

1 Neural correlates of conscious tactile perception: An analysis of  
2 BOLD activation patterns and graph metrics

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24 **Abstract**

25 Theories of human consciousness substantially vary in the proposed spatial extent of brain  
26 activity associated with conscious perception as well as in the assumed functional  
27 alterations within the involved brain regions. Here, we investigate which local and global  
28 changes in brain activity accompany conscious somatosensory perception following  
29 electrical finger nerve stimulation, and whether there are whole-brain functional network  
30 alterations by means of graph metrics. Thirty-eight healthy participants performed a  
31 somatosensory detection task and reported their decision confidence during fMRI. For  
32 conscious tactile perception in contrast to undetected near-threshold trials (misses), we  
33 observed increased BOLD activity in the precuneus, the intraparietal sulcus, the insula, the  
34 nucleus accumbens, the inferior frontal gyrus and the contralateral secondary  
35 somatosensory cortex. For misses compared to correct rejections, bilateral secondary  
36 somatosensory cortices, supplementary motor cortex and insula showed greater  
37 activations. The analysis of whole-brain functional network topology for hits, misses and  
38 correct rejections, did not result in any significant differences in modularity, participation,  
39 clustering or path length, which was supported by Bayes factor statistics. In conclusion, for  
40 conscious somatosensory perception, our results are consistent with an involvement of  
41 (probably) domain-general brain areas (precuneus, insula, inferior frontal gyrus) in addition  
42 to somatosensory regions; our data do not support the notion of specific changes in graph  
43 metrics associated with conscious experience. For the employed somatosensory  
44 submodality of fine electrical current stimulation, this speaks for a global broadcasting of  
45 sensory content across the brain without substantial reconfiguration of the whole-brain  
46 functional network resulting in an integrative conscious experience.

47 **Keywords:** somatosensory processing, perceptual awareness, consciousness, functional  
48 connectivity, graph theory, fMRI

## 49 **Introduction**

50 In the debate on the neural correlates of consciousness, several crucial issues are still not  
51 resolved. First, regarding the involved brain regions, some studies assume only areas  
52 related to the particular perceptual modality to be necessary (Auksztulewicz et al., 2012;  
53 Schröder et al., 2019), others emphasize the role of a parietal hot zone (Boly et al., 2017;  
54 Koch et al., 2016) whereas some theories - most notably the global workspace theory  
55 (Baars, 1988; Dehaene et al., 2006; Mashour et al., 2020) - assume conscious experience  
56 to depend on the involvement of widespread particularly fronto-parietal brain regions  
57 (Naghavi and Nyberg, 2005; Rees et al., 2002). Second, regarding the neurophysiological  
58 processes occurring *within* the involved brain regions, recent studies are suggesting  
59 specific alterations in their connectivity which can be identified by effects of transcranial  
60 stimulation (Casali et al., 2013) or using graph-theoretical metrics on fMRI data (Godwin et  
61 al., 2015; Sadaghiani et al., 2015).

62 For the somatosensory domain, previous fMRI activation studies have suggested  
63 the ipsilateral and contralateral secondary somatosensory cortices as the most promising  
64 candidates for conscious tactile perception (Moore et al., 2013; Schröder et al., 2019).  
65 Furthermore, recurrent interaction of S2 with S1 may play an important role for tactile  
66 detection (Auksztulewicz et al., 2012). Research focusing on tactile illusions has shown  
67 that S1 is activated somatotopically in correspondence with the illusory percept and body  
68 ownership (Blankenburg et al., 2006; Martuzzi et al., 2015). In this context, the temporal  
69 parietal junction (TPJ) plays a major role for bodily self-consciousness (De Ridder et al.,  
70 2007; Ionta et al., 2014). The insula has been consistently reported to be associated with  
71 conscious tactile perception (Moore et al., 2013) and described as a central hub for  
72 interoception (Ronchi et al., 2015) and self-identification (Park and Blanke, 2019).  
73 Interestingly, in another recent study, the insula together with anterior cingulate cortex  
74 coded for uncertainty across stimulation intensities (Schröder et al., 2019). In the same

75 study, frontal and parietal activations in tactile detection paradigms have been interpreted  
76 as serving the task (e.g., reporting a percept) but not the conscious sensory experience  
77 (Schröder et al., 2019). Yet, the above-mentioned ideas of a “global workspace” involving  
78 mainly fronto-parietal activity (Dehaene et al., 2006), or of a posterior cortical hot zone  
79 integrating sensory cortices (Koch et al., 2016) are conceived to be domain-general thus  
80 also applying to the tactile consciousness.

