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## Research Report

# The influence of hand posture on tactile processing: Evidence from a 7T functional magnetic resonance imaging study



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## ABSTRACT

Although behavioral evidence has shown that postural changes influence the ability to localize or detect tactile stimuli, little is known regarding the brain areas that modulate these effects. This 7T functional magnetic resonance imaging (fMRI) study explores the effects of touch of the hand as a function of hand location (right or left side of the body) and hand configuration (open or closed). We predicted that changes in hand configuration would be represented in contralateral primary somatosensory cortex (S1) and the anterior intraparietal area (aIPS), whereas change in position of the hand would be associated with alterations in activation in the superior parietal lobule. Multivoxel pattern analysis and a region of interest approach partially supported our predictions. Decoding accuracy for hand location was above chance level in superior parietal lobule (SPL) and in the anterior intraparietal (aIPS) area; above chance classification of hand configuration was observed in SPL and S1. This evidence confirmed the role of the parietal cortex in postural effects on touch and the possible role of S1 in coding the body form representation of the hand.

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## 1. Introduction

To determine the behavioral relevance of a tactile stimulus it is imperative that information from multiple sources be integrated to create a neural representation of our body in space. Previously, we argued for three distinct but interactive types of information that collectively generate the on-line representation of the body in space that encodes the location of sensory stimuli and interacts with motor systems in the genesis of action. These putative representations include a somatosensory representation that codes the location of the stimulus on the body surface, a “body form” representation that codes the size and shape of the body and a “postural representation” that codes the position of the body in external space (Medina & Coslett, 2010). Although behavioral studies have provided evidence for the effects of these representations on touch, little is known about their neural correlates. We utilized high resolution functional MRI (fMRI) at 7 T to explore the anatomic bases of the representations that collectively define the location of the body in the environment.

Tactile stimuli are initially represented in somatotopic maps in primary somatosensory cortex (S1) (Kaas, 1983; Merzenich, Kaas, Sur, & Lin, 1978). Ultra-high field fMRI studies can resolve individual fingertip representations in S1. A number of investigators (Besle, Sánchez-Panchuelo, Bowtell, Francis, & Schluppeck, 2013; Sanchez-Panchuelo, Francis, Bowtell, & Schluppeck, 2010; Stringer, Chen, Friedman, Gatenby, & Gore, 2011; Martuzzi et al., 2014; van der Zwaag, Gruetter, & Martuzzi, 2015) have identified areas that selectively respond to stimulation of a single digit (Kolasinski, Makin, Jbabdi, et al., 2016) and areas of overlap across digits (Ejaz, Hamada, & Diedrichsen, 2015; Iwamura, Tanaka, Sakamoto, & Hikosaka, 1983; McKenna, Whitsel, & Dreyer, 1982). Although there is abundant electrophysiological evidence of plasticity in S1 after finger amputation or anesthesia (Calford & Tweedale, 1990) as well as brain injury (see Medina & Coslett, 2016 for review), somatosensory maps, as defined by fMRI, appear to persist after amputation of a limb (Kikkert et al., 2016; Wesselink et al., 2019) and remain consistent over time (Kolasinski, Makin, Logan, et al., 2016); maps in S1 do not differ as a function of attention to the tactile stimulus (Puckett, Bollmann, Barth, & Cunnington, 2017). Recently, Akselrod, Martuzzi, van der Zwaag, Blanke, and Serino (2021) provided evidence that hand form is also represented in S1. Using univariate, multivoxel, and connectivity analyses, Akselrod et al. (2021) investigated the whole hand representation in S1, including both fingers and palm, and confirmed the somatotopic organization in S1 from D1 to D5 and palm. In addition, the authors computed a number of different measures (cortical distances, cross-activations, multi-voxel activity patterns and functional connectivity) of dissimilarity between patterns of activation across conditions. They tested whether a “body model” reflecting the shape of the hand, a linear model, depicting the linear arrangement of fingers and palm, or a control-circular model could account for dissimilarity data and showed that the body model was the best predictor across dissimilarity measures. The authors concluded that the pattern of activation in S1 matched more

closely the hand form and shape rather than simply the relationships between somatotopic stimuli. Information about the location of touch on the body surface is not sufficient for processing all tactile information. For example, the knowledge of the size or shape of one's hand allow us to determine whether an object held between one's thumb and little finger is a lime or an orange. It has been suggested that body position in space can be coded following two main frames of references (Schwoebel et al., 2001); the first, representation codes body position in an “intrinsic” body-centered representations that specifies the relationship between body parts. The second codes body position in an “extrinsic” or environment-based frame of reference that specifies body position in relation to the external environment. Evidence that both these representations influence tactile processing has been reported examining the effects of the location of the hand with respect to the body (left or right) and the hand configurations (open or closed hand).

Evidence for the influence of intrinsic-egocentric postural changes (hand open or closed) on tactile processing (e.g., whether the hand is open or closed; Overvliet, Anema, Brenner, Dijkerman, & Smeets, 2011; Tamè, Dransfield, Quettier, & Longo, 2017; Zampini, Harris, & Spence, 2005) has been provided in studies of neurotypical and brain-damaged (Coslett, 1998; Coslett & Lie, 2004) individuals. Overvliet et al. (2011) tested whether tactile localization in healthy adults changed if the fingers were spread apart (both hands open), with fingers in close proximity or with hands overlapping and fingers from both hands interdigitated. Participants made fewer errors identifying which hand was stimulated when the hands were in open configuration than in both the other conditions (which did not differ). Similar effects have also been reported in an individual suffering from left parietal damage (Coslett, 1998).

