

The gradient-based intrinsic coordinate system of the tactile cortex in the hand: a 7T fMRI study

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Abstract

Somatotopy is an important organizing principle in the somatosensory system, where the spatial location information of each body part constitutes its topology. The somatosensory homunculus, which is derived from electrophysiological studies, depicts the topology of the tactile representation within the primary somatosensory cortex (SI). However, how to construct a tactile intrinsic coordinate system in the brain to describe the underlying distribution mechanism of the topology map remains unclear. In this study, we depicted a detailed tactile topology map and an intrinsic coordinate system of the hand using high-resolution 7 Tesla task-state functional magnetic resonance imaging (7T ts-fMRI) and T1 imaging. Twelve participants (four females, aged 22–29 years, mean age 25.8) were evaluated. We investigated the topology map of the nondominant hand using a population receptive field (pRF) model, revealing a clear and orderly topological map in the between- and within-digit dimensions. In the between-digit dimension, the five digits and the palm were arranged along the postcentral gyrus from ventral to dorsal. The within-digit dimension suggests the existence of four mirrored within-finger maps in four subregions of the SI. Furthermore, we investigated the functional and structural gradients within the SI. The primary functional gradient and secondary structural gradient were first proposed as the core organizational axes of the tactile cortex, and a tactile intrinsic coordinate system was constructed. Exploring the human somatosensory cortex along these intrinsic dimensions can provide deeper insights into the distinct topographical organization of the hand across both between- and within-digit dimensions.

1. Introduction

The human hand and brain are deeply interconnected, enabling the exploration of the physical world and the ability to reshape selected segments of it according to human intentions¹. These functions rely heavily on accurate descriptions of mechanical events when objects come in contact with the hand. Mechanoreceptors located in the hairless skin of the palm play a key role in providing this sensory information¹. Tactile sensation arises through contact between tactile receptors in the skin and mechanical stimuli². The skin of the hands is highly specialized for detecting spatial and temporal cues that support the perception of an object's texture and form, particularly in the hairless skin of the palm³. The anatomical differences between the volar aspect and the dorsal hairy portions of the hand reflect their different roles in physiological function: the volar aspect of the hand is responsible for fine motor tasks and grip strength, whereas the dorsal hairy portions of the hand are mainly responsible for finger extension and motor control. Therefore, the hairless skin sensation of the hand is an important source of information about the external environment, and it is also the focus of this paper.

The tactile topology map of the hand is crucial for understanding the human somatosensory system, as well as for rehabilitation and other clinical therapies⁴. Beginning in the 1930s, Penfield and his colleagues mapped the human primary somatosensory cortex (SI) using direct cortical stimulation, and discovered that the hand occupies the largest area within the SI⁵. With the development of magnetic resonance imaging (MRI), many studies have focused on noninvasive methods to generate

topographical maps of SI⁶. The postural organization of the hand has already been established in SI, with the position of the thumb located far below and laterally, whereas the positions of the other fingers are increasingly above and medial, followed by the palm^{7,8}. The functional mapping of individual fingers and their phalanges on the cortex is of great interest. Functional magnetic resonance imaging (fMRI) investigations have demonstrated a correlation between spatial tactile acuity and the cortical representation of fingertips in the SI, particularly within Brodmann areas (BAs) 3b and BA1^{9,10}. Blankenburg et al.¹¹ identified a systematic anterior-to-posterior arrangement with mirrored cluster patterns in these regions at the group level, whereas such patterns were not observed in individual subjects. In contrast, Schweisfurth et al.⁹ did not identify somatotopic organization within the index finger but did reveal a medial-to-lateral gradient from the base to the tip of the little finger within BA3b in individual subjects. Overall, most of the current studies are limited to the topology of limited fingers in dominant or nondominant hands, and the results are not consistent. This inconsistency may be related to individual differences in the use of dominant hands¹², or may be due to the failure to effectively integrate external tactile stimuli with the receptive field properties of cerebral cortical neurons. The use of ultrahigh-field fMRI allows for the study of brain responses to single-finger stimuli¹³. Therefore, it is particularly important to study the tactile topology of the non-dominant hand by 7 Tesla (7T) fMRI technology and establish a unified tactile intrinsic coordinate system in the brain to describe the characteristics of tactile topology distribution.

Constructing an intrinsic coordinate system for the human tactile cortex of the hand presents significant challenges. However, using gradients offers a novel perspective for understanding the tactile cortex in relation to its inherent dimensions. A gradient represents an axis of variation in cortical characteristics, along which regions are arranged in a spatially continuous manner¹⁴. This gradient embodies a fundamental dimension of the intrinsic coordinate system of the human cerebral cortex¹⁵. Global connectivity patterns have revealed a sensorimotor to transmodal gradient that is closely associated with local microstructural features and intrinsic cortical geometry¹⁶. In addition, many studies have investigated the gradient distribution patterns of localized brain regions and obtained hierarchical axes within these regions, such as the thalamus¹⁷, cerebellum¹⁸ and corpus callosum¹⁹. Using fMRI, as well as sensitive spectral analysis, a somatotopic gradient was found in the precuneus²⁰. Moreover, in patients with sensory impairment, the gradient continuity of the SI and the supplementary motor area (SMA) was found to be disturbed²¹. The above studies provide a research basis for gradient research in tactile brain areas and provide the possibility for establishing a tactile intrinsic coordinate system. Therefore, we may be able to identify the principal axis of the intrinsic coordinate system within the tactile cortex of the hand through functional and structural gradient analysis methods, which will provide deeper insights into the interpretation of tactile topology maps.

In this study, we designed a phase-encoding experiment utilizing 7T fMRI to assess SI activation. We recruited right-handed participants and employed the population receptive field (pRF) model to assess the topographical organization within the SI of individual participants. To elucidate the spatial

organization mechanisms underlying the tactile topology map, we conducted functional and gradient analyses. We hypothesized that the tactile topography of the hand has an orderly representation along the postcentral gyrus and that there is a different topographical organization across between-digit and within-digit dimensions. This pattern of organization may be related to a gradient-based intrinsic coordinate system within the human tactile cortex of the hand.

