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1 Title: **Locating primary somatosensory cortex in human brain stimulation**  
2 **studies: Experimental evidence**

3

4 Running head: Locating S1 in human brain stimulation studies

5

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16

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25 **Abstract**

26 Transcranial magnetic stimulation (TMS) over human primary somatosensory cortex  
27 (S1) does not produce immediate outputs. Researchers must therefore rely on  
28 indirect methods for TMS coil positioning. The 'gold standard' is to use individual  
29 functional and structural magnetic resonance imaging (MRI) data, but the majority of  
30 studies don't do this. The most common method to locate the hand area of S1 (S1-  
31 hand) is to move the coil posteriorly from the hand area of primary motor cortex (M1-  
32 hand). Yet, S1-hand is not directly posterior to M1-hand. We localised the index finger  
33 area of S1-hand experimentally in four ways. First, we re-analysed functional MRI  
34 data from 20 participants who received vibrotactile stimulation to their 10 digits.  
35 Second, to assist the localisation of S1-hand without MRI data, we constructed a  
36 probabilistic atlas of the central sulcus from 100 healthy adult MRIs, and measured  
37 the likely scalp location of S1-index. Third, we conducted two experiments mapping  
38 the effects of TMS across the scalp on tactile discrimination performance. Fourth, we  
39 examined all available neuronavigation data from our laboratory on the scalp location  
40 of S1-index. Contrary to the prevailing method, and consistent with systematic review  
41 evidence, S1-index is close to the C3/C4 electroencephalography (EEG) electrode  
42 locations on the scalp, approximately 7-8 cm lateral to the vertex, and approximately  
43 2 cm lateral and 0.5 cm posterior to the M1-FDI scalp location. These results suggest  
44 that an immediate revision to the most commonly-used heuristic to locate S1-hand is  
45 required. The results of many TMS studies of S1-hand need reassessment.

46 **New and noteworthy**

47 Non-invasive human brain stimulation requires indirect methods to target particular  
48 brain areas. Magnetic stimulation studies of human primary somatosensory cortex  
49 have used scalp-based heuristics to find the target, typically locating it 2cm posterior  
50 to the motor cortex. We measured the scalp location of the hand area of primary  
51 somatosensory cortex, and found that it is approximately 2 cm lateral to motor cortex.  
52 Our results suggest an immediate revision of the prevailing method is required.

53

54 Keywords: S1, SI, TMS, TDCS, vibrotactile

55 **1. Introduction**

56 Transcranial magnetic stimulation (TMS, Barker et al. 1985) can be used to study the  
57 healthy human brain non-invasively, by stimulating brain tissue electromagnetically.  
58 TMS therefore requires indirect methods of locating the brain area of interest.  
59 Primary motor cortex (M1) can be located relatively easily, by moving the TMS coil  
60 around on the scalp, applying single pulses of TMS, and observing or recording  
61 muscle responses, however, for most other brain areas, there is no similar,  
62 immediate and objective output that researchers can use, on a pulse-by-pulse basis,  
63 to ensure correct TMS coil position. The 'gold standard' in this field is to acquire, for  
64 every participant, structural and functional brain imaging data and use frameless  
65 stereotaxy (Sparing et al. 2010).

66

67 When MRI is not available, researchers have used scalp-based heuristics to target  
68 the hand area of primary somatosensory cortex (S1-hand, Holmes & Tamè, in press;  
69 preprints available at: <https://osf.io/c8nhj/>). These heuristics have included using the  
70 10-20 or 10-10 electroencephalographic system (Jasper 1958; Koessler et al. 2009;  
71 Lagerlund et al. 1993; Okamoto et al. 2004; Towle et al. 1993; Vitali et al. 2002; Xiao  
72 et al. 2018), functionally-identified scalp locations for motor cortex (e.g., Balslev et al.  
73 2004), changes in reaction times or errors (e.g., Convento et al. 2018), or changes in  
74 sensation (e.g., Sugishita & Takayama 1993; Cowey & Walsh 2000). Systematic  
75 review revealed the most common heuristic involves positioning the coil 2 cm  
76 posterior to the M1 representation of hand muscles (e.g., first dorsal interosseus,  
77 FDI, or abductor pollicis brevis, APB), yet S1-hand is lateral, not posterior to M1-hand  
78 (Holmes & Tamè, in press). In previous work using individual fMRI-guided

79 neuronavigation (Tamè & Holmes, 2016), we noticed that, in all 20 of our participants,  
80 the scalp location above S1-index was indeed lateral, not directly posterior, to M1.

81

82 Here, we ask: “what is the optimal location on the scalp to magnetically stimulate the  
83 somatosensory cortex (Brodmann's areas BA3b & BA1, Geyer et al. 1999)

84 representations of the index finger (S1-index)? The index finger and the FDI muscles  
85 are the most commonly stimulated and recorded body parts in the relevant literature,

86 respectively, so we focused on them. We focused on the BA3b and BA1 subregions

87 of S1 because they show a clear somatotopy for individual fingers (Nelson & Chen

88 2008), because our fMRI protocol was not able to distinguish between them, and, for

89 the purposes of applying TMS on the scalp, because the representations of each

90 finger in BA3b and BA1 lie very close to each other (e.g., Figure 2 in Holmes & Tamè,

91 in press). We answered the question in four ways: First, by re-analysing functional

92 MRI data from our laboratory (Tamè & Holmes, 2016); Second, by creating a

93 probabilistic atlas of the central sulcus from 100 structural MRIs, and measuring

94 between-participant variability in central sulcus location at the likely position of S1-

95 index; Third, by conducting two experiments which systematically mapped the effect

96 of TMS on vibrotactile discrimination performance across the scalp, and; Fourth, by

97 summarizing all our available data from individual (F)MRI-neuronavigated TMS

98 experiments targeting S1-index. Together, these independent and converging lines of

99 evidence strongly support the immediate revision of the most commonly-used

100 heuristic for locating human primary somatosensory cortex in TMS studies.

101

102

103 **Materials and methods**

104 Studies were approved by research ethics committees (UREC11/58, University of  
105 Reading, UK; SoPEC916, University of Nottingham, UK), conducted in accordance  
106 with TMS safety guidelines (Rossi et al. 2009) and the Declaration of Helsinki (2008  
107 version, which does not require pre-registration).

108

109 *Participants*

110 fMRI experiment: Twenty healthy participants (mean±SD age=27.6±8.7 years, 15  
111 female, 3 left-handed by self-report). Structural MRI: 100 right-handed participants  
112 (mean±SD age=25.1±6.2 years, 64 female; Holmes et al., 2008; Tamè and Holmes,  
113 2016, unpublished datasets). Experiment 1: nine participants (mean±SD  
114 age=33.2±11.6 years, 5 female, 1 ambidextrous; 13 were recruited, 4 were removed).  
115 Experiment 2: twelve participants (mean±SD age=23.7±5.6 years, 5 females, 12  
116 right-handed). Participants met TMS safety inclusion criteria (Rossi et al. 2009), with  
117 no neuropsychiatric disorder. Neuronavigation: 37 localisations of S1-index from 15  
118 participants, separately for left (N=11, mean±SD=25.4±6.1 years, 7 female) and right  
119 hemispheres (N=9, mean±SD=26.2±6.3 years, 3 female).