The neural correlates of the effects of hand posture on touch, indexed by presenting tactile stimuli with the hands open versus closed, have been explored with electroencephalogram (EEG) and magnetoencephalography (Gherri, Zhao, & Ambron, 2021; Hamada & Suzuki, 2003, 2005). Using magnetoencephalography, Hamada and Suzuki (2003) showed that somatosensory evoked potentials (SEP) in S1 varied depending on the hand configuration, showing opposites effects in N20m and P40m components. On one hand, the ratio between thumb and index SEP was larger when participants had their hands closed than open when looking at N20m, a component that may reflect the overlap in the cortical representation between fingers. The opposite pattern (open > closed) was observed for P40m, a component that indexes an increase in lateral inhibition. The authors suggested that two possible mechanisms may give rise to the effects of hand configuration, one consisting of an increase in lateral inhibition contributing to differentiation between fingers when the hands are open and another mediated by an increase in activity of overlapping interneurons when the hand is closed. Similar effects of posture have also been reported looking at S2 (Hamada & Suzuki, 2005): the Euclidian distance in the equivalent current dipole of thumb and index was larger when the hand was closed rather than open.

More recently, Gherri et al. (2021) used the hand open and closed manipulation to test the effect of external and

somatotopic distance in a tactile selective attention task. Target and singleton distractor were always presented on the same hand, either on contiguous (near somatotopic distance) or non-contiguous fingers (far somatotopic distance), with the hand in an open or closed position. Both behavioral and EEG results showed two independent effects: one for the somatotopic and one for the external distance. Contrary to [Overvliet et al. \(2011\)](#), the behavioral results showed an advantage in target identification when the stimuli were at a close location in both somatotopic (e.g., target and distractor presented on neighboring digits) and external (e.g., hand in closed configuration) frames of reference. In particular, target identification was better when the fingers of the hand were in contact (closed hand configuration) rather than apart (open hand configuration), when target and distractor were presented in continuous fingers. Event-related potentials (ERP) results showed that the N140 cc, a component recorded from the somatosensory areas and known to represent tactile selection, was highest with non-contiguous stimuli in a somatotopic frame of reference at an earlier time window (120–260 ms). The effect of hand configuration was noted in a later time window (260–400 ms), with the N140 cc being higher in closed than open hand configuration. The authors argue that attention is spread and diluted across the different fingers (causing a decrease of the N140 cc) as different units when the hand is open, while the close hand configuration may have enhanced the attention towards the hand as a whole and favored the perceptual grouping of the tactile stimuli.

Additional studies have explored the extrinsic-egocentric spatial coding as indexed by the position of the hand with respect to the body (left or right). For example, [Lloyd, Shore, Spence, and Calvert \(2003\)](#) stimulated the thumb of the right hand of healthy subjects while the hand was resting on the right or left side of space as defined by the body. The contrast between the hand in left versus right side of space demonstrated significant ipsilateral activation in the ventral intraparietal sulcus when participants kept their eyes closed during the tactile stimulation. The activation encompassed more areas when the eyes were open during the task, including the premotor cortex, and ventral and medial intraparietal sulcus of the left hemisphere. Similar results were also observed with the left hand, suggesting that the intraparietal sulcus might be involved in coding the hand posture of both hands. Furthermore, recruitment of the contralateral superior parietal lobule (SPL) was also observed in this condition, suggesting that this region might also play a role. Behavioral studies with individuals with brain damage affecting parietal regions ([Medina & Rapp, 2008](#); or extinction; see [Medina & Coslett, 2016](#)) have implicated the parietal lobes in the computation of the position of the body in space. For instance, [Medina and Rapp \(2008\)](#) reported a subject with fronto-parietal damage who, when touched on the ipsilesional hand with both hands situated in the contralesional hemisphere, reported that both hands had been touched (a phenomenon termed “synchiria”); this misperception was not reported with the hands in the ipsilesional side of space. Similar evidence has been noted in patients with extinction ([Auclair, Barra, & Raibaut, 2012](#), [Moro, Zampini, & Aglioti,](#)

[2004](#)); a symptom consisting of the perception of a unilateral stimulation in the ipsilesional hand when both hands are touched (see also [Medina & Coslett, 2016](#) for review). In some cases, this symptom is more severe when the contralesional hand is resting in the contralesional rather than in the ipsilesional hemisphere.

In the present study, we used 7T fMRI to explore the neuroanatomical basis of the somatotopic and external (intrinsic and extrinsic) hand representation on tactile processing. First, we sought to localize and distinguish with high precision the cortical areas of the stimulated fingers in S1 by stimulating the index or middle fingers. Second, using a block design, we manipulated hand configuration (fingers spread or together) and hand location (left and right with respect to the body midline) to test the effect of intrinsic and extrinsic postural changes of the hand on tactile processing. We predicted that both intrinsic and extrinsic postural changes of the hand would modulate the activation in multisensory areas of the parietal cortex. More specifically, we expected the location of the hand on the right or left side of the body to be associated with changes in aIPS ([Brozzoli, Gentile, & Ehrsson, 2012](#); [de Lange, Helmich, & Toni, 2006](#); [Lloyd et al., 2003](#)) or the superior parietal lobule (SPL), an area known to be involved in coding body posture and body schema ([Felician et al., 2004](#); [Pellijeff, Bonilha, Morgan, McKenzie, & Jackson, 2006](#)). Changes in hand configuration (fingers opened or closed) were expected to be coded in the aIPS, as this area represents postural changes of the hand ([Buxbaum, Kyle, Tang, & Detre, 2006](#); [Makin, Holmes, & Zohary, 2007](#)).

However, several studies have also shown that aIPS is part of a fronto-parietal circuit involved in grasping ([Binkofski, Kunesch, Classen, Seitz, & Freund, 2001](#); [Borra & Luppino, 2019](#); [Borra et al., 2008](#)) and plays a crucial role in sensorimotor transformations ([Binkofski et al., 1999](#); [Devare et al., 2007](#); see also [Borra & Luppino, 2019](#); [Borra et al., 2008](#) for evidence from animal studies) and/or the extraction of grasping related affordances ([Binkofski et al., 1998](#); [Borra et al., 2008](#); [Devare et al., 2007](#)). Therefore, aIPS may code complex postural changes ([Klaes et al., 2015](#)), but its contribution might be primarily related to grasping ([Binkofski et al., 1999](#); [Devare et al., 2007](#)) and/or affordances extraction ([Binkofski et al., 1998](#); [Devare et al., 2007](#)). If so, activation of aIPS may not occur in our task, in which postural changes do not involve visuo-motor transformation, affordances and grasping.