2. Materials and Methods

2.1 Participants

Twelve right-handed individuals (four females, aged 22–29 years, mean age 25.8 years) participated in the study. To ensure experimental rigor, all participants were assessed by the Edinburgh Handedness Inventory (EHI)²². The evaluation confirmed that all the participants were right-handed, with a mean EHI score of 95 and a standard deviation of 8.3. In this experiment, in order to eliminate the error caused by the difference in the use of the dominant hand, we chose to stimulate the hairless skin on the palm side of the left hand of the participants. Moreover, according to the brain lateralization effect²³, we analyzed the activation of the right hemisphere. The participants were in good health, with normal visual, auditory, and tactile functions, and no history of neurological or psychiatric conditions. Owing to excessive head motion, MRI data from two participants were excluded, leaving 10 participants for the final analysis. The study protocol was approved by the Ethics Committee of Beijing Institute of Technology (IRB/ethics board approval number: BIT-EC-H-2024162) and was conducted in accordance with the Declaration of Helsinki. Prior to the experiment, all participants provided written informed consent after receiving a comprehensive explanation of the study details.

2.2 Stimuli and paradigm

Vibrotactile stimuli was applied to the thumb (D1), index finger (D2), middle finger (D3), ring finger (D4), little finger (D5), and palm of the hairless skin on the left hand through twenty-three independently controlled MR-compatible piezoelectric actuators. These actuators were strategically positioned at the proximal, middle, and distal phalanges of each finger (Fig. 1A). Each actuator generated a vibrotactile stimulus at a frequency of 21 Hz, targeting approximately 1 cm² of glabrous skin at each stimulation site. Neuroscience studies have confirmed that this frequency can trigger significant somatosensory cortical activation²⁴, and can avoid causing discomfort while meeting the intensity of tactile activation. Under different frequency ranges and stimulation types, different skin mechanoreceptors can be activated. The 21 Hz vibratory stimulation selected in this paper can activate the Meissner corpuscle of the FAI type and the Merkel corpuscle of the SAI type in the hairless skin of the palm^{1,2}.

The vibratory stimulation was delivered using a phase-encoding paradigm, where each finger was stimulated sequentially, starting from the thumb and progressing to the little finger (from the distal to the proximal phalanx for each finger) and then to the palm (Fig. 1A). A total of 23 distinct locations were stimulated, with each location receiving stimulation for 8 seconds before transitioning to the next

location (7 seconds of continuous stimulation followed by a 1-second pause to minimize adaptation effects). After the 14 locations on the fingers were stimulated, an 8-second rest period was introduced, followed by stimulation of the 9 locations on the palm, after which a 16-second rest period ensued. Consequently, a full stimulation cycle lasted 216 seconds. Each fMRI run consisted of 8 such cycles, resulting in a total run time of 1672 seconds. This protocol facilitated the somatotopic mapping of the fingers and palm in the SI, as well as the generation of mirrored maps representing the proximal-to-distal surfaces of the fingers. To ensure participants maintained attention, a "+" visual stimulus was provided as a fixation point (Fig. 1B). More details of the experiment can be found in the supplementary video.

2.3 MRI data acquisition

The data were collected using a MAGNETOM 7T whole-body research scanner (Siemens Healthcare, Erlangen, Germany), equipped with a 32-channel head coil (Nova Medical, Wilmington, USA). Functional imaging was performed with a gradient echo-planar imaging (EPI) sequence, featuring the following acquisition parameters: repetition time (TR) = 2000 ms, echo time (TE) = 25 ms, flip angle (FA) = 67°, and field of view (FoV) = 200mm × 200 mm. A simultaneous multislice excitation EPI sequence with 836 transverse slices aligned along the anterior commissure-posterior commissure (AC-PC) plane was employed. This sequence utilized a multiband acceleration factor of 3 and achieved an isotropic spatial resolution of 1.5 mm³. Additionally, whole-brain high-resolution anatomical images were obtained using an MP2RAGE sequence with the following specifications: TR = 4300 ms, TE = 2.35 ms, FA = 4°, FoV = 230 mm × 210 mm, initial inversion time (TI1) = 1000 ms, and isotropic voxel resolution = 0.64 mm.

2.4 MRI preprocessing

Standard data preprocessing was conducted using BrainVoyager QX (version 3.6.2: Brain Innovation B.V., Maastricht, Netherlands). Anatomical datasets were transformed to the AC-PC space following preprocessing. Since intensity inhomogeneities in MR images can significantly compromise the accuracy of segmentation and registration, we applied an intensity inhomogeneity correction protocol. This protocol involved background noise removal, brain extraction, white matter identification, and bias field estimation within white matter voxels. To ensure accurate delineation of the white matter (WM)-grey matter (GM) and GM-cerebrospinal fluid (CSF) boundaries, advanced segmentation techniques were employed. These steps included the exclusion of subcortical structures and the cerebellum, enhancement of tissue contrast and uniformity, segmentation of the WM-GM interface, segmentation of the GM-CSF interface, and the reconstruction of cortical hemispheres. The resulting segmentations were utilized to generate high-quality cortical reconstructions, facilitating the visualization of high-resolution functional data. For the task-state fMRI (ts-fMRI) data, the preprocessing steps included 3D motion correction (using trilinear interpolation for detection and sinc interpolation for correction), slice timing correction, and high-pass filtering (cut-off: 2 cycles per scan). Notably, no spatial smoothing was applied. The preprocessed data were then coregistered to anatomical datasets, and both volume time course (VTC) and mesh time course (MTC) datasets were extracted for population receptive field analysis.

For the construction of functional and structural networks, the ts-fMRI and high-resolution T1-weighted MRI data were processed according to standard preprocessing implemented in DPABI (<http://www.rfmri.org/dpabi>). Specifically, preprocessing of the T1-weighted images involved several key steps: correction for intensity nonuniformity, skull stripping, and the extraction and segmentation of cortical WM and GM. For each participant in the study, we derived five morphometric characteristics: grey matter volume, surface area (SA), cortical thickness (CT), Gaussian curvature (GC), and sulcus depth (CS). These features were assessed across 24,044 vertices located within the postcentral gyrus of the right hemisphere. Structural networks were established by calculating Pearson's correlation coefficients among these feature vectors. The ts-fMRI data underwent several preprocessing steps, including the removal of the initial ten frames, slice timing correction, realignment, normalization, smoothing, and filtering. For each participant, we extracted time series data from voxels within the postcentral gyrus to construct voxelwise functional networks, comprising 2,083 nodes. Both the functional and structural networks were constructed utilizing the Schaefer 400 templates²⁵.

2.5 Population receptive field analysis

Population receptive field (pRF) analyses were conducted utilizing BrainVoyager software. This pRF methodology estimates a model representation of the receptive field of individual voxels within the tactile cortex, aiming to best explain the fMRI responses elicited by a range of tactile stimuli. The pRF approach comprises two primary components: first, the stimulus data are employed to compute the predicted model time courses; second, the fitting of the actual model is executed. A time course can be generated from the model by sampling the tactile stimuli that fall within the receptive field during the experimental procedure. The characteristics of the model, specifically its position and size, yield a model time course that demonstrates positive responses whenever a stimulus occurs within its receptive field. Conversely, a receptive field located elsewhere will produce a distinct time course, as the stimuli will typically engage different receptive fields at varying time points. By comparing the predicted time courses from multiple pRF models to the measured time course of a specific voxel (or vertex), the model whose time course most accurately accounts for the observed data is identified for that voxel.