120

121 **Functional MRI data**

122 Data reported by Tamè and Holmes (2016) were re-analysed. Participants underwent  
123 10x280 s scans, each comprising 10x11.5 s vibrotactile stimulation blocks interleaved  
124 with 10x12.5 s rest. Stimuli were produced by MRI-compatible piezoelectric wafers  
125 driving a 2.5 mm diameter plastic rod (~100Hz, 8x1 s, 0.5 s pause). One scan  
126 (Siemens Trio 3T, 3x3x3 mm) was collected for each digit on each hand, in

127 pseudorandomised order. FMRI data were processed with FSL5  
128 (<http://www.fmrib.ox.ac.uk/fsl>): 3D spatial smoothing (5 mm FWHM), 6- and 12-  
129 degree-of-freedom linear registration to the anatomical (MPRAGE, 1x1x1 mm) and  
130 MNI152 (2x2x2 mm) template brains, respectively. Data were modeled as square-  
131 wave regressors convolved with canonical hemodynamic response functions. Two  
132 contrasts were made with each set of 10 scans: Single digit contrasts of vibration  
133 versus rest, within scans; Differential contrasts of each digit against the other four of  
134 that hand, across scans (e.g., left index finger (D2) contrasted against the left thumb  
135 (D1), middle (D3), ring (D4), and little (D5) digits, weights: [-1,4,-1,-1,-1]). Group  
136 means were calculated for each digit and each contrast (20 group-level images). The  
137 voxel with maximum Z-score in postcentral gyrus of presumed primary  
138 somatosensory cortex of each group image was recorded. Harvard-Oxford and  
139 Juelich atlases (Eickhoff et al. 2005) within FSLView were used to assign probabilistic  
140 anatomical and functional labels to voxels.

141

#### 142 ***Probabilistic atlas of the central sulcus, and S1-index scalp location***

143 Structural MRI scans were used to create a probabilistic central sulcus atlas. The  
144 location of S1-index on the scalp was estimated by measuring seven points along the  
145 scalp between midline and the scalp overlying S1-index (MNI[-48,-21,50], Holmes &  
146 Tamè, in press). 112 scans (MPRAGE, 1x1x1 mm) were acquired from: Siemens  
147 Sonata 1.5T (N=43, University of Oxford, UK); Siemens Magnetom Trio 3T (N=20,  
148 University of Reading, UK), and Philips Achieva 3T (N=49, University of Nottingham,  
149 UK). 8 were excluded for self-reported left-handedness, 1 for scan quality (artefacts),  
150 and 1 for poor health (severe uncorrected visual deficits). 2 scans which did not



151 include the full scalp, nasion, andinion were also removed.  
152  
153 Each image was viewed in axial/transverse plane, by NPH or SZ. Using a 2 mm  
154 'pencil', the complete bilateral course of the central sulcus was drawn on the image,  
155 starting at the hand knob, moving superiorly then inferiorly and laterally from the hand  
156 area. We filled all gaps between pre- and postcentral gyri to provide a liberal estimate  
157 of central sulcus location and width. Five landmarks were drawn on the images with  
158 3x3x3 mm masks: nasion, inion, left and right pre-auricular points, vertex (Figure 1H).  
159 Nasion and pre-auricular points were easily identified, but inion prominence varied  
160 greatly. Vertex was estimated by calculating a line orthogonal to and through the  
161 intersection of nasion-inion and pre-auricular lines, then using ruler and protractor to  
162 find the scalp location 90 degrees from the intersection. A best guess for vertex  
163 location was then taken, considering three image planes. It is not known how these  
164 locations correspond to those measured on participants' heads during S1-index TMS.  
165  
166 Participants' brain images were extracted using BET, and both head and brain were  
167 registered to MNI152 1x1x1 mm templates using FLIRT (12 degrees of freedom). The  
168 two transformations (head, brain) were applied to central sulcus mask images to  
169 create masks in standard MNI space. 100 masks were summed to create a  
170 probabilistic atlas of the central sulcus where voxel intensity is the percentage of  
171 participants with central sulcus passing through.  
172  
173 S1-index location was estimated relative to vertex using a mask of meta-analytic  
174 mean MNI coordinates for S1-index (MNI[-48,-21,50]), transformed into

175 scanner/anatomical space per MRI. To account for non-alignment between head and  
176 scanner axes, nasion, inion, and vertex on each image were used to form a plane,  
177 NIV (i.e., mid-sagittal). The nearest voxel to S1-index on the scalp was estimated,  
178 and projected orthogonally onto NIV. This projection was used to generate six pairs of  
179 coordinates (x,y) between S1-index and NIV. Each pair's Z-coordinate was recorded  
180 as the most superior scalp voxel where x- and y-coordinates matched the projection.  
181 Distances between adjacent points, and the distance between S1-index and vertex  
182 were calculated. For anterior distances, the y-coordinate of the S1-index projection  
183 onto NIV was subtracted from the vertex y-coordinate and divided by the cosine of  
184 the angle between nasion-inion and scanner y-axis.

185

#### 186 ***Experiment 1: Mapping effects of TMS on tactile discrimination thresholds***

187 Participants trained to detect and discriminate vibrotactile stimuli (150 Hz, 50 ms,  
188 Oticon bone-conductor) on their right index finger. The first training was 48 trials of 2-  
189 interval forced choice (2IFC) detection, in which a pseudorandom interval contained a  
190 target. 1s intervals were preceded by a 250 ms light emitting diode (LED) flash on the  
191 left (first) or right (second interval). Targets were presented mid-interval, and were  
192 followed by a 2.5 s response period. Participants released a pedal under their left  
193 (indicating the target was in the first) or right foot (second interval). Incorrect  
194 responses were followed by 2x250 ms flashes from both LEDs. Trials were separated  
195 by 1 s. Target intensity began at 0.8 (arbitrary units), adjusted by QUEST (Watson  
196 and Pelli, 1983) implemented in PsychToolBox3 (Brainard, 1997). The second  
197 training was 2IFC intensity discrimination. One interval contained a 'weak' (1.5x  
198 detection threshold), the other a 'strong' vibration (starting at 1.8x weak intensity).

199 Participants responded with left feet for strong (targets) in the first, and right for the  
200 second interval. Threshold for 2IFC tasks was ~76 % correct, taken as the final trial's  
201 value of QUESTMean. The third training was 1IFC intensity discrimination. Half the  
202 intervals contained a weak (1.5x detection threshold), and half a strong vibration  
203 (starting at 1.8x weak intensity). Participants classified stimuli as 'strong' (left) or  
204 'weak' (right pedal). The strong intensity was adjusted with QUEST. Threshold was  
205 69 % correct (equivalent to 76 % in 2IFC). A single pulse of TMS at 50 % maximum  
206 stimulator output (MSO) was presented ~30 cm away from the participant's head, 25  
207 ms after the onset of each vibration.