Our second hypothesis was that the open versus closed hand comparison would also be indexed by changes in S1 ([Akselrod et al., 2021](#); see also [Ambron et al., 2018](#)). Indeed, if the hand is processed as a whole ([Gherri et al., 2021](#)), changes in the hand configuration may also be processed as modification of the hand form and shape and represented within S1. Multivoxel Pattern Analyses (MVPA) showed support for both hypotheses. Indeed, we observed alterations of parietal lobe activation in coding for both postural changes but with differential involvement of aIPS and SPL regions in hand localization and configuration. Furthermore, we provided evidence that the hand configuration is represented also at the level of S1 and possibly coded as changes in hand form representation.

## 2. Methods

### 2.1. Transparency and data availability statement

In the following paragraph, we report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion were established prior to data analysis, all manipulations, and all measures in the study. Participants' informed consent did not include permission to make data publicly available and for this reason data are not publicly available. Requests for data can be made to the corresponding authors [EA, FEG] and Institutional Review Board at the University of Pennsylvania will review and approve each request. Scripts used for preprocessing and data analysis are available at the following link <https://osf.io/edy5f/>.

No part of the study procedures or analysis was preregistered prior to the research being conducted.

### 2.2. Participants

Twenty individuals from the University of Pennsylvania participated in the study in exchange for payment. All participants were right-handed with normal or corrected-to-normal vision and no history of neurological illness. All participants gave written informed consent in accordance with the Institutional Review Board at the University of Pennsylvania. Three participants were removed because they did not complete at least four runs of the task; one participant's data were removed due to excessive motion throughout each run (>30% data loss after motion censoring); one additional participant was removed due to issues co-registering the functional and structural MRI data. All subsequent analyses were performed over the remaining fifteen participants.

### 2.3. General experimental procedure

Stimulus presentation was controlled with E-Prime Professional Software 2.0 (Psychology Software Tools, Inc., Sharpsburg, PA). All participants viewed the stimuli binocularly through a mirror attached to the head coil adjusted to allow for foveal viewing of a back-projected monitor (temporal resolution = 60 Hz). Each participant took part in one scanning session which began with a high resolution T1 anatomical scan; each participant then took part in at least 4 runs of the somatosensory mapping experiment.

### 2.4. Somatosensory mapping fMRI experiment

There were 8 cells in the design: Finger Stimulated (2 levels; index, middle), Hand configuration (2 levels; fingers opened, fingers closed) and Hand location (2 levels; left side, right side). Each run consisted of 8 mini blocks, each 48 sec in duration. Each mini block started with the presentation of a word to instruct participants where to place the hand (left or right side), and hand configuration (open or closed). Participants were given 16 sec to position the right hand following the instructions and to then close their eyes. The examiner visually monitored the change in position. After a delay of 8 sec, a

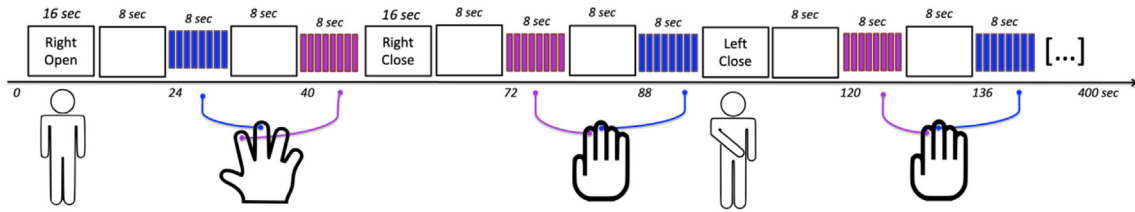
vibro-tactile stimulation was delivered randomly to the index or middle finger for 8 sec. Following an 8 sec inter-trial interval, a second somatosensory stimulation was delivered to the other finger for 8 sec. After the second stimulation event, a tactile stimulus was presented on both fingers simultaneously to signal participants to open their eyes and read the instructions. A new word stimulus was presented and participants were asked to configure the fingers according to the instruction (see Fig. 1). Within each 8-sec event, the index or middle finger was stimulated with sixteen vibro-tactile 400 msec (ms) bursts, interspersed with 100 ms of silence; stimuli were presented with an MR-compatible piezoelectric device (Dancer Design). Hand location and hand configuration were counterbalanced across mini blocks within a run, such that after 16 stimulation events each cell of the design was replicated twice per run (64 trials across four runs).

### 2.5. MRI parameters

Whole brain BOLD imaging was conducted on a 7-T Siemens TERRA scanner with a 32-channel head coil located at the University of Pennsylvania. High-resolution structural T1 contrast images were acquired using a magnetization-prepared rapid gradient echo (MP-RAGE) pulse sequence at the start of each participant's first scanning session (TR = 2300 ms, TE = 3.69 ms, flip angle = 7°, FOV = 192 × 256 mm, matrix = 192 × 256, 160 left-to-right slices, voxel size = 1x1x1 mm). An echo-planar imaging sequence was used for T2\* contrast was utilized (multi-band factor = 4, TR = 2000 ms, TE = 34.80 ms, flip angle = 70°, FOV = 220 × 220 mm, 76 inferior-to-superior slices, voxel size = 1x1x2 mm). The first 6 volumes of each run were discarded to allow for signal equilibration (4 volumes during image acquisition and 2 at preprocessing).