2.6 Gradient analysis

The gradient analysis pipeline was implemented using the BrainSpace toolbox²⁶. For each participant, we constructed a functional and a structural connectivity matrices. To quantify the connectivity similarity between brain regions, a cosine similarity matrix was computed. Subsequently, diffusion embedding¹⁴ was employed to extract the principal gradient components that account for the variance in the connectivity patterns. In essence, this method derives a low-dimensional embedding from a high-dimensional connectome matrix. A key parameter in this algorithm is α , which regulates the influence of the sampling point density on the manifold ($\alpha = 0$, maximal influence; $\alpha = 1$, no influence). Consistent with prior research, we set α to 0.5 to preserve global relationships between data points within the embedded space. The resulting gradient maps were further aligned across participants using iterative Procrustes rotation²⁷.

We subsequently conducted a quantitative analysis of the gradient values. On the basis of the individual hand activation patterns derived from the pRF analysis, we identified the hand region within the right postcentral gyrus. From these regions, we extracted the principal functional gradient values and the second structural gradient values for further analysis.

2.7 Statistical analysis

Statistical analyses were conducted using MATLAB, with a significance threshold set at $p < 0.05$, adjusted for multiple comparisons using the false discovery rate (FDR) correction. The analysis controlled for covariates, including sex and age. Descriptive statistics for continuous variables are reported as the means with standard deviations.

General linear model analysis

A general linear model (GLM) analysis was conducted using BrainVoyager. First, the experimental design was defined by constructing a design matrix that outlined the timing and duration of the tactile stimuli as well as the control conditions. Next, on the basis of the activation results, volumes of interest (VOIs) were delineated for the five fingers, palm, and four Brodmann areas (BA3a, BA3b, BA1 and BA2), which were then converted into masks. By utilizing these masks and the predefined design matrix, the GLM was applied to the fMRI data using the ordinary least squares (OLS) method to estimate the β coefficients (regression weights). These coefficients represent the magnitude of the relationship between the experimental conditions and the observed fMRI signal. Although the precise interpretation of the β values depends on the design matrix specifics, a high positive (or negative) β coefficient generally suggests strong activation (or deactivation) relative to the baseline during the experimental conditions being modelled. Thus, these β values reflect the degree of activation or brain activity change within each region under various experimental conditions. Finally, a t test was performed to assess the statistical significance of the estimated β values.

fMRI response analysis

The fMRI time series data were transformed into percentage signal change (PSC) values for further statistical analysis. This approach provides a relative measure of signal variation compared with a baseline or reference condition. By normalizing the data through percentage signal change calculations, we enhanced the comparability of the data across different scans and participants. This method enables the focus to be placed on the dynamic fluctuations in brain activity in response to stimuli or tasks rather than on the absolute signal intensity, which may be influenced by nonneuronal factors. Consequently, prior to statistical analysis, each value was converted to its PSC relative to the mean of the voxel's time course using the following equation:

$$p = \frac{y_i - \bar{y}}{\bar{y}} \cdot 100$$

where the mean of the voxel signal time course is subtracted from the signal y in a voxel at each time point i . The resulting value is then normalized by dividing it by the mean of the voxel's signal time course and multiplying by 100. The resulting value is then normalized by dividing it by the mean of the voxel's signal time course and multiplying by 100. This transformation ensures that the mean of the time course is consistent across all voxels and subjects (in the case of multisubject analyses), and expresses the variations in the time course as percentage deviations from the mean. This method facilitates a more straightforward assessment of the observed effect magnitudes in the data.

3. Results

3.1 Tactile topology map of the hand in the SI

We investigated the tactile topographic representation of the hand using pRF analysis. The activation patterns, defined by a threshold of $r > 0.25$ with a significance level of $p < 0.05$ (FDR corrected), revealed a distinct and specific organization in the right postcentral gyrus. We separately presented the results for the longitudinal and horizontal dimensions. In the longitudinal (between-digit) dimension, the hand's somatotopic representation followed a systematic arrangement along the central sulcus: thumb (D1), index (D2), middle (D3), ring (D4), little finger (D5), and palm (P) (Fig. 2A). For the horizontal (within-digit) dimension, a mirrored somatotopic organization was evident across BA3a, BA3b, BA1, and BA2, with the proximal (base), middle, and distal (tip) phalanges arranged sequentially in areas BA3a and BA1 and in reverse order (tip to base) in areas BA3b and BA2 (Fig. 2B). These findings highlight distinct organizational patterns for the hand's tactile map between and within individual digits.

3.2 Connection between the functional gradient and longitudinal representation

Tactile topology maps representing the hand were constructed in both the longitudinal and horizontal dimensions. In the longitudinal dimension, the fingers D1, D2, D3, D4, D5, and the palm (P) were sequentially arranged along the postcentral gyrus (Fig. 2A). We then derived the principal functional gradient map of the postcentral gyrus using voxel-level task-state functional connectivity analysis. This principal functional gradient accounted for approximately 20% of the total variance in connectivity (Figure S1A). On the basis of the tactile topology map of the hand, we delineated a gradient region for further analysis, which is highlighted with a black dashed box. Notably, the principal functional gradient within the designated regions exhibited a decreasing organizational pattern along the postcentral gyrus, extending from the bottom to the top (Fig. 3A). This observation aligns with the longitudinal tactile topology map of the hand (Fig. 2A).

3.3 Connection between the structural gradient and horizontal representation

We constructed a structural gradient map of the postcentral gyrus using vertex-level structural connectivity data and subsequently analysed both the principal and secondary structural gradients (Figs. 3B and 3C). These gradients accounted for approximately 76% and 8% of the total variance in connectivity, respectively (Figure S1B). The principal structural gradient map demonstrated anteroposterior symmetry within the postcentral gyrus, delineating three distinct regions (Fig. 3B). Similarly, the secondary structural gradient map exhibited anteroposterior symmetry, revealing a more intricate subdivision of brain regions within the postcentral gyrus (Fig. 3C). Following the approach used in functional gradient analysis, we identified specific gradient regions for further examination on the basis of the tactile topology map of the hand, highlighted by a black dashed box. The secondary structural gradient map for these selected regions displayed a mirrored arrangement at the borders of BA3a, BA3b, BA1 and BA2. Specifically, in BA3b and BA1, the gradient values ranged from high to low, whereas in BA3a and BA2, they exhibited the opposite distribution from low to high. This arrangement reflects a symmetrical relationship between the two pairs of adjacent areas, as well as an overall mirror distribution across the four regions. Notably, this observation aligns with the horizontal (within-digit) dimension of the tactile topology map of the hand (Fig. 2B).