81 While most of the above-mentioned studies relied on the analysis of BOLD  
82 activation patterns, the question, whether functional connectivity changes or not, can be  
83 assessed using graph metrics (Bassett and Sporns, 2017). For this purpose, cortical and  
84 subcortical regions of interest (ROIs) are defined as nodes and their temporal relationships  
85 as edges (i.e., their connection; Bullmore and Bassett, 2011). The resulting network  
86 topologies are assessed with graph-theoretical measures such as modularity and  
87 clustering coefficient and compared between aware and unaware target trials (Godwin et  
88 al., 2015; Sadaghiani et al., 2015; Weisz et al., 2014). *Modularity* captures the global  
89 organization of nodes in subnetworks, whereas the *clustering coefficient* indicates whether  
90 a node’s neighbors are also connected, thus forming local clusters. Measures of  
91 integration (e.g., *characteristic path length*) describe the general connectivity between all  
92 nodes, whereas measures of centrality (e.g., *participation coefficient*) reveal important  
93 nodes in the network. In this framework, visual awareness has recently been suggested to  
94 be accompanied by a decreased modularity and increased participation coefficient of the  
95 post-stimulus network topology in fMRI (Godwin et al., 2015). Importantly, these topologies  
96 had explanatory power beyond local BOLD amplitudes and baseline functional  
97 connectivity (Godwin et al., 2015). Globally, this indicates a lower segregation of nodes  
98 into distinct networks and locally a higher centrality of all nodes. A more integrated state  
99 accompanying stimulus awareness (Godwin et al., 2015) is supposed to facilitate  
100 broadcasting of sensory information to other brain areas (Dehaene et al., 2006; Dehaene

101 and Changeux, 2011). These widespread changes in functional connectivity have been  
102 interpreted as evidence supporting global models of awareness, e.g., the global  
103 workspace theory (Dehaene et al., 2006; Dehaene and Changeux, 2011). Whether these  
104 changes in graph metrics generalize to other sensory modalities is not yet answered.

105 In the present study, building on our previous experience in studies on neural  
106 processes underlying conscious and unconscious somatosensory processing  
107 (Blankenburg et al., 2003; Forschack et al., 2020; 2017; Nierhaus et al., 2015; Schubert et  
108 al., 2006), we used a “classical” fMRI detection paradigm in which aware and unaware  
109 trials of physically identical near-threshold stimuli are contrasted (Aru et al., 2012; Baars,  
110 1988). Notably, our fMRI paradigm included a nine-second pause between stimulation and  
111 report, which made the assessment of functional network topologies with graph metrics  
112 possible. Therefore, our study design allowed to assess BOLD activity patterns and graph  
113 metrics independently, as well as to relate the two measures directly.

114 Two other features of our paradigm are important: (i) a confidence rating was  
115 included for each trial allowing for an analysis of confident decisions only and (ii) the  
116 paradigm included 25% catch trials. By comparing the contrast of undetected stimuli to  
117 correctly rejected catch trials, neural processes associated with non-conscious stimulus  
118 processing of near-threshold stimuli can be assessed. In a previous study on subthreshold  
119 stimuli, we had shown that they were associated with a deactivation of somatosensory  
120 brain regions (Blankenburg et al., 2003); however, it is not clear whether this is also true  
121 for stronger stimuli near the detection threshold.