### 2.6. Preprocessing of fMRI data

fMRI data were pre-processed with AFNI and in-house scripts drawing on the NeuroElf toolbox in MATLAB (<https://github.com/neuroelf/neuroelf-matlab>). T1 anatomical datasets were warped to MNI space using non-linear registration (3dQwarp). Preprocessing of the functional data included, in the following order, slice time alignment (3dTShift), co-registration of functional data to anatomical data, functional voxel interpolation to 1.5 mm<sup>3</sup>, motion correction (3dvolreg), spatial smoothing of the functional data (3 mm FWHM), and voxel-wise scaling such that the mean of each voxel's time series was equal to 100. Motion correction included the censoring of volumes with excessive motion (volumes with motion greater than .3 mm of Euclidean distance from the previous volume were censored). A general linear model (GLM) was used to derive beta estimates of each experiment conditional (collapsing across repetitions within a run). Experimental events were convolved with a hemodynamic response function 8 sec in duration. Slow linear trends and the first derivatives of 3D motion correction from each run were modeled as predictors of no interest prior to modelling experimental events. AFNI's 3dREMLfit was used to model experimental events while controlling for temporal autocorrelation at the voxel level. We then contrasted all conditions (weighted equally) against the 8-sec resting event that immediately



**Fig. 1 – Representation of the task performed in each run. The interstimulus interval was increase to 16 sec when participants switched positions.**

preceded it to derive a whole-brain map of the regions eliciting robust BOLD across conditions.

#### 4. Data analysis

##### 4.1. Univariate analysis

*Region-Of-Interest (ROI) Localization at the Participant Level.* All ROIs were spheres 1 cm in diameter (for precedent, see [Chen, Garcea, Jacobs, & Mahon, 2018](#); [Chen, Garcea, & Mahon, 2016](#); [Garcea et al., 2019](#); [Garcea & Buxbaum, 2019](#); [Garcea, Chen, Vargas, Narayan, & Mahon, 2018](#); [Shay, Chen, Garcea, & Mahon, 2019](#)). The left somatosensory cortex (S1) was localized at the single-subject level using the ‘All Conditions [weighted equally] > Rest’ contrast (see [Table 1](#)). The left anterior IPS (aIPS) and the left superior parietal lobule (SPL) were manually localized at the single-subject level using the T1-weighted anatomical data prior to the analysis of the fMRI data by co-author HBC. The aIPS ROI was defined as the anterior-most portion of the intraparietal sulcus medial to the left supramarginal gyrus (mean XYZ = -36, -40, 39). The SPL ROI was defined as the posterior portion of the SPL in the vicinity of Brodmann Area 7 (mean XYZ = -16, -65, 56; see [Table 1](#)).

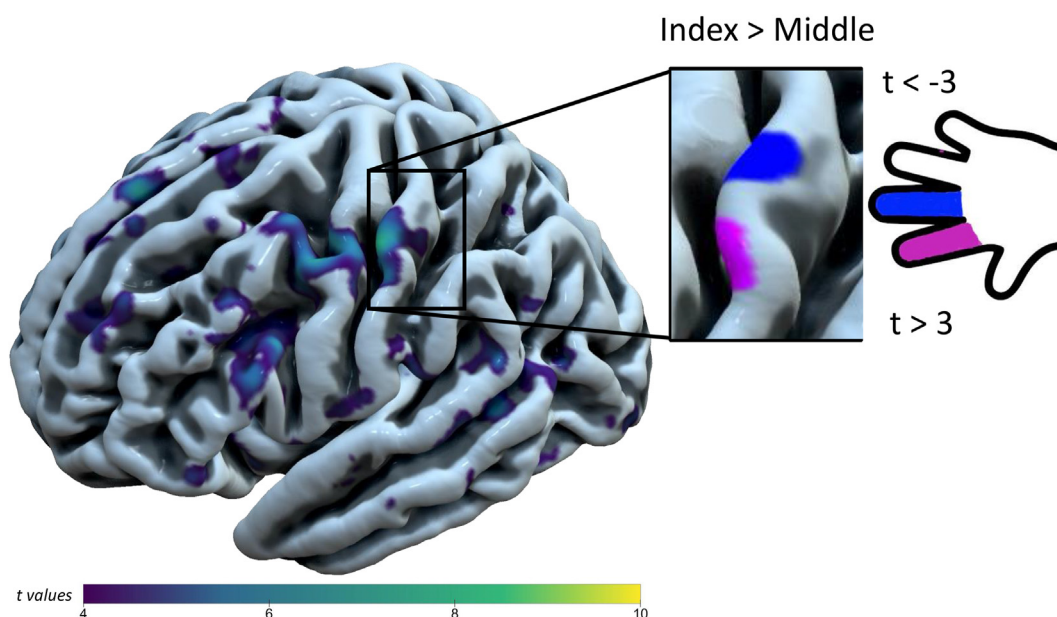
*Group-level Whole-brain Contrast.* We localized the left S1 at the group level using the ‘All Conditions [weighted equally] > Rest’ contrast at the group-level (see [Fig. 2](#)). We then ran a whole-brain analysis contrasting finger stimulation events (index finger stimulation > middle finger stimulation), hand configuration events (hand closed > hand open), and hemispace stimulation events (left hemispace > right hemispace). False Discovery Rate (FDR) correction was applied to each map to adjust for multiple comparisons (minimum q-value set to .05). Clusters with 200 contiguous voxels or less were removed from the analysis.