208

209 We refer to scalp and brain coordinates thus: ORIGIN(lateral, anterior). Right and  
210 anterior are positive, left and posterior negative. For example, 5 cm left and 1 cm  
211 anterior to vertex: Cz(-5,1); 2 cm posterior to the optimal FDI location: FDI(0,-2). MNI  
212 neuroimaging coordinates are: MNI(X,Y,Z), in mm. Resting motor threshold (RMT) for  
213 the FDI was estimated using motor evoked potentials (MEPs) in the electromyograph  
214 (EMG, AD Instruments Powerlab 16/30; BioAmplifier, silver/silver-chloride electrodes  
215 over FDI belly and distal second metacarpal, Criswell, 2011; monophasic Magstim  
216 200<sup>2</sup> BiStim module, standard BiStim mode, figure-of-8, 100 mm outer diameter  
217 coil). Test pulses ~5-10 s apart were presented while the coil was moved around, at  
218 approximately Cz(-5,1), starting at 50 % MSO, increasing and decreasing to find the  
219 threshold (i.e., 5/10 trials with minimum peak-to-peak MEP amplitude of 50  $\mu$ V, both  
220 peaks within 20-60 ms). The coil handle pointed posterolaterally, approximately 45  
221 degrees to the midline; current anterior-to-posterior.

222

223 The mapping experiment was 10 blocks of 48 trials of 1IFC intensity discrimination,  
224 with TMS at one of 10 pseudorandomly ordered locations (Fig. 1F, white circles). A  
225 grid of ten locations was placed on participants' heads, with the origin, location 2,  
226 L2=FDI(0,0). The 9 other locations were: L1=FDI(+2,-2), L3=FDI(0,-2), L4=FDI(0,-4),  
227 L5=FDI(-2,+2), L6=FDI(-2,0), L7=FDI(-2,-2), L8=FDI(-2,-4), L9=FDI(-4,0), and  
228 L10=FDI(-4,-2).

229

230 Two participants (#3, #8) could not perform training. Two participants (#10, #12)  
231 performed poorly with TMS (i.e., floor effects, QUEST reached ceiling) on 8 blocks.  
232 #7 showed floor effects on six, #11 on two, and #5, #6, and #9 on one block each.  
233 Floor effects reduce variability at lower performance ranges (Holmes, 2009). A  
234 scatterplot of participants' across-block means against across-block SDs revealed  
235 two outliers (#10, #12), with low coefficient of variation (SD/mean). These participants  
236 were removed; the reported mean effects of TMS are therefore likely under-  
237 estimated.

238

### 239 ***Experiment 2: Controlling for non-specific effects of TMS***

240 Experiment 1 contained one task and 10 locations. Changes in performance across  
241 locations could be due to differences in TMS-related discomfort rather than effects on  
242 the brain (Meteyard & Holmes, 2018; Holmes & Meteyard 2018; [http://tms-](http://tms-smart.info)  
243 [smart.info](http://tms-smart.info)). Experiment 2 improved TMS localization and participant performance.  
244 Participants also performed auditory intensity discrimination to control for non-specific  
245 TMS effects.

246

247 EMG data were recorded from electrodes over FDI and flexor digitorum superficialis  
248 (FDS; Criswell, 2011). M1 was systematically mapped at 20 grid locations oriented  
249 ~45 degrees to midline (Fig. 1A, white circles). During discrimination, seven TMS  
250 locations were stimulated (4x2 grid, 2 cm spacing). An extra location was added, at  
251 FDI(-1,-1), as our best guess (at the time) of optimal S1-index location: L1=FDI(0,0),  
252 L2=FDI(0,-2), L3=FDI(-1,-1), L4=FDI(-2,0), L5=FDI(-2,-2), L6=FDI(-4,0), and  
253 L7=FDI(-4,-2), see Fig. 1C (white circles). Participants performed two  
254 counterbalanced 1IFC intensity discrimination tasks (vibrotactile, auditory). In  
255 auditory blocks, a speaker was positioned near participants' hands. Target frequency  
256 was 200 Hz. Weak intensity was 2x detection threshold, strong was 1.5x  
257 discrimination threshold above the weak intensity. 20 trials with fixed intensity were  
258 used. Based on unpublished data, TMS was triggered 50 ms after stimulus onset  
259 (i.e., approximately mid-way through stimulus processing, assuming ~25ms  
260 conduction time). A 75 mm outer diameter TMS coil was used.

261

262 Participants' heads were measured. Five pulses of TMS were presented at each of  
263 20 locations on the 5(medial-lateral)x4(anterior-posterior) grid (Figure 1A, white  
264 circles), with 1 cm spacing, centered on Cz(-5,1). The mean MEP amplitude across 5  
265 trials at each location was recorded. The 20 locations were tested sequentially,  
266 starting anteromedially, #1, Cz(-3,2.5), proceeding posterolaterally to #4, Cz(-3,-0.5),  
267 then #5, Cz(-4,2.5), finishing at #20, Cz(-7,-0.5). The location with maximal mean  
268 MEP amplitude per participant was designated M1-FDI; RMT was measured here.

269

270 Participants performed tactile and auditory tasks in two counterbalanced ~60 minute

271 sessions. Two training tasks were performed per session: 2IFC detection, 2IFC  
272 intensity discrimination. The experiment included seven blocks of 20 trials, each with  
273 TMS over one pseudorandomised location. Data were analyzed as proportion  
274 correct,  $d\text{-prime} = Z(\text{Hits}) - Z(\text{False alarms})$ , and  $\text{criterion} = -0.5 * (Z(\text{Hits}) + Z(\text{False}$   
275  $\text{alarms}))$ , Tamè & Holmes, 2016). The coil was held at ~45 degrees to midline, handle  
276 posterolaterally, current anterior-to-posterior.

277

### 278 ***Scalp measurements of S1-index***

279 The scalp locations of S1-index across all our available neuronavigated TMS data  
280 from nine unpublished experiments were summarised. For all measurements we had  
281 a recent structural MRI scan, and used atlas coordinates derived either from  
282 individual fMRI data, from group (N=20) fMRI data, or from meta-analysis (Holmes  
283 & Tamè, in press). All available sources of information were used. The target was on  
284 the anterior bank and/or crown of postcentral gyrus. Anatomical criteria (i.e., over  
285 postcentral gyrus, posterior to central sulcus) were prioritised over fMRI data. fMRI  
286 coordinates, whether based on individual, group, or meta-analysis, indicated that S1-  
287 index was, in every participant, lateral to or on the lateral border of the precentral  
288 gyrus 'hand knob' (Yoursy et al., 1997).

289

### 290 ***Analytic strategy***

291 This report provides multiple independent estimates of the optimal scalp location to  
292 stimulate S1-index. The analysis was largely exploratory, to estimate rather than  
293 hypothesis-test. Means and SDs are given for distances, locations, and TMS  
294 parameters; means and standard errors (SE) are given for behavioral performance,

295 muscle responses, and between condition differences, where statistical comparisons  
296 are made. Our experimental question is: are there consistencies in optimal TMS  
297 location across the samples typically used in similar TMS experiments ( $N \approx 12$ ).  
298 Reported p-values are uncorrected, unless otherwise stated. We believe minimizing  
299 sample size is important for human brain stimulation experiments, to reduce the risk  
300 that TMS poses - three of our participants have suffered syncope or fainting (Reader  
301 et al., 2017). Our approach is therefore to search for large, consistent effects (Smith  
302 & Little, 2018), and accumulate multiple, independent, converging sources of  
303 evidence. Where statistical tests are used, we are comfortable with the conventional  
304 long-run false positive error rate of 5 % (Lakens et al. 2018). Data, scripts, and  
305 previous versions of our work are freely available at <https://osf.io/c8nhj/>.