122 Thus, our study aimed to address the following main questions:

- 123 • Do BOLD activation patterns following somatosensory near-threshold stimuli  
124 match the predictions of major consciousness theories, i.e., does the contrast  
125 detected/undetected lead to increased activity only in somatosensory areas  
126 (Schröder et al., 2019), in a fronto-parietal network (global workspace theory), or in  
127 a more restricted temporo-parietal-occipital hot zone (Koch et al., 2016)?
- 128 • Do graph metrics change with the conscious experience of somatosensory stimuli  
129 as shown for the visual system by Godwin et al. (2015), and do the affected areas  
130 match activated brain areas?
- 131 • Which neural changes are associated with non-perceived, but near-threshold  
132 somatosensory stimuli?

## 133 **Materials & Methods**

### 134 **Participants**

135 Thirty-eight healthy humans (19 women; mean age = 27.3, age range: 23-36) participated  
136 in the study. They had normal or corrected-to-normal vision and were right-handed (mean  
137 laterality index = 85, range: 60-100; Oldfield, 1971).

138

### 139 **Ethics statement**

140 All participants provided informed consent (including no contra-indication for MRI), and all  
141 experimental procedures were approved by the ethics commission at the medical faculty of  
142 the University of Leipzig.

143

### 144 **Experimental design and statistical analysis**

145 The experimental design of the tactile detection task had the intention to generate different  
146 sensory experiences for physically identical stimulus presentations. Brain activity  
147 accompanying these sensory experiences was sampled with BOLD fMRI (see fMRI data  
148 acquisition for details). The tactile stimulation was applied as a single electrical pulse to  
149 the left index finger. The stimulation intensity was set to the individual sensory threshold,  
150 before each of the four acquisition blocks, such that participants reported a stimulus  
151 detection (“hit”) in about 50% of the trials. One hundred near-threshold trials were  
152 intermingled with 20 clearly perceivable, supra-threshold trials and 40 catch trials without  
153 stimulation as control conditions. Participants had to report their perception (yes/no) and  
154 decision confidence (see “behavioral paradigm” for details). This led to three within-  
155 participant factors of interest: (a) rejected catch trials without stimulation (correct  
156 rejections), (b) non-perceived near-threshold trials (misses), and (c) perceived near-  
157 threshold trials (hits). We did not include false alarms (reported “yes” in catch trials without

158 stimulation) due to the low false alarm rate (mean FAR = 3.3%,  $SD = 6.0\%$ ). 17 of 31  
159 participants reported zero false alarms.

160 We compared the graph metrics between hits, misses and correct rejections across  
161 participants with the Wilcoxon's signed-rank test (see Graph-theoretical analysis for  
162 details). For each graph metric, the  $p$ -values of the 24 paired Wilcoxon's signed-rank tests  
163 were corrected for multiple comparisons with a false discovery rate (FDR) of 5%  
164 (Benjamini and Hochberg, 1995). The BOLD response amplitudes were modeled for the  
165 three (detection related) within-participant factors and compared them with a mixed-effects  
166 meta-analysis (3dMEMA; Chen et al., 2012). We controlled for multiple comparisons with  
167 family-wise error correction (see fMRI contrast analysis for details).

168

#### 169 **Data and code availability**

170 The code to run the experiment, the behavioral data, and the code to analyze the  
171 behavioral and MRI data are available at <http://github.com/grundm/graphCA>. Due to a lack  
172 of consent of the participants, structural and functional MRI data cannot be shared  
173 publicly, and can only be made available upon reasonable request if data privacy can be  
174 guaranteed according to the rules of the European General Data Protection Regulation  
175 (EU GDPR). The respective research group has to sign a data use agreement to follow  
176 these rules. This statement is in line with our institute's policies and requirements by our  
177 funding bodies.

178

#### 179 **Behavioral paradigm**

180 Participants had both to report the perception (yes/no) of electrical pulses applied to their  
181 left index finger and rate their confidence about their decision. Single square-wave pulses  
182 (0.2 ms) were generated with a constant current stimulator (DS5; Digitimer, United  
183 Kingdom) at individually assessed intensities near (mean intensity = 1.85 mA, range: 1.01-