##### 4.2. Multivoxel analysis

Each subject’s functional data were pre-processed a second time without spatial smoothing. Trial-level data were modeled (16 trials per run; 4 runs per subject), resulting in 8 repetitions per cell of the design per subject within each voxel. We then conducted a whole brain searchlight multivoxel pattern analysis (MVPA) using the CoSMoMVPA toolbox ([Oosterhof, Connolly, & Haxby, 2016](#)) with a spherical searchlight of 125 voxels. Input data were z-normalized trial-level  $\beta$  weights. A linear support vector machine was trained to learn the difference between experimental conditions;

**Table 1 – MNI coordinates of the functionally defined Left S1 and the anatomically defined Left aIPS and Left SPL. All ROIs were spheres 1 cm in diameter centered on the listed coordinate.**

Participant	Left S1				Left aIPS			Left SPL		
	X	Y	Z	Statistical value	X	Y	Z	X	Y	Z
1	-49	-24	60	t = 13.93, p < .001	-35	-38	38	-12	-68	56
2	-51	-24	57	t = 9.78, p < .001	-35	-40	38	-20	-68	56
3	-42	-32	42	t = 8.12, p < .001	-35	-40	38	-16	-68	56
4	-53	-17	47	t = 9.11, p < .001	-34	-38	37	-20	-69	53
5	-41	-12	59	t = 5.55, p < .001	-36	-38	40	-14	-68	56
6	-42	-18	51	t = 6.25, p < .001	-35	-38	36	-14	-66	52
7	-60	-20	48	t = 12.84, p < .001	-40	-38	36	-16	-66	52
8	-46	-21	57	t = 12.09, p < .001	-34	-41	36	-18	-62	60
9	-53	-18	36	t = 11.68, p < .001	-32	-39	45	-17	-62	57
10	-42	-26	51	t = 7.54, p < .001	-34	-39	40	-16	-62	57
11	-56	-14	57	t = 6.55, p < .001	-36	-47	39	-17	-69	55
12	-53	-18	45	t = 3.02, p < .01	-36	-40	40	-16	-60	58
13	-54	-18	50	t = 8.65, p < .001	-36	-39	41	-16	-60	54
14	-57	-30	59	t = 9.39, p < .001	-39	-45	39	-14	-60	60
15	-56	-26	54	t = 10.65, p < .001	-40	-45	40	-19	-63	57
Average	-50	-21	52		-36	-40	39	-16	-65	56
SD	6.3	5.7	7		2.3	2.9	2.4	2.3	3.5	2.5



**Fig. 2** – The group-level whole-brain contrast for ‘All Conditions [weighted equally] > Rest’ (FDR corrected) is projected on a surface map (left); on the right is the contrast of ‘Index Finger Stimulation > Middle Finger Stimulation’ (FDR uncorrected).

decoding accuracy was estimated using an even-odd split such that the classifier was trained with odd trials and tested with even trials, and vice versa. For each subject, three main analyses were conducted to explore which regions could accurately decode whether the index or middle finger was stimulated (fingers stimulation – somatosensory coding), whether the fingers were open or closed (hand configuration -intrinsic spatial coding) and whether the hand was on the right or left side of the body (hand location – extrinsic spatial coding). Maps of all the subjects were submitted to a 10,000 iterations Monte Carlo Test permutation analysis with Threshold-Free Cluster Enhancement (TFCE; Smith &

Nichols, 2009) implemented using Cosmo Monte Carlo Cluster Stat function of CoSMoMVPA toolbox (Oosterhof et al., 2016).

The same MVPA analysis was also carried out at an ROI level using CoSMoMVPA toolbox. Z-normalized  $\beta$  weights were extracted for each trial from the S1, aIPS and SPL regions (see Table 1) using an identical even and odd split analysis. One tail t-tests analyses were used to test our *a priori* hypotheses that decoding accuracy would be above chance (.5) in specific regions; (a) in S1 for finger decoding; b) aIPS and/or SPL for location decoding; c) in S1 and in the aIPS for configuration decoding.

**Table 2** – The peak MNI coordinate of clusters identified in the whole-brain contrast of ‘All Conditions [weighted equally] > Rest’. Clusters smaller than 200 contiguous voxels were removed from the analysis.

Region Name	Cluster Size	Peak X	Peak Y	Peak Z
Left Somato-motor cortex	13,367	-45	-16.5	51
Right Supplementary motor Area	7106	3	9	57
Left Primary Visual Cortex	3756	-3	-89	0
Right Precentral Gyrus	2899	35	11	29
Left Middle Cingulate Cortex	2614	-2	-24	48
Right Superior Temporal Gyrus	1729	68	-41	21
Right Rolandic Operculum	1202	57	-20	17
Left Lateral Occipital Cortex	1162	-36	-93	-15
Right Anterior Insula	918	33	24	9
Left Cerebellum	706	-14	-56	-38
Right Caudate Nucleus	414	8	8	2
Right Anterior Superior Temporal Sulcus	376	48	-15	-12
Right Lateral Occipital Cortex	260	17	-89	-11
Left Superior Parietal Lobule	253	-32	-60	51
Right Dorsal Occipital Cortex	249	32	-74	20
Left Posterior Thalamus	208	-3	-23	-2

## 5. Results

### 5.1. Univariate analysis

#### 5.1.1. Whole brain analysis

We tested whether there was a significant BOLD response in the left S1 when participants' fingers were stimulated. As hypothesized, the 'All Conditions [weighted equally] > Rest' contrast induced a significant BOLD response in several regions, including left S1 (See Fig. 2; see Table 2). Also, we observed a significant BOLD response in right and left parietal operculum (sometimes designated the second somatosensory area), areas associated with light touch (Eickhoff, Schleicher, Zilles, & Amunts, 2006). In addition, finger-specific sub-regions within the left S1 were identified with the contrast of 'Index > Middle' (see Fig. 2). Neither the Hand Configuration ('Closed Hand > Open Hand') nor the Hand Location ('Right Hemisphere > Left Hemisphere') contrast significantly impacted the magnitude of activation in S1.