306

## 307 **Results and statistical analyses**

308 *Functional MRI data.* The group peak voxel locations and probabilistic anatomy for  
309 BOLD responses to vibrotactile stimulation of ten digits are in Table 1. The data are  
310 unable to resolve different S1 subregions, so only peak S1 voxels are reported. The  
311 differential contrasts, of each digit against the other four, resulted in lower BOLD Z-  
312 scores (across-digit mean $\pm$ SD  $Z=2.69\pm 0.86$ ) than single condition contrasts  
313 (mean $\pm$ SD  $Z=4.14\pm 0.65$ ), as expected – the single contrasts do not account for  
314 general task-related or finger non-specific activity common to all conditions in  
315 contrast with rest. The peak voxels in the two contrasts were mean $\pm$ SD  $5.44\pm 4.05$   
316 mm apart. Left hemisphere peak voxel locations ranged superiorly from MNI(-40,-  
317 30,64) for the little, to MNI(-50,-18,44) for the index; right hemisphere ranged from  
318 MNI(40,-30,66) for the ring, to MNI(56,-12,46) for the index finger. The peak

319 differential contrast voxels for S1-index were MNI(-48,-14,50) for left, and MNI(48,-  
320 12,54) for right hemisphere.

321

322 *Probabilistic atlas of the central sulcus, and S1-index scalp location.* The 100 central  
323 sulcus masks were summed into a single image, indicating the percentage of  
324 participants whose central sulcus included each voxel (Fig. 1B, left panel). The brain  
325 registration was less variable than the head registration (Fig. 1B, right panel). The  
326 between-participant range in Y-axis position of the central sulcus at the level of S1-  
327 index, MNI(-48,-21,50), was around 2-3 cm. The mean±SD location of S1-index  
328 projected onto the scalp was 6.8±0.4 cm lateral and 0.6±0.7 cm posterior to the  
329 vertex (Fig. 1B, 1D, 1E, blue square; Table 2).

330

331 *Experiment 1: Mapping effects of TMS on tactile discrimination thresholds.* In training,  
332 nine participants' mean±SE 2IFC detection threshold was 0.473±0.105 (A.U.); 2IFC  
333 discrimination threshold was 1.50±0.09 times weak intensity (1.71±0.26 dB, D'Amour  
334 and Harris 2014; Tamè et al. 2014); and 1IFC discrimination threshold was 1.52±0.15  
335 times weak intensity (1.64±0.41 dB). Mean±SD RMT=44.3±4.9 % MSO. TMS was  
336 applied at mean±SD=119±1.7 % RMT (mean±SD=52.7±5.3 % MSO). Due to  
337 researchers not recording data, scalp locations for M1-FDI were available for only  
338 seven participants, with mean±SD Cz(6.0±1.0,0.9±0.6) cm. Overall mean±SE  
339 discrimination threshold across 10 locations was 2.73±0.26 dB (Fig. 1F), with best  
340 performance (2.3±0.4 dB) at FDI(0,-2), and worst (3.36±0.31 dB) at FDI(-2,2) (Fig.  
341 1D, 1F, black cross). Thresholds were higher (worse) than in training, with locations  
342 5, 6, and 9 significantly (.012≤p≤.032). Pairwise comparisons between all 10 sites



343 revealed significant differences between FDI(-2,2), and locations 2, 3, 4, 6, 8, and 10  
344 ( $.026 \leq p \leq .049$ ). Across locations, mean $\pm$ SE MEPs were  $0.178 \pm 0.039$  mV, from  
345  $0.106 \pm 0.027$  mV at FDI(0,-4), to  $0.439 \pm 0.186$  mV at FDI(0,0). Within-participant  
346 correlations between MEP amplitude and discrimination threshold across 10  
347 locations varied from  $r(8) = -0.499$  to  $r(8) = .417$  (uncorrected two-tailed  $p > .14$ ). R-  
348 values were converted to Z-scores to allow parametric analysis; across participants,  
349 mean $\pm$ SE Z-score was small ( $0.100 \pm 0.110$ ,  $t(8) = 0.905$ ,  $p = .389$ ).

350

351 *Experiment 2: Controlling for non-specific effects of TMS.* Training performance on  
352 2IFC detection was mean $\pm$ SE =  $0.0483 \pm 0.0112$  (A.U.) for tactile, and  $0.0319 \pm 0.0029$   
353 for auditory stimuli,  $t(11) = 0.145$ ,  $p = .887$ . 2IFC intensity discrimination performance  
354 was  $0.352 \pm 0.055$  ( $1.27 \pm 0.16$  dB) for tactile, and  $0.524 \pm 0.113$  ( $1.71 \pm 0.30$  dB) for  
355 auditory,  $t(11) = .876$ ,  $p = .160$ . Participants' head sizes were a mean $\pm$ SD =  $38.0 \pm 2.3$  cm  
356 from nasion-inion, and  $36.5 \pm 1.8$  cm between pre-auricular points. Across locations,  
357 mean $\pm$ SE MEP amplitude =  $0.197 \pm 0.056$  mV, from  $0.003 \pm 0.002$  mV at Cz(-5.4,3.5), to  
358  $0.526 \pm 0.283$  mV at Cz(-6.1,-0.1) (Fig. 1A). Locations 3, 6, 9-11, and 15 produced  
359 MEPs significantly greater than zero ( $.005 \leq p \leq .020$ ). Pairwise comparisons revealed  
360 no clear pattern of differences. Across participants, Cz(-4.7,-1.5), Cz(-3.9,2.1), Cz(-  
361 4.7,1.4), Cz(-5.4,2.1), and Cz(-6.8,0.7) produced maximal MEPs in one participant,  
362 Cz(-3.2,1.4) and Cz(-6.1,-0.1) in two, and Cz(-5.4,0.7) in three. Mean $\pm$ SD optimal  
363 location was Cz(-5.0 $\pm$ 1.1,0.8 $\pm$ 1.0). Mean $\pm$ SD RMT at this site was  $40.4 \pm 7.0\%$ MSO.

364

365 TMS was presented during the experiment at a mean $\pm$ SD of  $120 \pm 0.6\%$  RMT  
366 ( $48.4 \pm 8.4\%$  MSO). Performance was worse with tactile (mean $\pm$ SE d-