3.4 Quantitative analysis of brain activity

In our analysis of both longitudinal (between-digit) and horizontal (within-digit) dimensions, we generated group analysis plots for the β values, fMRI responses, and functional gradient values from ten participants, as illustrated in Figs. 4A and 4B. The individualized data can be found in Figures S2, S3, and S4. In the longitudinal dimension, the β and fMRI response curves exhibited a similar trajectory, demonstrating a gradual increase from D1 to D3, followed by a decrease at D4, an increase at D5, and a subsequent decrease at P (Fig. 4A). Additionally, we produced a pseudocolour plot of the average fMRI response across eight cycles, which aligned with the observed changes in the fMRI response curve. For the quantitative assessment of functional gradients, we extracted the gradient values from six regions of interest (ROIs) within the Schaefer 400 templates, specifically focusing on brain regions 19, 21, 23, 25, 27, and 29 of the right hemisphere's somatosensory motor network, on the basis of the tactile topology map of the hand in the SI. The resulting curve (Fig. 4A) demonstrated a consistent decline in gradient values from the ventral to dorsal aspects along the postcentral gyrus, in line with the tactile topology distribution of the hand.

The horizontal dimension exhibited an orderly pattern of β and fMRI response variation in a direction orthogonal to the longitudinal dimension, with reversals consistent with the mirrored representations in adjacent Brodmann's subregions (Fig. 4B). Individualized outcomes are presented in Figures S2, S3, and S5. We examined these six functionally defined ROIs for anatomical variations in the secondary structural gradient. Comparative analyses of β values and secondary structural gradient metrics across Brodmann's areas (BA1, BA2, BA3a, BA3b) revealed a mirrored distribution within adjacent regions. The fMRI response curves for each phalanx exhibited trends parallel to those of the β values, with both metrics peaking in the middle phalanges (Fig. 4B). Furthermore, we constructed a pseudocolour plot

reflecting the average fMRI response over eight cycles, which confirmed the observed alterations in the fMRI response curve.

3.5 Tactile intrinsic coordinate system

Based on activation results, gradient results and analysis results of various quantitative indicators, we conclude that the primary functional gradient and the secondary structural gradient can not only describe the topological organization of the hand tactile brain area, but also constitute the two core organization axes of the human tactile cortex, and establish the tactile intrinsic coordinate system, as illustrated in Fig. 5. The primary functional gradient constitutes the vertical axis of this system, whereas the secondary structural gradient forms the horizontal axis. Together, these axes establish a coordinate framework that effectively encapsulates the two-dimensional nature of the tactile topology map.

4. Discussion

In this study, we utilized high-resolution fMRI at 7T to investigate the tactile topology map of hairless skin on the left hand within the SI of right-handed participants. The tactile topology map is characterized by two primary dimensions. In the longitudinal dimension, the five digits and palm were arranged along the postcentral gyrus from ventral to dorsal. In the horizontal dimension, each finger exhibits "mirror" symmetry across the four subregions of the SI (BA1, BA2, BA3a and BA3b). Specifically, in BA3a and BA1, the proximal (base), middle and distal (tip) phalanges of each finger are arranged in turn. In BA3b and BA2, the phalanges of each finger are arranged in reverse order (tip to base), so there is a mirror symmetrical distribution in adjacent subregions. Through functional and structural gradient analysis, we reveal that the longitudinal dimension of hand tactile topology is related to brain function, while the horizontal dimension of hand tactile topology is determined by brain structure. It is concluded that the primary functional gradient and the secondary structural gradient explain the spatial distribution mechanism of the tactile topological map, constitute the two core organization axes of the human tactile cortex, and then establish the tactile inner coordinate system.

4.1 Tactile topology map of the hand in the SI

In the longitudinal dimension, the pRF analysis indicated an ordered arrangement of the thumb (D1), index (D2), middle (D3), ring (D4), little finger (D5), and palm (P) along the postcentral gyrus. Specifically, the thumb is positioned most inferiorly and laterally, whereas the representations of the other digits are located progressively superiorly and medially, with the palm following suit (Fig. 2A and Fig. 5A). This finding is consistent with prior research focused on the right hand^{28,29}. Investigations that stimulated the five proximal phalanges of the left hand have reported the consistent somatotopic organization within the right hemisphere^{7,30}. Notably, the representations of both the left and right hands exhibited similar sequential arrangements within individual brains or normalized spaces³¹. Furthermore, the analysis of pRF maps revealed variations in the aspect ratios of the ellipses corresponding to different fingers, with those of D5 and the palm exhibiting a more rounded shape, whereas the pRFs for the other digits were

more elongated³². This finding implies distinct processing characteristics for each finger's sensory information.

In the horizontal dimension, we observed that the tactile topology map within the finger shows a mirror symmetric distribution in the subregions of the SI. Specifically, we identified the most anterior fingertip reversal between BA3a and BA3b, a base reversal between BA3b and BA1, and a posterior fingertip reversal between BA1 and BA2. Furthermore, the tactile topology maps we generated demonstrated a high degree of reproducibility across participants. In primate studies, the locations of reversals within the tactile topology maps of individual fingers, identified through electrophysiological methods^{33–35}, have consistently aligned with cytoarchitectonic boundaries, which is consistent with our study. Schweisfurth et al²⁹ examined the tactile maps for digits D1 to D5 and reported that only D4 and D5 exhibited orthogonal and orderly patterns in BA3b. However, some investigations have failed to establish a consistent tactile topology map within digits^{29,36,37}. This variability underscores the necessity of conducting mapping studies in individual participants to produce dependable within-digit maps.

Some studies have consistently demonstrated that neural activation correlates with increased blood oxygen level-dependent (BOLD) signals, whereas inactivation is associated with a decrease in these signals^{38–40}. Thus, variations in BOLD signals across voxels may reflect changes in the overall activation and deactivation of neurons within the voxel rather than individual neuronal events³⁹. Specifically, increases in BOLD signals are likely indicative of heightened activation relative to deactivation, whereas decreases suggest a predominance of deactivation over activation. Most fMRI investigations utilize BOLD signal change analysis through the General Linear Model (GLM) to pinpoint regions of the brain that exhibit activity or inactivity during specific cognitive tasks⁴¹. In this work, the β weight value representing the activation intensity of each finger was obtained by GLM analysis, which quantified the activation level or the fluctuation in the brain activity of different fingers in the brain region. The trend of the β curve is consistent with the distribution of the topological map, which explains the topological distribution mechanism.