### 5.2. ROI analysis

**Univariate Analysis.** For each contrast of interest, a one-way Analysis of the Variance (ANOVA) was carried out on the extracted beta weights. A main effect of the ROI was found for the 'All Conditions [weighted equally] > Rest' contrast ( $F_{2,42} = 40, p < .001$ ), driven by the larger BOLD response in left S1 compared to the left aIPS and left SPL ( $p < .001$  in both comparisons; see Fig. 3, top panel). We did not observe a significant modulation-by-region effect for the 'Hand Closed > Hand Open' and 'Right Hemisphere > Left Hemisphere' contrast. We then tested whether the beta weights differed from zero using a one sample t-test. The analysis showed a reliable difference in the left S1 ( $t_{14} = 8.98, p < .001$ ) and the left aIPS ( $t_{14} = 3.5, p = .001$ ) for the 'All Conditions [weighted

equally] > Rest contrast, and in the left aIPS for the 'Right Hemisphere > Left Hemisphere' contrast ( $t_{14} = 1.84, p = .04$ ; see Fig. 3, top panel). In addition, we specifically interrogated the parietal operculum due to its involvement in light touch (Eickhoff et al., 2006) and complex objects manipulation (Binkofski et al., 1999); the results confirmed ipsilateral and contralateral activation of the parietal operculum.

**MVPA.** We tested the hypotheses that (i) Within the left S1 we could decode which finger had been stimulated (index vs middle); (ii) Within the left SPL and/or left aIPS we could decode hand location (right vs left); and (iii) Within the left aIPS and S1 we could decode the hand configuration (Hand Closed vs Hand Open). After deriving each subject's decoding accuracy, a t-test against chance (.5) was used to test these hypotheses (see Table 3). Our hypotheses were partially supported. As predicted, above-chance finger decoding was found in the left S1, and above-chance hand location was decoded in the left aIPS and left SPL. Though we identified above-chance hand configuration decoding in the left S1 and (more surprisingly) left SPL, we did not observe the predicted effect in the left aIPS (see Fig. 3, bottom panel, and Table 3). We explored these results further by looking at whether finger decoding varied as a function of hand posture across ROIs. When looking at decoding accuracy for the two postures separately, finger decoding was classified above-chance only in S1 for both hand configurations and the decoding accuracy was not different between the open and closed configuration (see Table 4).

#### 5.2.1. Searchlight MVPA results

For each subject, a classifier was trained to decode the finger stimulated (index/middle), the location (right/left) and configuration (open/closed) using the even trials and then tested the classification on the odd trials, and vice versa. Using Monte Carlo permutation, we tested whether classification accuracy was greater than chance (.5) across participants. No

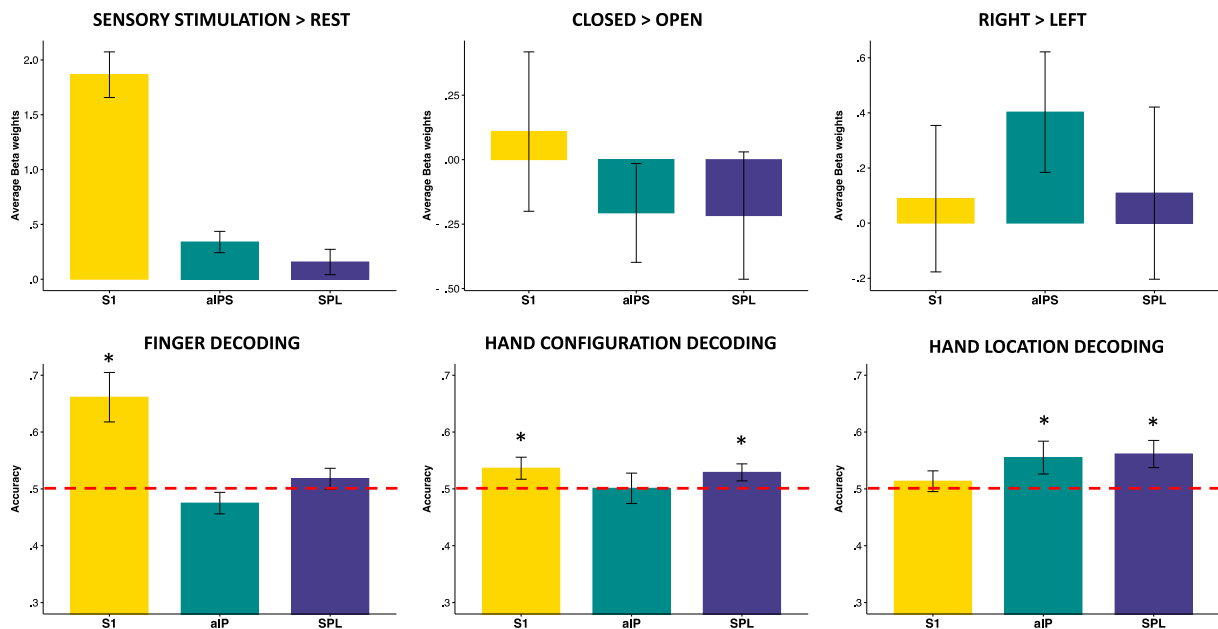


Fig. 3 – Univariate (top panel) and MVPA (bottom panel) results of the ROI analysis.

**Table 3 – Mean decoding accuracy ( $\bar{x}$ ) and one-sample t-tests for each ROI and experimental condition.**

	Finger (Index vs Middle)	Configuration (Open vs Closed)	Location (Right vs Left)
S1	$\bar{x} = .66; t_{14} = 4.55, p < .001$	$\bar{x} = .53; t_{14} = 2.33, p = .035$	$\bar{x} = .51; t_{14} = 1.24, p = .23$
aIPS	$\bar{x} = .48; t_{14} = -1.76, p = .10$	$\bar{x} = .50; t_{14} = .72, p = .48$	$\bar{x} = .55; t_{14} = 2.36, p = .03$
SPL	$\bar{x} = .52; t_{14} = 1.42, p = .17$	$\bar{x} = .53; t_{14} = 2.40, p = .03$	$\bar{x} = .56; t_{14} = 3.09, p = .008$

regions exhibited above-chance classification accuracy ( $z > 1.65, p < .05$ ) that also survived permutation correction.