367 prime= $1.06 \pm 0.12$ ) than auditory targets ( $1.61 \pm 0.2$ ,  $t(11)=2.78$ ,  $p=.018$ ). Response  
368 biases (tendency to respond 'stronger') were negligible, and comparable between  
369 touch (mean $\pm$ SE criterion= $-0.005 \pm 0.039$ ) and audition ( $0.055 \pm 0.054$ ,  $t(11)=0.938$ ,  
370  $p=.369$ ). Effects of TMS were assessed by differences between auditory and tactile  
371 tasks per location. TMS over FDI(-2,0) resulted in the largest decrement in  
372 performance (tactile mean $\pm$ SE  $d'=1.05 \pm 0.30$  vs. auditory= $1.93 \pm 0.30$ , mean $\pm$ SE  
373 difference= $0.880 \pm 0.265$ ,  $t(11)=3.32$ ,  $p=.007$ ), with FDI(0,0) second largest  
374 ( $0.942 \pm 0.194$  vs.  $1.73 \pm 0.346$ , difference= $0.788 \pm 0.318$ ,  $t(11)=2.48$ ,  $p=.031$ , Fig. 1C,  
375 1D black 'target'; Table 2). All other sites showed worse performance for tactile  
376 targets, but none significantly. None of the response biases differed between auditory  
377 and tactile tasks, but participants were more likely to report 'weaker' tactile targets  
378 with TMS over FDI(0,0) (mean $\pm$ SE criterion= $-.136 \pm 0.075$ ), than FDI(-2,0)  
379 ( $0.120 \pm 0.087$ ,  $t(11)=2.39$ ,  $p=.036$ ), or FDI(-2,-2) ( $0.130 \pm 0.110$ ,  $t(11)=2.26$ ,  $p=.045$ ).  
380  
381 MEPs were recorded from FDI and FDS, were monitored during experiments, but  
382 data were saved only for eight participants (#5-12). During the tactile task, mean $\pm$ SE  
383 MEPs were smallest at FDI(-4,0) (FDI= $0.058 \pm 0.026$  mV) and FDI(-2,-2)  
384 (FDS= $0.014 \pm 0.010$  mV) and largest at FDI(0,0) (FDI= $1.51 \pm 0.49$  mV, FDS= $1.22 \pm 0.43$   
385 mV). During the auditory task, MEPs were smallest at FDI(-2,-2) (FDI= $0.01 \pm 0.01$  mV;  
386 FDS= $0.01 \pm 0.01$  mV) and largest at FDI(0,0) (FDI= $0.79 \pm 0.29$  mV, FDS= $0.55 \pm 0.21$   
387 mV). The smallest 'MEPs' ( $\sim 0.01$  mV) were not different from zero, much lower than  
388 the MEP threshold, and likely reflect electrical noise. Comparing auditory and tactile  
389 tasks, MEPs were not significantly different at any location. There were no significant  
390 correlations between performance ( $d'$ ) and MEP amplitude, either for tactile or

391 auditory tasks alone, the differences between them, for either muscle, or for both  
392 muscles combined (nine comparisons on Z-scores, all  $t(7) \leq 1.75$ , all uncorrected  
393  $p \geq .125$ ).

394

395 *Scalp measurements of S1-index.* The mean $\pm$ SD scalp location of S1-index was Cz(-  
396  $8.0 \pm 0.9, -0.4 \pm 1.0$ ) (left hemisphere, Fig. 1D, magenta circle; Table 2), and  
397 Cz( $8.4 \pm 1.1, -0.4 \pm 0.5$ ) (right hemisphere). Combining hemispheres across 15  
398 participants, S1-index was at Cz( $\pm 8.1 \pm 1.0, -0.3 \pm 0.8$ ). For seven participants,  
399 mean $\pm$ SD S1-index was at FDI( $\pm 2.4 \pm 1.0, -0.5 \pm 1.3$ ).

400

#### 401 **Discussion**

402 Re-analysis of fMRI data revealed the peak voxel for right index finger was very  
403 close to the meta-analytic mean location of S1-index in BA3b and BA1. The  
404 probabilistic central sulcus atlas revealed a 2-3 cm anterior-posterior range in central  
405 sulcus location at the level of S1-index. This implies that researchers using template  
406 MRI to position TMS coils are likely to make Y-axis errors of several cm in locating  
407 the central sulcus. Projected onto the scalp, S1-index is 7 cm lateral, and 0.5 cm  
408 posterior to vertex. These distances are likely to be slight underestimates, given that  
409 participants typically have hair (not visible on MRI), and a bathing or EEG cap  
410 between scalp and TMS coil. This underestimation is between 0.2 and 1.0 cm (Table  
411 2). In Experiment 1, the location of maximal interference of TMS with tactile intensity  
412 discrimination thresholds was 2 cm lateral, and 2 cm anterior to M1-FDI. Experiment  
413 1, however, is relatively weak: two participants could not complete the task, two were  
414 removed, and the statistical tests did not pass conservative multiple comparison

415 corrections. Instead, Experiment 2 provides strong evidence that maximal  
416 interference with tactile intensity discrimination is 2 cm lateral to M1-FDI. Experiment  
417 2 allows greater confidence that M1-FDI was optimally localized and that tactile  
418 interference was due to a specific worsening of tactile relative to auditory  
419 discrimination. Conservative correction for multiple comparisons revealed that the  
420 only significant effect of TMS on tactile intensity discrimination was 2 cm lateral to  
421 M1-FDI.

422

423 The more anterior location found in Experiment 1 than 2 may be due to the different  
424 tasks used (threshold estimation vs. discrimination); to between-participant  
425 differences in central sulcus anatomy or head shape; to variability in the precision of  
426 our TMS methods and head measurements; or to increased TMS-related discomfort  
427 at the most anterior site in Experiment 1 (Meteyard & Holmes, 2018; Holmes &  
428 Meteyard, 2018). Experiment 2 included a control task so that TMS-related  
429 discomfort was matched, and task-related differences were the dependent variable.  
430 Without independent MRI evidence, the most likely cause is measurement error and  
431 increased TMS-related discomfort at the most anterior site in Experiment 1.

432

433 Here, we reported multiple independent lines of evidence (Table 2, Figure 1) which  
434 supports findings from a recent systematic review (Holmes & Tamè, in press): the  
435 optimal location for stimulating the hand area of primary somatosensory cortex, on  
436 average, is ~2 cm lateral, and ~0.5 cm posterior to M1-FDI. This finding of S1-hand  
437 being more lateral than M1-hand is consistent with studies in which both M1-hand  
438 and S1-hand are measured together (e.g., Blatow et al. 2011), and with the work of

439 Seyal and colleagues (1997), who systematically mapped TMS effects on tactile  
440 detection and discrimination at 25 locations in a grid centered on M1-hand. They  
441 found maximal interference when the TMS coil was 4 cm lateral and 0-2 cm posterior  
442 to M1-hand (Figure 2a and 2b in Seyal et al. 1997).

443

444 Assuming previous TMS studies found M1-FDI/APB in a similar location to our data,  
445 these results imply that TMS studies targeting S1-index have been, on average, 2.25  
446 cm away from their target (Table 1). This is not a trivial distance. The mean figure-of-  
447 eight TMS coil used in these studies has a 7.5 cm outer wing diameter, implying an  
448 error of 30% of coil diameter. This is likely to impede stimulation effectiveness. TMS  
449 over motor cortex is sensitive to coil position changes of a few millimeters (e.g.,  
450 Raffin et al., 2015). These large distances between the likely location of S1-index,  
451 and the locations targeted in prior experiments may explain why otherwise well-  
452 designed experiments may fail to interfere significantly with tactile perception (e.g.,  
453 Convento et al. 2018, reviewed by Holmes and Tamè, 2018). Below, we discuss  
454 possible sources of variability in stimulating S1 using TMS.