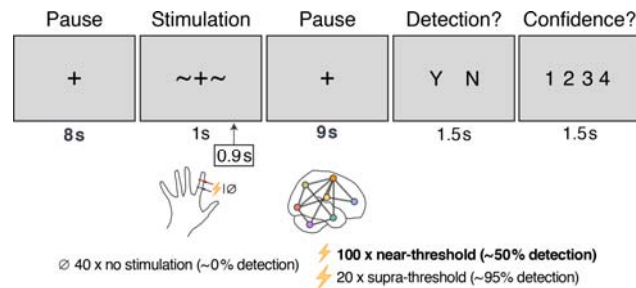


184 3.48 mA) and supra (mean intensity = 2.18 mA, range: 1.19-3.89 mA) perceptual threshold  
185 reflecting 50% and 100% detection rate. Additionally, 25% of all trials were catch trials  
186 without stimulation.

187 Each trial (21 s) started with a fixation cross (1 s), followed by a cue (1 s) indicating  
188 an electrical pulse was soon to follow (Figure 1). The stimulation onset was always 100 ms  
189 before cue offset in order to temporally align the stimulation with the detection decisions.  
190 For aware trials participants' detection decisions presumably occur the instant the  
191 stimulation is noticed. However, for unaware trials they can only conclude there was no  
192 stimulus at cue offset. If the stimulus onsets had been pseudo-randomized across the cue  
193 window, the yes-decision would have occurred on average half of the cue window earlier  
194 than the no-decision. The actual reporting of the decision was delayed by 9 s to allow a  
195 movement-free time window for analyses. Participants had 1.5 s to report if they felt the  
196 stimulus or not by pressing the corresponding button for yes or no. Subsequently they had  
197 another 1.5 s to report their confidence about the yes/no-decision on a scale from 1 (very  
198 unconfident) to 4 (very confident). Any remaining time in the confidence rating window,  
199 following the rating, was added to a 7 s fixation cross creating an inter-trial interval of at  
200 least 7 s. Participants were instructed to place their right four fingers on a four-button box.  
201 The second and third buttons were controlled by the right middle finger and the ring finger  
202 to report the decision for yes or no. The outer buttons were controlled by the index finger  
203 and the little finger additionally to report the confidence decision on the full four-point  
204 scale. All button-response mappings were counterbalanced across participants. Hence  
205 depending on the mapping, the middle finger or the ring finger indicated "yes", and the  
206 four-point confidence scale started with "very confident" or "very unconfident" at the index  
207 finger.

208 Each block had in total 40 trials and lasted 14 min: 10 trials without stimulation, 25 with  
209 near-threshold intensity, and 5 with supra-threshold intensity, delivered in pseudo-

210 randomized order. Before each block, individual thresholds were assessed with an up-and-  
211 down method followed by the psi method from the Palamedes Toolbox (Kingdom and  
212 Prins, 2009). The threshold procedure followed that of the actual experimental trials but  
213 excluded the long pause and confidence response. Participants performed 4 blocks  
214 sequentially (circa 80 min). The experimental procedure was controlled by custom  
215 MATLAB scripts (The MathWorks Inc., Natick, Massachusetts) using Psychophysics  
216 Toolbox (Kleiner et al., 2007).



217

218 **Figure 1.** Experimental paradigm visualized across one trial (21 s). The tiles represent the  
219 participant's visual display and the times given below indicate the presentation duration. In  
220 total, each participant completed 160 trials across 4 blocks, including 100 near-threshold  
221 trials. Electrical nerve stimulation was applied to the left index finger 0.9 s after cue onset  
222 (~+~) to temporally align yes/no-decisions, which presumably had to be made at cue  
223 offset. Participants only reported their target detection decision (yes/no) following a long  
224 pause of 9 s in order to model the brain's post-stimulus functional network without a button  
225 press-related signal. The detection decision was followed by a confidence rating on a  
226 scale from 1 (very unconfident) to 4 (very confident). Every 0.75 s, a full MRI brain volume  
227 (BOLD) was acquired with a 3-mm isotropic resolution.