4.2 Functional gradients representing the longitudinal topology

A functional gradient refers to the presence of a continuous or gradual pattern in the anatomical organization of the cerebral cortex associated with a specific function or attribute¹⁵. This phenomenon indicates that adjacent cortical areas may exhibit functional similarities while also demonstrating a trend of gradual change across distances. In this study, the tactile topology map of the human hand illustrates that various regions of the hand are systematically arranged on the cortex in a manner that mirrors their spatial configuration on the body. This organization aligns with the notion of a functional gradient, where neighbouring cortical regions share functional characteristics but progressively diverge. Consequently, the hierarchical organization and spatial distribution of different regions associated with the hand can be understood as a reflection of functional gradients, whereby distinct areas exhibit varying functional properties when processing tactile stimuli from different parts of the hand.

Functional gradients show the concept that specific sensory information is anatomically represented in a continuous, spatially organized manner within the cerebral cortex⁴². This organizational structure enables the brain to effectively process tactile information from various regions of the body. In this study, we selected gradient regions for analysis on the basis of findings from task-related functional activation. The primary functional gradient within the identified regions exhibited a systematic bottom-up decrease along the postcentral gyrus (Fig. 3A), aligning with the longitudinal arrangement of the tactile topology map for the hand (Fig. 2A). This finding suggests that the longitudinal division of the hand posture map may be correlated with its distinct functions in the processing of tactile information. Consequently, the primary functional gradient serves as the vertical axis of the intrinsic coordinate system.

4.3 Structural gradient representing the horizontal topology

Previous studies have demonstrated a robust correlation between the myelin sensitivity observed via MRI and cortical thickness, indicating an anatomical relationship between myelin distribution and both cortical thickness and folding patterns⁴³. Quantitative analyses of cortical thickness measurements have revealed regional variations within the SI, likely reflecting alterations in myelin content across these subregions. Specifically, the myelin content shows a decreasing gradient from BA3b to BA3a, whereas the relative myelin content between BA1 and BA3b appears to exhibit a reversal, decreasing from BA1 to BA2. These findings collectively indicate the presence of structural discrepancies among various subregions of the SI. Research by Gordon revealed that as functional differences converge, metrics of brain structure differ across subregions of the SI⁴⁴. In this study, we extracted five morphometric features, including grey matter volume, surface area, cortical thickness, Gaussian curvature and sulcal depth, across 24,044 vertices of the posterior central gyrus in the right hemisphere, derived from structural MRI (T1-weighted) data. This dataset was utilized to construct structural gradients, validate the structural differences within the four subregions of the SI, and derive more nuanced results, thereby confirming that the within-digit topological distribution within these areas is intrinsically linked to their structural distinctions.

Classical neuroanatomical theories propose that the spatial arrangement of cortical areas is not random but is instead the result of developmental processes influenced by evolutionary selection⁴⁵. By analyzing the structural characteristics of various brain regions, researchers can more effectively categorize the brain into areas with distinct functions, including perception, movement, language, and memory. These areas are traditionally organized on the basis of the extent of their microstructural differentiation⁴⁶. Structural gradients serve as a critical means of delineating functional regions within the brain⁴⁷. Information derived from structural gradients can be employed to construct brain maps, which enhance our understanding of the organization and connectivity of the brain. In this study, the secondary structural gradient map revealed anteroposterior symmetry within the postcentral gyrus, facilitating a more precise delineation of brain regions in this area (Fig. 3C). Furthermore, a mirrored arrangement was

observed at the borders of BA3a, BA3b, BA1 and BA2, aligning with the distribution of the tactile topographic map of the hand in the horizontal dimension (Fig. 2B). We suggest that the longitudinal mapping of the hand may be linked to variations in the anatomical structure of the tactile area. Therefore, the secondary structural gradient represents the horizontal axis of the intrinsic coordinate system of the hand's tactile cortex.

4.4 Limitations of the study

There are several limitations in our study. First, the present study focused only on the hand, and our approach could clearly be expanded to other body surfaces. Therefore, the tactile topology of other body parts can be studied by improving the tactile stimulation device. Second, the coordinate system we propose serves merely as a preliminary working model, with both the number and precise arrangement of its dimensions yet to be fully defined. Nonetheless, this model provides insights into the relative positioning of cortical areas within functional and structural hierarchies, thereby reflecting the inherent organization of the tactile cortex itself.

5. Conclusions

Establishing a definitive intrinsic coordinate system within the human tactile cortex associated with the hand presents considerable challenges. In this study, we utilized high-resolution fMRI at 7T to investigate tactile topology maps across between- and within-digit dimensions. To understand the spatial organization mechanism of tactile topology, we conducted analyses of functional and structural gradients. Our findings indicate that the arrangement of hand tactile topology within two dimensions of the SI correlates with the intrinsic coordinate framework of the tactile cortex. We propose that the primary functional gradient and secondary structural gradient constitute the two essential organizing axes of the human tactile cortex, and then construct the tactile intrinsic coordinate system.

Declarations

Data and Code Availability

Owing to the sensitive nature of participant data, we uploaded the data of two participants on Google Drive to help readers assess the scientific nature of the study (https://drive.google.com/drive/folders/1HzdrezzQgDw_DwWp9XTfGQQfGZaUEkUu?usp=drive_link). The remaining neuroimaging data and the code used in the present study are available from the corresponding author (zhangjian2023@bit.edu.cn) upon request.

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Author contributions

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Competing interests

The authors declare no competing interests.

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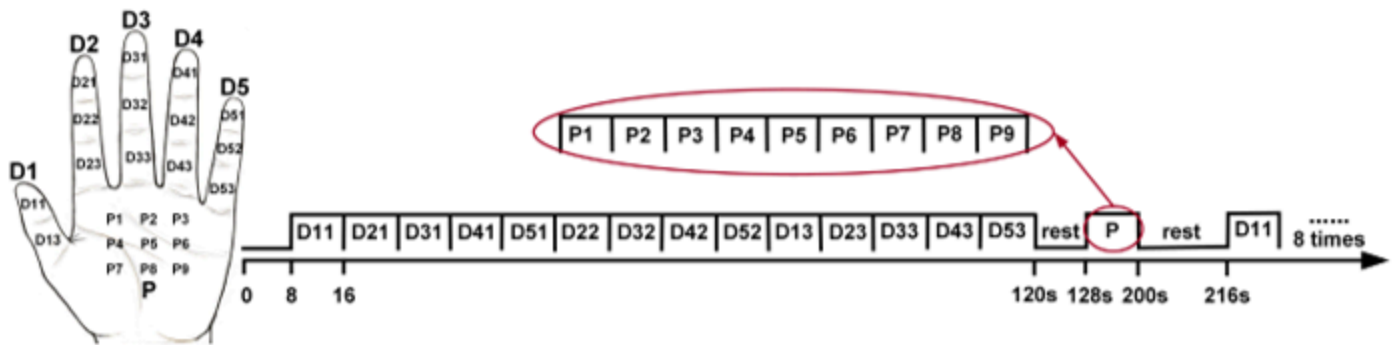
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Figures