455

#### 456 ***Sources of variability in stimulating S1***

457 Variability in TMS studies arises from participants, experimenters, and procedures.  
458 Participant-associated variability includes head size and shape (Zilles et al. 2002;  
459 Xiao et al. 2018), brain area size, shape, folding, location, and function.  
460 Experimenter-associated variability arises from the selection, measurement, and  
461 registration of anatomical landmarks and reference points (nasion,inion, vertex), and  
462 the positioning and orientation of the coil. Procedure-associated variability includes

463 the target, timing, intensity, orientation, waveform, frequency, and orientation of TMS.  
464  
465 We were surprised by the large within-participant and between-session/experimenter  
466 variability during our studies. This variability may explain the potentially surprising  
467 finding of Experiment 1, with maximal thresholds 2 cm lateral and 2 cm *anterior* to  
468 M1-FDI. Measurements on the scalp varied, laterally and anteriorly, by 3-4 cm  
469 between participants for M1-FDI relative to vertex (Niskanen et al. 2010), S1-index  
470 relative to vertex, and S1-index relative to M1-FDI. In part, this is due to errors in  
471 scalp measurement, MRI registration, and locating M1-FDI. In large part, however, it  
472 likely reflects between participant anatomical differences. Better training,  
473 communication, and day-to-day practice will minimize experimenter error; better  
474 understanding of M1-hand and S1-hand are required to optimise TMS protocols.  
475 Given the potential sources of variability in stimulating S1, we recommend consistent,  
476 systematic, and numerical reporting of every aspect and stage of TMS studies (Rossi  
477 et al. 2009; Rossini et al. 1994, 2015; Chipchase et al. 2012). This should be done for  
478 all studies, regardless of whether neuronavigation was used.

479

#### 480 ***Limitations***

481 Our approach relied on numerous sources of information which, we argued,  
482 converged on the result that S1-index is 2 cm lateral to M1-FDI. Despite this  
483 convergence, one might question whether meta-analysis of reported FMRI  
484 coordinates, or averaging FMRI data across participants is sufficient. We cannot  
485 distinguish between Brodmann's area BA3b, BA1, or BA2 with our FMRI data, as our  
486 localizers were not sufficiently powerful. Similar limitations may apply to our TMS

487 data (Fox et al. 2004). We also cannot account for biases intrinsic to fMRI – the data  
488 rely on oxygenation changes rather than neural activity, and may be biased by non-  
489 neural structures (Schweisfurth et al., 2014). Further, single peak voxel coordinates  
490 derived from multiple studies and participants do not reflect the likely extent of S1  
491 activation following index finger stimulation, nor the total S1 territory involved. Better  
492 methods to estimate the optimal scalp location for S1-index TMS may be to combine  
493 probabilistic maps of S1 with the likelihood of TMS, accounting for individual brain  
494 anatomy (Petrov et al. 2017). The overlap or convolution of these probabilistic maps  
495 might provide more accurate estimates of the scalp locations necessary to stimulate  
496 S1-index. This approach represents a clear goal for future work, and would be  
497 extremely useful for interpreting previous results and planning new studies (Xiao et  
498 al., 2018). Generating such a statistic will need to account for TMS coil size, shape,  
499 position, and orientation, intensity, waveform, frequency, and pattern; scalp-to-brain  
500 distance, cortical folding, and the size and function of the cortical area under study.

501

502 We have criticized the standard heuristic based on M1-FDI to locate S1-index, but  
503 our methods also rely on TMS over M1-FDI: the origin of our maps was M1-FDI; TMS  
504 intensity was set according to M1-FDI threshold. These practices are very common in  
505 TMS research, but we must be cautious about the circularity. There may be no  
506 reason why S1-index is best localized using M1-FDI as a reference, and no reason  
507 why parameters optimal for M1-FDI should be optimal for S1-index. Addressing this  
508 circularity is outside the present scope, but is important for future studies.

509

510 ***Recommendations for locating S1-index in transcranial stimulation studies***

511 Depending on available equipment and funding, transcranial stimulation studies may  
512 need different methods to locate their targets. Ideally, neuronavigation with a recent  
513 high-resolution structural MRI and functional localizer will be used for each  
514 participant. Systematic review showed that very few studies met this ‘gold standard’  
515 (Holmes & Tamè, in press). If individual fMRI is unavailable, individual MRI with  
516 group-level localizers or coordinates may suffice. The fMRI data need to be  
517 interpreted in conjunction with anatomical criteria. Registration of the participant’s  
518 head to the MRI needs to be done carefully; we recommend recording head and  
519 scalp measurements systematically - in one participant, we noticed scalp coordinates  
520 well outside other participants’; re-registering the MRI revealed that the wrong  
521 calibration file had been used, leading to ~3 cm coil positioning error. If a participant’s  
522 MRI is unavailable, then standard MRI templates, registered onto the participant’s  
523 scalp, provide only an approximate localization. The probabilistic central sulcus atlas  
524 we reported (Fig. 1B), suggests registration errors of several centimeters are likely.  
525 Without neuronavigation, scalp measurements using the 10:20 or 10:10 systems may  
526 be the only, very approximate, localization method. If the location of a target is  
527 estimated relative to that of primary motor cortex (i.e., using muscle twitches or  
528 motor-evoked potentials), or other functionally-defined locations, then researchers  
529 should use as many relevant sources of evidence to justify any heuristics used. Our  
530 work suggests that even very-commonly reported heuristics are not optimal for  
531 locating the intended target. Such heuristics may not be evidence-based.

532

533



534 **Conclusion**

535 More than a century after the first electrical stimulation of human somatosensory  
536 cortex (Cushing, 1909), the accuracy of TMS coil positioning remains questionable.  
537 The localization error in previous TMS studies of S1-hand is likely about 2.25 cm.  
538 Evidence from the independent sources reported here converged on the finding that  
539 S1-index is about 7-8 cm lateral to the vertex, or about 2 cm lateral and 0.5 cm  
540 posterior to the scalp location for eliciting MEPs in the FDI muscle. These estimates  
541 cannot be relied upon for any single participant – the range of scalp locations across  
542 participants was 3-4 cm in each direction for each location. Multiple sources of  
543 evidence for target location – probabilistic anatomy, group data, scalp measurements,  
544 meta-analyses, and the gold standard of individual (F)MRI – should be sought in  
545 every TMS study. To improve localization methods, we recommend systematic  
546 reporting of participants' head sizes and all locations targeted, both along the scalp  
547 and, if available, in MRI scanner/anatomical and standard (e.g., MNI152)  
548 coordinates. The results of previous TMS studies targeting the index finger area of S1  
549 need reassessment.