228

## 229 **fMRI data acquisition**

230 While participants performed the task, we acquired whole-brain BOLD contrast images  
231 with a 32-channel head coil on a Siemens MAGNETOM Prisma 3 Tesla scanner. For sub-  
232 second, whole-brain images, we used a Multi-Band (MB) echo-planar imaging (EPI)

233 sequence (Moeller et al., 2010; Setsompop et al., 2012) with an MB acceleration factor of  
234 3 (TR = 750 ms, TE = 25 ms, flip angle = 55°, receiver bandwidth = 1815 Hz/px, partial  
235 Fourier = 7/8). No GRAPPA acceleration was applied (iPAT factor = 1). In each of the 4  
236 blocks we acquired 1120 brain volumes (14 min), each consisting of 36 axial slices with a  
237 field of view of 192 x 192 mm<sup>2</sup> (64 x 64 voxel) and a 0.5-mm gap resulting in 3-mm  
238 isotropic voxels.

239 For magnetic distortion correction of the EPI scans, B0 images were obtained from  
240 double-echo GRE images (TR = 750 ms, TE<sub>1</sub> = 4.92 ms, ΔTE = 2.46 ms, echo spacing =  
241 0.66 ms, flip angle = 45°), with the same voxel geometry as used for the EPI scans. The  
242 receiver bandwidth was 822 Hz/pixel.

243 For normalizing the EPI scans and extracting nuisance regressors of core white  
244 matter voxels and ventricles, we used previously acquired T1-sensitive brain images of the  
245 participants with a 32-channel head coil or for two participants with a 20-channel  
246 head/neck coil on 3-Tesla Siemens MAGNETOM Prisma, Skyra, TrioTim or Verio scanner.  
247 The MPRAGE sequence covered the whole brain (176 x 240 x 256 mm<sup>3</sup>) with an isotropic  
248 voxel resolution of 1 mm and slightly varied regarding the echo time and the receiver  
249 bandwidth across participants (TR = 2.3 s, TE = [2.01 (2), 2.96 (9), 2.98 (19), 4.21 (5)] ms,  
250 inversion time TI = 900 ms, flip angle = 9°, bandwidth = [238 (10), 240 (16), 241 (9)]  
251 Hz/px). For two participants, the sequence parameters were more different (TR = 1.3 s, TE  
252 = 3.5 ms, inversion time = 650 ms, flip angle = 8°/10°, bandwidth = 190 Hz/px).

253

## 254 **Behavioral data analysis**

255 The behavioral data was analyzed with R 3.6.0 in RStudio 1.2.1335. Data by four  
256 participants was incomplete due to technical issues and failed data acquisition. The blocks  
257 of the remaining 34 participants were evaluated for successful near-threshold  
258 assessments if at least 4 null and 17 near-threshold trials with a yes/no and confidence

259 response were recorded. This meant that only blocks with a hit rate at least 5 percentage  
260 points larger than the false alarm rate and participants with an average hit rate of 20-80%  
261 were further processed. This resulted in 31 participants with on average 89 near-threshold  
262 trials (range: 66-100). The distribution of mean detection rates is visualized in Figure 2a.  
263 For the confidence ratings, we calculated conditional probabilities for each confidence  
264 rating given a stimulus-response condition: correct rejection, near-threshold miss, near-  
265 threshold hit, and supra-threshold hit (Figure 2b). The conditional probabilities were  
266 compared with paired *t*-tests between neighboring conditions (correct rejection vs. near-  
267 miss, near-miss vs. near-hit, near-hit vs. supra-hit). The twelve *p*-values were FDR-  
268 corrected with a false discovery rate of 5% (Benjamini and Hochberg, 1995) and visualized  
269 with the means in Figure 2b.