A. Phase encoding experimental design



B. fMRI experiments with tactile stimuli

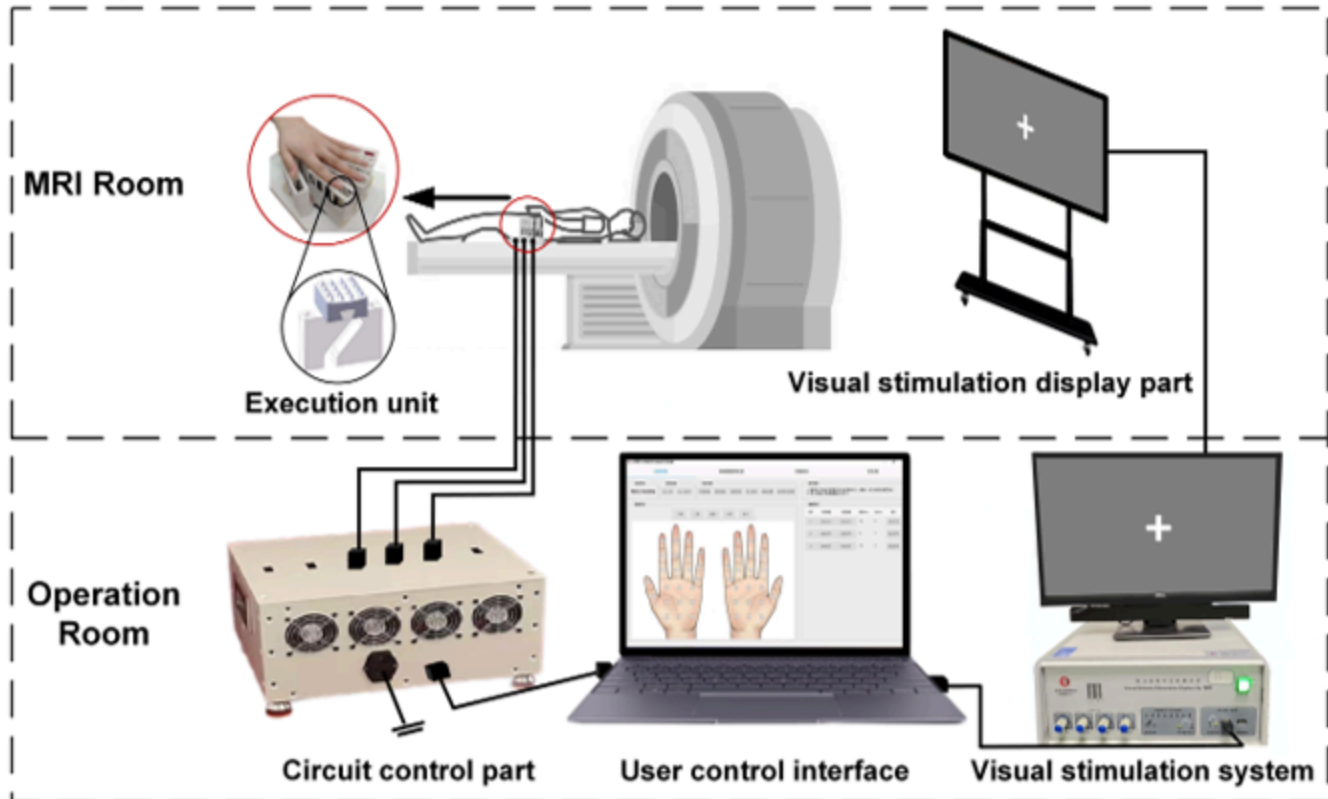


Figure 1

Tactile experimental design and fMRI data collection. A. Phase-encoded stimulation paradigm. B. fMRI experiments with tactile stimuli. D1, thumb; D2, index finger; D3, middle finger; D4, ring finger; D5, little finger; P, palm.