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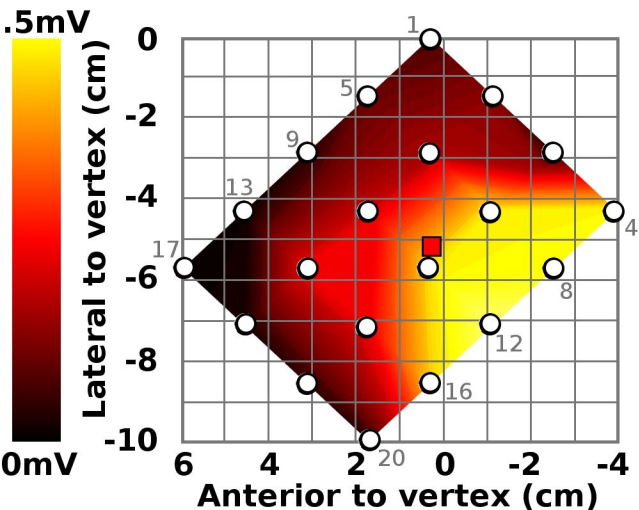
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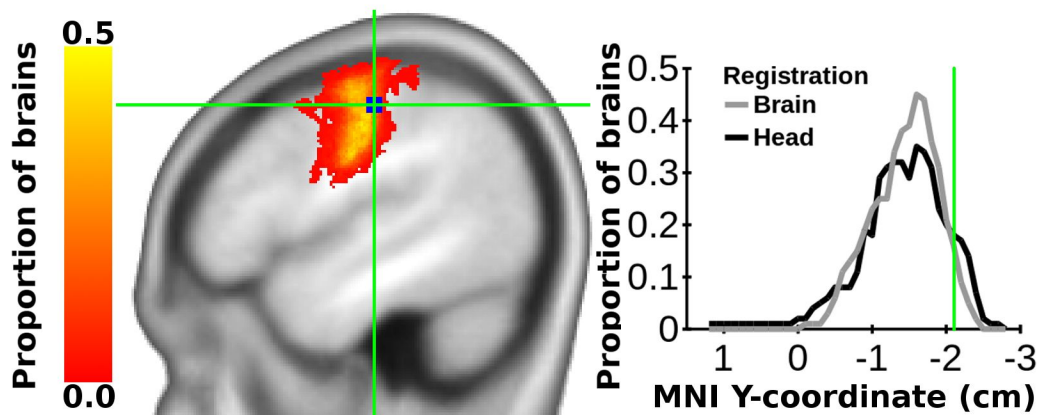
705 **Fig. 1: Locating primary somatosensory cortex in human brain stimulation**  
706 **studies.** Evidence for the scalp location of the primary somatosensory cortex  
707 representation of the right index finger (S1-index). All coordinates are in centimetres (  
708 cm) lateral to (i.e., left of) and anterior to (i.e., forward of) the vertex (Cz), or in MNI  
709 space. **A.** Mean motor evoked potential (MEP) amplitude during systematic mapping  
710 of the first dorsal interosseus muscle's primary motor cortex representation (M1-FDI)  
711 on the scalp in Experiment 2. Red square at Cz(-5.2,0.4): mean location of M1-FDI  
712 from all available studies conducted in the laboratory (N=56); white circles: locations  
713 tested. **B.** Probabilistic anatomy of the central sulcus, as estimated from 100 MRI  
714 scans. Colours on the brain scan represent the proportion of participants with central  
715 sulcus at that location. Blue square and green cross-hairs: mean reported MNI  
716 coordinate for the location of S1-index across 54 fMRI studies, MNI(-48,-21,50). The  
717 graph shows a cross-section along the MNI Y-axis for the selected coordinate. The  
718 range of likely central sulcus distances along this axis, after transformation of either  
719 the whole head (black), or the brain (grey), is 2-3 cm. **C.** TMS-related interference  
720 with tactile intensity discrimination (N=12, Auditory d' – Tactile d', t(11)-scores), is  
721 highest 7 cm lateral, and 0.76 cm anterior to the vertex. Thin black contour:  
722 uncorrected 1-tailed statistical significance (alpha) threshold ( $p \leq .05$ ); thick black  
723 contour: alpha threshold Bonferroni corrected for 7 locations ( $p \leq .007$ ); black 'target':  
724 maximum tactile interference; red square: M1-FDI; white circles: locations tested. **D.**  
725 Summary of all scalp locations ( $M \pm SD$ ) studied in this report and those from a recent  
726 systematic review. Magenta circle: S1-index based on individual fMRI-guided TMS  
727 neuronavigation; yellow triangle: Mean C3 location on 101 participants' heads; open  
728 squares: estimated mean scalp location targeted for 43 TMS studies using M1-FDI as

729 a reference point (black); 16 TMS studies using M1-thenar as a reference point (mid  
730 grey); 21 TMS studies using hand movement as a reference point (light grey); black  
731 triangle: estimated mean scalp location targeted for 16 TMS studies using C3 as a  
732 reference point; black diamond: estimated mean scalp location of M1-FDI according  
733 to a meta-analysis. Black cross: mean location of maximum intensity discrimination  
734 thresholds in Experiment 1; black 'target': mean location of maximum difference  
735 between auditory and tactile intensity discrimination performance in Experiment 2. **E.**  
736 *fMRI data. Re-analysis of fMRI data from Tamè and Holmes (2016): red-yellow*  
737 *shading shows the contrast between the right index finger versus all other fingers on*  
738 *the right hand. F. Mean tactile intensity discrimination thresholds for 9 participants in*  
739 *Experiment 1. White circles: locations tested. G. Mean±95% confidence ellipsoids for*  
740 *M1-FDI (red) and S1-index (magenta) locations, as used by Tamè and Holmes*  
741 *(2016). H. Scalp landmarks used in the 10:20 electrode positioning system. White*  
742 *circle: vertex; green circles: other scalp landmarks and electrode positions, including*  
743 *C3', often positioned as indicated, at 2 cm posterior to C3, though likely located ~3.6*  
744 *cm posterior to C3.*

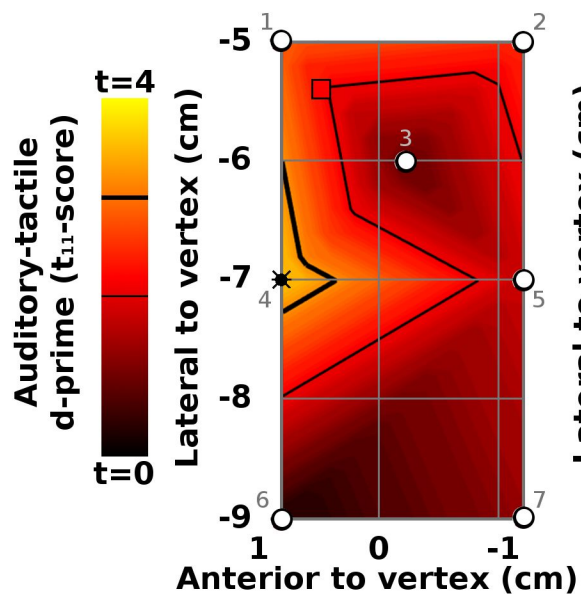
### A. MEP map (E2)



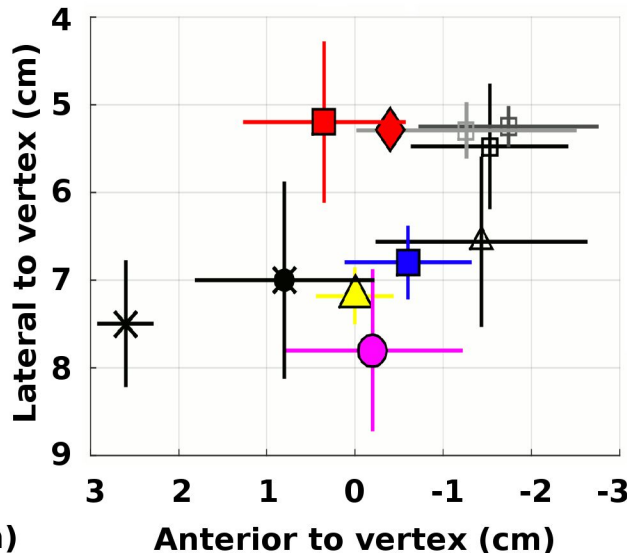
### B. Probabilistic central sulcus anatomy