270

## 271 **fMRI preprocessing**

272 Each EPI block was preprocessed with custom bash scripts using AFNI 18.2.17, FSL  
273 5.0.11, and FreeSurfer 6.0.0 (Cox, 1996; Fischl, 2012; Smith et al., 2004). The code is  
274 available on <http://github.com/grundm/graphCA>. After removing the initial 10 volumes, the  
275 time series were despiked and corrected for slice timing. Subsequently, the volumes were  
276 corrected for motion and distortion using field maps acquired at the beginning of the  
277 experiment. We applied a non-linear normalization to MNI space (AFNI 3dQwarp). Next to  
278 the realignment to correct for motion, we calculated the euclidean norm (enorm) to censor  
279 volumes with large motion for the functional connectivity and BOLD contrast analyses.  
280 Volumes were ignored when they exceeded motion > 0.3 mm (enorm = sqrt(sum squares)  
281 of motion parameters; AFNI 1d\_tool.py -censor\_motion). Compared to the framewise  
282 displacement (FD = sum(abs) of motion parameters; Power et al., 2012), the euclidean  
283 norm has the advantage to represent appropriately large motion, e.g., the six parameters  
284 “6 0 0 0 0 0” and “1 1 1 1 1 1” would be the same for FD (FD = 6) in contrast to a enorm of

285 6 and 2.45, respectively. Modeling the functional connectivity and the BOLD contrasts was  
286 done with AFNI 19.1.05.

287

### 288 **fMRI whole-brain contrast analysis**

289 For the BOLD contrast analysis, the data was additionally smoothed with a 7-mm FWHM  
290 kernel and scaled to a mean of 100 and maximum of 200. In the final step, we calculated a  
291 nuisance regression to control for (a) motion with Friston's 24-parameter model (Friston et  
292 al., 1996), (b) signal outliers and their derivatives, (c) each 3 first principal components of  
293 core voxels in ventricle and white matter masks separately, and (d) a constant and trends  
294 up to polynomial of degree six (~high-pass filter > 0.0046 Hz) separately for each block.

295 We calculated an individual general linear model (GLM) for each participant with  
296 AFNI 3dREMLfit that combined all blocks and modeled the BOLD response as a gamma  
297 function for the following conditions: correct rejections, near-threshold misses, and near-  
298 threshold hits. A second model included confident correct rejections, confident misses, and  
299 confident hits (pooled confidence ratings of 3 and 4). Furthermore, two BOLD response  
300 regressors for the button presses of the yes/no-decision and the confidence rating were  
301 included. The regressors of the nuisance regression served as baseline regressors (AFNI  
302 3dDeconvolve -ortvec).

303 The estimated regression coefficients for the aware and unaware condition were  
304 tested against each other with a mixed-effects meta-analysis (3dMEMA; Chen et al.,  
305 2012). This approach accounts for within-participant variability by using the corresponding  
306  $t$ -statistics of the regression coefficients from each participant. Additionally, the detection  
307 rate was used as a covariate to account for the interindividual variance. The resulting  
308 volumes with  $t$ -values were corrected for multiple comparisons by thresholding voxels at  
309  $p_{\text{voxel}} < 0.0005$  and the resulting clusters at  $k$  voxels ( $p_{\text{cluster}} = 0.05$ ). The cluster size  
310 threshold  $k$  was derived for each contrast separately based on 10,000 simulations without

311 a built-in math model for the spatial autocorrelation function as recommended by AFNI (for  
312 details see 3dttest++ with Clustsim option and Cox et al. (2017) as response to Eklund et  
313 al. (2016)). The rendered brain images were created with MRICron (Rorden and Brett,  
314 2000).

315

### 316 **fMRI contrast analysis in primary somatosensory cortex**

317 Furthermore, we wanted to evaluate the BOLD signal for the near-threshold stimulation in  
318 the primary somatosensory cortex. Unlike the fMRI contrast analysis for the whole brain  
319 described above, the BOLD data was not smoothed, scaled or part of a nuisance  
320 regression. We modeled the BOLD response for all near-threshold trials and trials without  
321 stimulation (independent of the yes/no-responses). The GLMs also included one regressor  
322 for each button press. The baseline regressors were limited to (a) Friston's 24-parameter  
323 model, (b) signal outliers and their derivatives, and (c) a constant and a linear trend  
324 separately for each block (polynomial of degree one). The estimated regression  
325 coefficients for the trials with and without near-threshold stimulation were compared with a  
326 mixed-effects meta-analysis (3dMEMA; Chen et al., 2012) that included the detection rate  
327 as a covariate. Additionally to reporting the contrast "stimulus present > absent" for the  
328 whole-brain, this analysis was limited to the right primary somatosensory cortex (Area 3b  
329 and Area 1) as defined by a multi-modal parcellation based brain atlas (Glasser et al.,  
330 2016).