## 6. Discussion

This study tested the neuroanatomical correlates of tactile stimulation of the index and middle fingers while varying the configuration (open and closed hand) and location (hand on the right or left side of the body) of the hand using 7T fMRI. We expected activation patterns in S1 to distinguish stimulation of the index and middle fingers. We predicted that the location and configuration of the hand would both be represented in multimodal parietal areas, but that effect of the hand configuration would also be noted also in primary somatosensory cortex (Gherri et al., 2021; Hamada & Suzuki, 2003, 2005). The results partially supported our hypotheses and will be discussed in turn.

First, we tested whether tactile stimulation induced a reliable activation in the somatosensory cortex and whether we could distinguish the index and middle finger representation in S1. Both univariate and multivariate analyses showed this to be the case. Indeed, whole brain and ROI univariate analyses showed a reliable recruitment of the somatosensory cortex when the tactile stimulation was presented. We were also able to localize index and middle finger activation using a contrast between these two conditions and to show a cortical mapping in line with the somatosensory homunculus (Puckett et al., 2017; Sanchez-Panchuelo et al., 2012). The Region of Interest MVPA analysis confirmed and reinforced this evidence, showing that it is possible to distinguish between tactile stimulation presented on the index and on the middle finger based on the difference in pattern of activations between these condition in S1.

Second, we investigated our hypotheses regarding the effects of postural changes of the hand on tactile processing. We predicted differential recruitment of the parietal cortex in the hand configuration (open vs closed) and hand location (right vs left) manipulations. We expected that changes in the hand location would be represented in aIPS and SPL (Brozzoli et al., 2012; de Lange et al., 2006; Lloyd et al., 2003), while changes in hand configuration would be coded in aIPS, reflecting

variation of the specific hand posture (Buxbaum et al., 2006; Makin et al., 2007). MVPA analysis conducted on these specific ROIs partially confirmed these predictions. As we predicted, both aIPS and SPL regions predicted changes in the location of the arm across hemispaces; however, SPL rather than aIPS coded for changes between open and close hand configuration. This evidence suggests that SPL can discriminate between patterns of activity that involve postural changes of both hand and arm, while aIPS may represent changes in the arm position. This result is not surprising as neural recoding (Lacquaniti, Guigon, Bianchi, Ferraina, & Caminiti, 1995) or lesion (Rushworth, Johansen-Berg, & Young, 1998) studies in macaque and fMRI studies in humans have shown evidence that SPL (Brodmann area 5) represent body-centered changes the position of the arm (Magri, Fabbri, Caramazza, & Lingnau, 2019; Pellijeff et al., 2006). Furthermore, SPL has also been shown to be involved in visuo-motor integration (Iacoboni & Zaidel, 2004) and in coding postural changes related to reaching movements (Matsumiya, 2022). Our results expand these observations and further suggest that these changes are not specific to action performance but may also involve tactile processing.

In addition to SPL, aIPS discriminated between changes in the localization of the hand relative to the body (extrinsic postural changes). This area has been shown to integrate tactile and proprioceptive inputs (Iwamura, 1998; Medina & Coslett, 2010) and was previously found to be associated with postural changes of the hand across hemispaces (Lloyd et al., 2003). While Lloyd et al. (2003) found a significant activation of this region when contrasting the activation with the hand placed on the left with the hand placed on the right, we did not observe significant results of the hand location in our univariate analysis. Instead, we showed that this area can accurately distinguish between the pattern of activation related to the hand location between hemispaces during tactile stimulation. One possible account for the difference between our results and those of Lloyd et al. (2003) relates to discrepancies in task designs. First, in Lloyd et al.'s (2003) study, the somatosensory stimulation was much longer (16 sec) and was followed by a longer rest period (24 sec) than in the present study (8 sec). Second, Lloyd et al. (2003) targeted the thumb, a digit with the largest somatosensory representation, while we stimulated

**Table 4 – Mean decoding accuracy ( $\bar{x}$ ) and one-sample t-tests for finger decoding (Index vs Middle) as function of hand configuration and location.**

	Open hand configuration	Closed hand configuration	Comparison between open and closed hand configurations
S1	$\bar{x} = .65; t_{14} = 4.04, p = .001$	$\bar{x} = .64; t_{14} = 4.07, p = .001$	$t_{14} = .84, p = .41$
aIPS	$\bar{x} = .53; t_{14} = 1.69, p = .11$	$\bar{x} = .45; t_{14} = 2.01, p = .06$	$t_{14} = 2.46, p = .03$
SPL	$\bar{x} = .50; t_{14} = .74, p = .46$	$\bar{x} = .51; t_{14} = 1.05, p = .30$	$t_{14} = .89, p = .38$



the index and middle fingers. Longer tactile stimulation on a finger with a larger cortical representation as in [Lloyd et al. \(2003\)](#) may have enhanced BOLD-related changes and permitted the investigators to capture the effect of changes in posture during passive tactile stimulation.

Our prediction that the effect of open-closed hand configuration would be observed in S1 was supported in the ROI analysis. Indeed, the decoding accuracy for hand configuration was above chance in S1. This evidence is in line with previous EEG studies showing an effect of hand configuration in S1 ([Gherri et al., 2021](#); [Hamada & Suzuki, 2003, 2005](#)). The involvement of S1 further suggests that the change of the hand configuration (open vs closed) is coded as a change in hand form or shape as suggested by [Akselrod et al. \(2021\)](#).