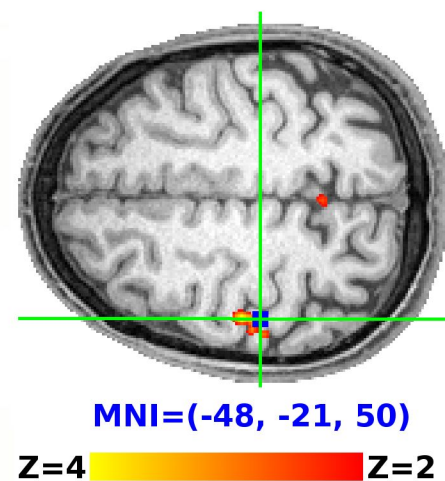
### C. Tactile interference (E2)



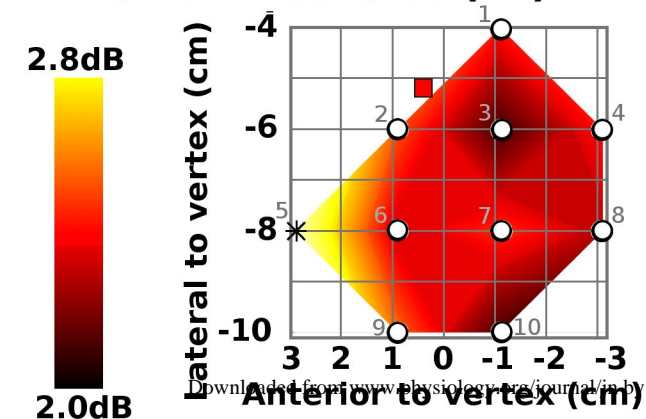
### D. Mean $\pm$ SD scalp positions



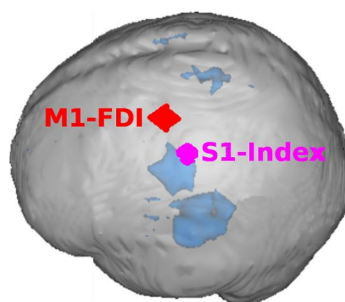
### E. FMRI data



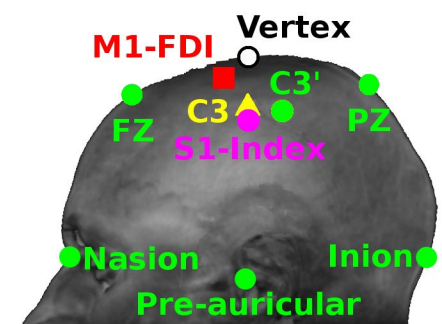
### F. Tactile thresholds (E1)



### G. TMS neuronavigation



### H. Scalp anatomy



**Table 1: Peak BOLD signal changes at the group level, to vibrotactile stimulation of left and right digits in 20 healthy participants**

Hand	Contrast	Digit	MNI			Z	Probabilistic anatomy (%)									
			x	y	z		Central gyri		Brodmann's area							
							Pre	Post	6	4a	4p	3b	1	2		
Left	Differential	1	56	-12	46	3.43	20	57	9	41	1	32	82	17		
		<b>2</b>	<b>48</b>	<b>-12</b>	<b>54</b>	<b>3.77</b>	<b>42</b>	<b>27</b>	<b>47</b>	<b>38</b>	<b>0</b>	<b>8</b>	<b>43</b>	<b>0</b>		
		3	42	-20	54	2.41	32	32	15	41	13	66	19	0		
		4	42	-22	62	2.83	28	34	49	38	0	21	55	0		
		5	40	-30	64	1.34	5	47	7	35	8	31	76	0		
	Single	1	56	-12	48	5.32	19	52	7	44	0	22	76	10		
		<b>2</b>	<b>50</b>	<b>-14</b>	<b>56</b>	<b>4.39</b>	<b>17</b>	<b>50</b>	<b>26</b>	<b>18</b>	<b>0</b>	<b>0</b>	<b>37</b>	<b>0</b>		
		3	46	-22	60	4.08	9	48	9	10	0	19	96	3		
		4	40	-30	66	4.1	5	58	14	38	6	12	65	0		
		5	40	-30	64	3.36	5	47	7	35	8	31	76	0		
Right	Differential	1	-50	-18	44	3.34	13	51	0	20	15	44	48	60		
		<b>2</b>	<b>-48</b>	<b>-14</b>	<b>50</b>	<b>3.55</b>	<b>35</b>	<b>37</b>	<b>33</b>	<b>45</b>	<b>1</b>	<b>31</b>	<b>48</b>	<b>6</b>		
		3	-42	-20	62	2.79	38	28	60	28	0	7	32	0		
		4	-44	-28	64	1.56	2	63	0	6	0	16	80	8		
		5	-46	-28	62	1.92	0	62	0	2	0	11	94	19		
	Single	1	-50	-20	44	4.42	6	51	0	9	11	43	50	72		
		<b>2</b>	<b>-54</b>	<b>-22</b>	<b>52</b>	<b>4.80</b>	<b>0</b>	<b>69</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>8</b>	<b>88</b>	<b>30</b>		
		3	-44	-20	62	4.17	24	41	48	19	0	5	32	0		
		4	-52	-26	56	3.28	0	57	0	0	0	0	86	26		
		5	-40	-30	64	3.44	5	49	2	40	0	15	71	8		

x: MNI x-coordinate in mm; y: MNI y-coordinate in mm; z: MNI z-coordinate in mm; Z: Z-score for the BOLD contrast; Post: postcentral gyrus; Pre: precentral gyrus. Probabilistic anatomy based on the Juelich probabilistic cytoarchitectural atlases viewed in FSL-view.

Data for the index finger are highlighted in bold text.

**Table 2: Scalp locations of M1-FDI, S1-index, and C3/C4 relative to vertex (Cz), from seven independent sources of evidence**

Location and source	Location relative to vertex (Cz) mean±SD cm (min:max)					
	N	Left hemisphere		N	Right hemisphere	
		Lateral	Anterior		Lateral	Anterior
M1-FDI, TMS studies (2011-18)	56	-5.2±0.8 (-7.0:-3.0)	0.4±0.9 (-2.6:2.0)	14	5.2±0.9 (3.5:7.5)	0.5±0.9 (-1:1.8)
S1-index, TMS meta-analysis (N=96 studies, 1991-2017)*	1693	-5.9±0.9 (-8.2:-4.4)	-1.3±1.0 (-3.6:0.4)	-	-	-
C3/4, head measurements (2016-18)	101	-7.2±0.3 (-7.8:-6.6)	0	-	-	-
S1-index, FMRI meta-analysis (LH N=425; RH N=316, 54 studies, 1999-2017), projected onto scalp in MRI	100	-6.8±0.4 (-9.4:-5.7)	-0.6±0.7 (-2.3:2.2)	100	6.9±0.4 (6.1:9.8)	-0.6±0.8 (-2.3:1.8)
S1-index, Experiment 1 (2014-15)	10	-7.5±0.7 (-9.0:-7.0)	2.6±0.3 (2.0:3.0)	-	-	-
S1-index, Experiment 2 (2017)	12	-7.0±1.1 (-8.8:-5.2)	0.8±1.0 (-1.5:2.1)	-	-	-
S1-index, FMRI study (N=20, 2012-14), group contrast projected onto scalp in navigated TMS studies (2016-18)	11	-7.8±0.9 (-10.0:-6.7)	-0.2±1.0 (-1.5:1.4)	9	8.4±1.1 (7.0:10.3)	-0.4±0.6 (-1.1:0.3)

\* Collapsed across hemispheres, and using assumed scalp locations for M1-FDI/M1-APB

representations where not reported