331

### 332 **Functional connectivity analysis**

333 For estimating the context-dependent functional connectivity between regions of interest  
334 (ROI), we used the generalized psychophysiological interaction (gPPI; McLaren et al.,  
335 2012) without the deconvolution step, as implemented in FSL (O'Reilly et al., 2012). The  
336 deconvolution algorithm tries to estimate the underlying neural activity to match it

337 temporally with the psychological context (Cisler et al., 2014; Gitelman et al., 2003;  
338 McLaren et al., 2012). However, it cannot be determined if this estimate is correct (Cole et  
339 al., 2013; O'Reilly et al., 2012). Furthermore, also Godwin et al. (2015) repeated their  
340 analysis without the deconvolution step. Hence, we followed the FSL implementation and  
341 convolved the psychological variable with a fixed-shaped HRF to temporally align it with  
342 the measured BOLD signal (O'Reilly et al., 2012). The gPPI model included (a) regressors  
343 for the BOLD response function for each condition, (b) a regressor for the baseline  
344 functional connectivity of a seed region of interest (ROI), and (c) regressors for the  
345 context-dependent functional connectivity of the ROI for each condition  
346 (psychophysiological interaction). For (b), the seed ROI average time series was extracted  
347 to be used as a regressor. For (c), this baseline regressor was masked for each condition  
348 separately to generate conditional interaction regressors. The mask for each condition was  
349 equivalent to the regressor that modeled the BOLD response for the corresponding  
350 condition, hence weighting the seed time series in the post-stimulus phase with the  
351 hemodynamic response. The interaction regressors for each condition allowed the  
352 estimation of (c) the context-dependent functional connectivity by accounting for (a) the  
353 BOLD response and (b) the baseline functional connectivity (Figure 5b). Additionally, the  
354 gPPI included baseline regressors: (a) Friston's 24-parameter model for motion, (b) signal  
355 outliers and their derivatives, and (c) a constant and a linear trend separately for each  
356 block (polynomial of degree one).

357         The gPPI was calculated with AFNI 3dREMLfit for a whole-brain network of 264  
358 nodes based on a resting-state functional connectivity atlas (Power et al., 2011). The  
359 nodes were defined as 4-mm radius, spherical ROIs at the atlas' MNI coordinates. The  
360 BOLD response model was a gamma function. AFNI 3dREMLfit has the advantage of  
361 allowing for serial correlations by estimating the temporal autocorrelation structure for each  
362 voxel separately.



363 For each node's gPPI, the coefficients of the context-dependent functional connectivity  
364 regressors were extracted from all other nodes separately by averaging across all voxels  
365 constituting the particular node. Subsequently, the beta values were combined in a  
366 symmetric connectivity matrix for each participant and each condition. As Godwin et al.  
367 (2015), we did not assume directionality and averaged the absolute values of reciprocal  
368 connections. Subsequently, the connectivity matrices were thresholded proportionally for  
369 the strongest connections and rescaled to the range [0,1] by dividing all values by the  
370 maximum value. The figures showing nodes and edges on a glass brain (Figure 5a,e)  
371 were created with BrainNet Viewer 1.6 (Xia et al., 2013).

372 After running the functional connectivity analysis as Godwin et al. (2015) for only  
373 confident trials, we repeated the analysis for all trials independent of their confidence  
374 response. Furthermore, we extended the preprocessing to include 7-mm smoothing,  
375 scaling and a nuisance regression and redid the analysis for both trial selections (confident  
376 only and all). For this analysis, the baseline regressors were (a) Friston's 24-parameter  
377 model, (b) signal outliers and their derivatives, (c) each three first principal components of  
378 core voxels in ventricle and white matter masks separately, and (d) separately for each  
379 block a constant and trends up to polynomial of degree six (~high-pass filter > 0.0046 Hz).

380

### 381 **Graph-theoretical analysis**

382 The context-dependent connectivity matrices were further processed with the Brain  
383 Connectivity Toolbox (BCT Version 2017-15-01; