plane. The coordinates were found by selecting the nearest local maximum within a search radius of 16 mm at a threshold of $p < 0.001$ (uncorrected). This was done for all stimulus conditions within each volunteer's first-level analysis.

manifest this variability [19]. The two-point discrimination distance, measuring the minimum distance of two solely perceived tactile stimuli, which in turn depends on the density of somatosensory receptors, of the forehead is more than five times larger (17 mm) than the distance measured at the cheek (3 mm) [22]. Stimulation of an area on the forehead may therefore activate a smaller portion of the postcentral gyrus than stimulation of an equally sized area on the cheek. As outlined above, subjects also perceived the tactile stimuli to the forehead as being weaker than those to the cheek or chin. Both factors may combine to explain why the number of subjects in whom we observed activation loci in SI differed depending on the location on the face being stimulated. The number of activation loci we observed when simulating the forehead was lower than the numbers for cheek and chin. To overcome this effect and achieve robust activation after stimulation of the forehead, it may be necessary to use different stimulation probes for different areas of the face.

Recently, other groups have reported that using tactile stimulation paradigms optimum BOLD responses can be achieved with stimulation frequencies between 3 Hz and 8 Hz [23–25]. There may be a significant signal loss using lower or higher frequencies. Moreover, pronounced habituation may occur in SI. Therefore, very short stimulation blocks (< 10 s in duration) or event-related paradigms should be used to achieve optimum results in SI. It has been reported that habituation is less relevant for SII. These findings may very well explain why we achieved a robust bilateral activation in SII but observed a rather weak activation in SI.

Activation of SII Following Tactile Stimulation

We observed a robust bilateral activation of SII after unilateral tactile stimulation of the face. Ruben et al. [8] also found bilateral activation of SII following tactile stimulation. According to Ruben et al. [8] these bilateral signal changes probably rely on afferent inputs reaching contra- as well as ipsilateral SII (see also [26, 27]). The coordinates we found regarding the representation of the face in SII were also in line with those reported by other groups. For example, following tactile stimulation of the right cheek Nguyen et al. [9] reported a coordinate of –54.3 –27.6, 19.4 (converted to MNI space) in a magnetoencephalography study.

Somatotopic Representation of the Face in SI

There is ample evidence that SI is organized in somatotopic order although it is also known that there may be considerable overlap between receptive fields [18, 28]. As outlined in the introduction, Penfield & Rasmussen [4] reported that the representation of the face in SI is organized along the central sulcus with the forehead in the superomedial region adjacent to the hand area, and the chin in the inferolateral region. This has been challenged by some authors who proposed that the representation of the face in SI is upside-down as compared to Penfield's homunculus [6]. We stimulated both sides of the face and used two different algorithms to identify activations within contralateral SI. However, we could not identify a statistically significant order of representation. Therefore, our results can neither support the model proposed by Penfield & Rasmussen [4] nor the model proposed by Servos et al. [6].

Somatotopic Representation of the Face in SII

Our knowledge about the organization of SII is still limited. There is some evidence on a somatotopic organization of SII although it might not be as strict as in SI. Using fMRI, Ruben et al. [8] were not able to show a somatotopy for neighboring body parts like digits, but they could show distinct receptive fields for the hallux and the representation of several fingers in SII. Their conclusion was that SII is probably less fine grained with receptive fields overlapping to a greater extent than in SI. There was a trend in our data that the representation of the cheek in SII was located more anterior to the representation of forehead and chin (see Figures 5 and 6). However, differences between coordinates were small and statistically not significant. Our results therefore do not provide evidence for a somatotopic organization of SII.

Several methodical approaches may be combined in order to be able to demonstrate somatotopy in future studies. (1) As mentioned above, it should be possible to increase the level of activation in SI by modifying the stimulation probes and by controlling the subjects' attention toward the stimuli. (2) Because of the inherently low signal-to-noise ratio of the 1.5-T MR scanner we used, we kept the voxel size rather large at $3.75 \times 3.75 \times 6.25$ mm^3. Future studies will be performed at higher field strengths enabling us to increase the geometric resolution.

Conclusion

In this study we were able to confirm the activation of SI and SII following tactile stimulation of the face but could not provide statistical evidence for a somatotopic representation of the different facial locations in SI or SII. Since there is evidence of such an organization, it is very likely that positive results can be obtained if the experimental approach is improved, and the results of this report will enable us to do so in future studies.

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Conflict of Interest Statement

The authors declare that there is no actual or potential conflict of interest in relation to this article.

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Address for Correspondence
PD Dr. Martin Wiesmann
Department of Neuroradiology
University of Munich
Marchioninistraße 15
81377 München
Germany
Phone (+49/89) 7095-2501, Fax -2509
e-mail: martin.wiesmann@med.uni-muenchen.de