Contrary to our expectations, aIPS did not show a significant activation or above chance decoding for hand configuration (open vs closed). One possible explanation for this null finding is that this region may be specifically involved in visuo-motor ([Jeannerod, Arbib, Rizzolatti, & Sakata, 1995](#)) and/or tactile-motor ([Binkofski et al., 1999](#); [Stoekel et al., 2003](#)) integration in the context of object manipulation. Our task did not require visuomotor transformation and the postural changes did not directly involve grasping. Postural changes occurred after the visual presentation of the instruction, but the tactile task was presented when participants had positioned their hand and closed their eyes. In addition, the hand configurations open and close did not evoke any form of grasping or object affordance. It is possible that aIPS may not play a general role in postural changes but its activation may be specific to hand configuration related to grasping ([Binkofski et al., 1999](#); [Devare et al., 2007](#); see also [Borra & Luppino, 2019](#); [Borra et al., 2008](#) for evidence from animal studies) or manipulation based on affordances and intrinsic characteristics of the objects ([Binkofski et al., 1998](#); [Borra et al., 2008](#); [Dafotakis et al., 2008](#); [Devare et al., 2007](#); [Georgieva, Peeters, Kolster, Todd, & Orban, 2009](#); [Monaco et al., 2015](#); [Tunik, Frey, & Grafton, 2005](#)).

Indeed, Studies have shown that aIPS is involved in shaping visually guided grasping movements to match the intrinsic characteristics of the objects ([Binkofski et al., 1998](#); [Monaco et al., 2015](#)); damage to the aIPS alters hand pre-shaping prior to contact with the object ([Jeannerod, 1986](#); [Binkofski et al., 1998](#)) and disrupts pre-shaping based on in object affordances ([Devare et al., 2007](#)). Similar observations were reported in fMRI studies showing that the aIPS is active during grasping movements that adjust to an object's shape and size ([Binkofski et al., 1999](#)) and in tactile exploration of complex objects ([Stoekel et al., 2003](#)). [Binkofski et al. \(1999\)](#) also reported activation of second somatosensory cortex (SII) and superior parietal lobule during manipulation of complex objects. They suggested that SII may represent the intrinsic characteristics of the objects whereas SPL may code hand posture as function of the object's characteristics and aIPS may have a crucial role in the initial stage of hand-object interaction ([Binkofski et al., 1999](#)). More recently, [Monaco et al. \(2015\)](#) confirmed the role of aIPS in grasping and compared the processing of intrinsic (size) and extrinsic (location) object attributes during simple looking and grasping tasks. They found that activation of extrinsic characteristic of the objects, like location, were associated with activation of

the superior parietal occipital sulcus, S1/M1, and supplementary motor area, while aIPS was involved in coding the intrinsic objects characteristic, like the object size, in relation to the grasping and interacting with the object.

Across the different portions of the IPS (middle, caudal or anterior), [Rice, Tunik, and Grafton \(2006\)](#) found that aIPS plays a crucial role the execution of the grasping component during both movement execution and correction as a consequence of perturbation, suggesting that aIPS may be essential for combining motor goal and sensory information during online grasping execution. The potential role of aIPS in online correction of the grasping and scaling of the grip as consequence of perturbation has been tested using manipulations of object size ([Tunik et al., 2005](#)) and weight ([Dafotakis et al., 2008](#)). For instance, TMS studies creating a virtual lesion over the aIPS demonstrated that different grasping components were altered (grip size or the forearm rotation) depending on the goals of the action ([Tunik et al., 2005](#)); the impairment in grasping was evident not only at the onset of the reaching but also as the peak aperture was achieved ([Dafotakis et al., 2008](#)). Taken together, this evidence suggests that aIPS has a crucial role in dynamic motor planning in response to the intrinsic properties of objects and in updating the plan to reflect changes and perturbations ([Dafotakis et al., 2008](#)).

Finally, aIPS activation is not only observed with grasping, but also in visual and motor imagery ([Klaes et al., 2015](#)). In a tetraplegic subject, [Klaes et al. \(2015\)](#) used an adapted version of the Rock-Paper-Scissors game and direct neuronal recording to show that neurons in aIPS decode complex hand shapes and grasping movements. Therefore, taking into consideration this literature, our null findings are not surprising as aIPS may be specifically involved in coding grasping-related body postures.

A second possible explanation and a potential limitation of our study is that the absence of a task or behavioral relevance of the stimulation may have minimized neural response to the tactile stimulation and minimized the effect of posture on touch. It may be relevant that behavioral evidence demonstrating effects of posture on touch ([Coslett, 1998](#); [Gherri et al., 2021](#); [Overliet et al., 2011](#)) were obtained in studies requiring an explicit response. It is possible that the neural effect of hand configuration may vary as a function of the tactile task performed. For instance, a hand open configuration may be beneficial for the exploration of the environment, while the hand closed could enhance sensitivity to tactile input in tasks involving manipulation of an object. In the current study, the absence of a task did not force participants to pay attention to hand or use the postural information to achieve a goal. If passive tactile stimulation is sufficient for mapping the hand representation in S1, it might not be enough to induce strong effects in parietal association cortices coding hand configuration. Finally, though all MVPA analyses were cross-validated across even and odd data folds to ensure the independence of data for model training and model testing, there was a relatively small number of trials entered in each analysis ( $N = 32$ ). Future study should investigate further how task demands and the total number of stimulation trials modulate the effect of posture on tactile perception and whether different brain areas are responsible for these effects.

To conclude, this study confirmed that intrinsic and extrinsic postural changes of the hand in space during tactile stimulation are represented in posterior parietal regions. We also showed that changes in the hand configuration are represented as both postural changes, and coded in SPL, and as changes in the shape of the hand, as coded in S1.

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### CRediT authorship contribution statement

**Elisabetta Ambron:** Conceptualization; Methodology; Software; Validation; Formal analysis; Investigation; Data curation; Writing – original draft; Writing – review & editing; Visualization. **Frank E. Garcea:** Conceptualization; Methodology; Software; Validation; Formal analysis; Investigation; Data curation; Writing – original draft; Writing – review & editing; Visualization. **Samuel Cason:** Conceptualization; Investigation; Project administration. **Jared Medina:** Conceptualization; Methodology; Writing – review & editing. **John A. Detre:** Conceptualization; Methodology; Writing – review & editing. **H. Branch Coslett:** Conceptualization; Methodology; Supervision; Funding acquisition; Writing – review & editing.

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### Conflict of interest

The authors declare no conflict of interest.

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