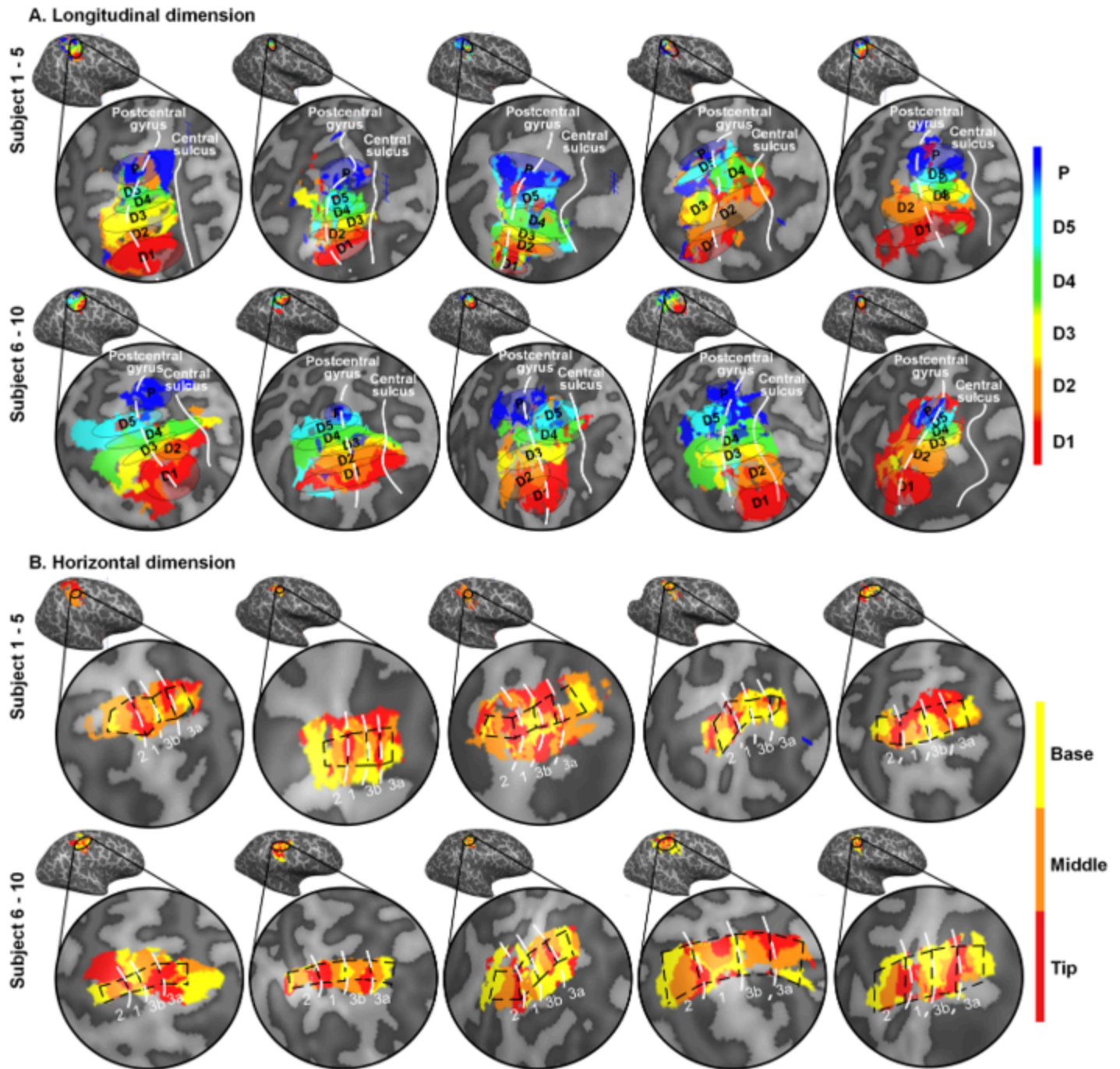


Figure 2

Tactile topography maps. A. Longitudinal dimension (between-digit) tactile topography. Each row represents data from a single participant, displayed on an inflated cortical surface model. Dark grey, regions of negative curvature (sulci); light grey, regions of positive curvature (gyri). The organized mapping of digits (D1 - D2 - D3 - D4 - D5 - P) is shown along the posterior bank of the central sulcus (solid white line) and the postcentral gyrus (dashed white line). **B. Horizontal dimension (within-digit) tactile topography.** The black lines indicate the boundaries of Brodmann areas, which are based on mirrored representations. Base, proximal phalanges; Middle, middle phalanges; Tip, distal phalanges.

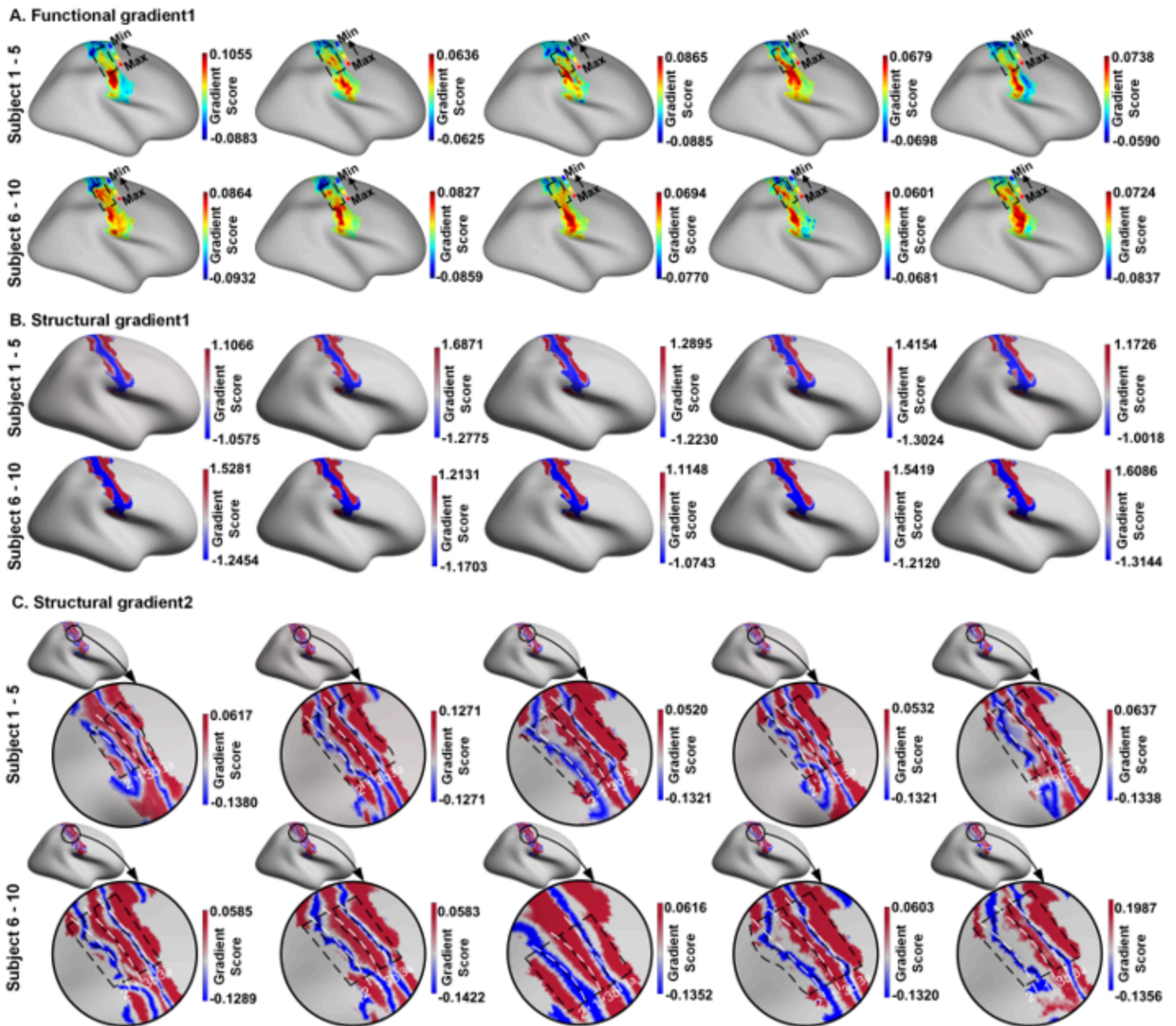


Figure 3

Gradient analysis of the postcentral gyrus. A. Primary functional gradient map for the postcentral gyrus. The primary functional gradient within selected regions decreased organizationally along the postcentral gyrus from bottom to top. **B. Primary and secondary structural gradients within the postcentral gyrus.** The principal and secondary structural gradient maps revealed an occurrence of anteroposterior symmetry within the postcentral gyrus.

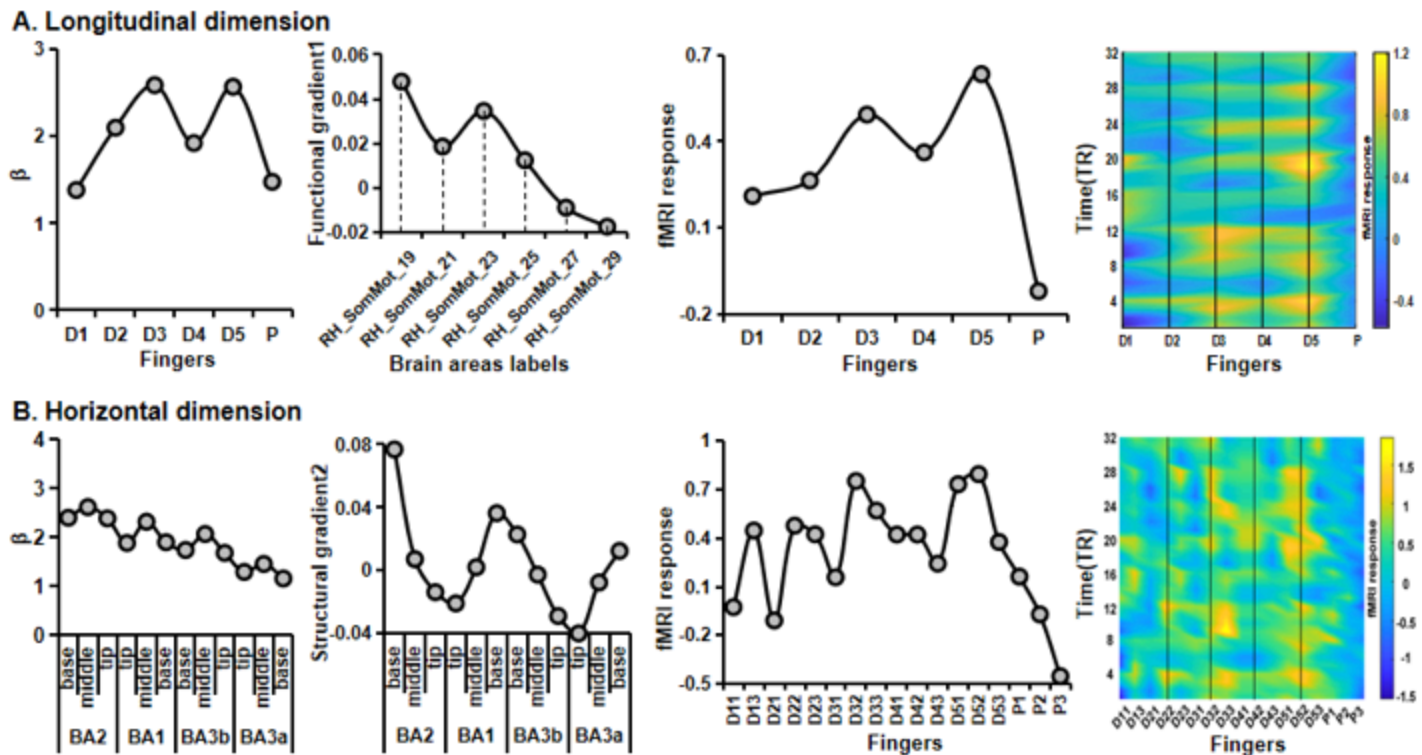


Figure 4

Results of the statistical analysis and the inherent coordinate system of the hand's tactile cortex. A and B represent the group analysis results of β values, fMRI responses and gradient values in the longitudinal and horizontal dimensions, respectively. The fMRI responses were represented visually as images, with the pseudo color plot illustrating the average responses. In this plot, the vertical axis denotes the time progression within a cycle, whereas the horizontal axis corresponds to the fingers and palms (or phalanges). Each longitudinal trace within this two-dimensional representation reflects the averaged fMRI time course associated with a specific finger.

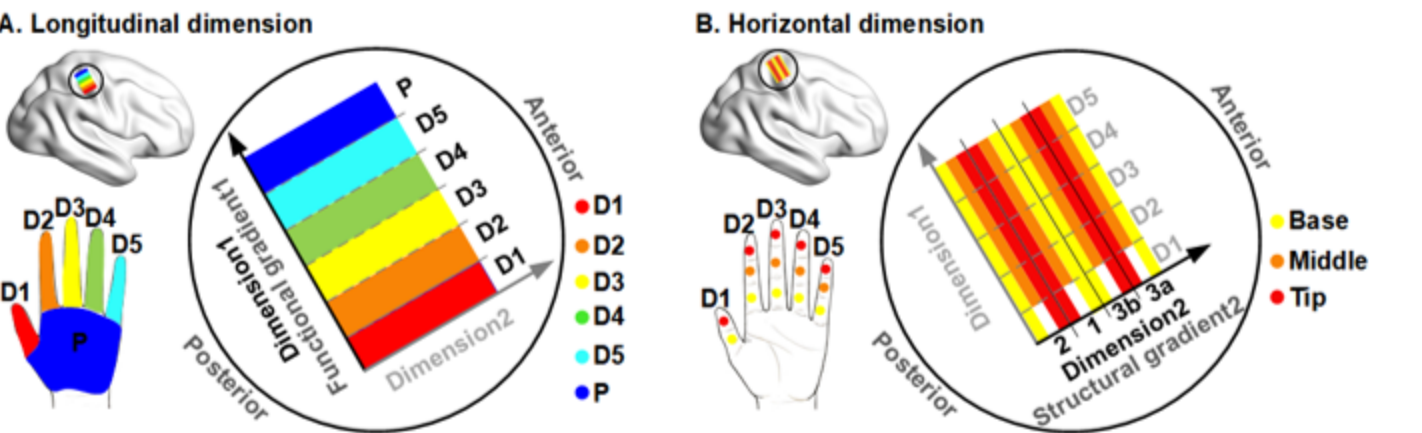


Figure 5

The intrinsic coordinate system of the tactile cortex of the hand. A. Longitudinal dimension. The arrangement of the five fingers and palm along the postcentral gyrus follows this sequence: D1 - D2 - D3 - D4 - D5 - P, represented by a colour spectrum transitioning from red to blue. **B. Horizontal dimension.** Within the fingers, the organization across the four Brodmann areas is as follows: in BA3a, the arrangement is from Base to Middle to Tip; in BA3b, it progresses from Tip to Middle to Base; in BA1, the sequence is from Base to Middle to Tip; and in BA2, it is arranged from Tip to Middle to Base.

Supplementary Files

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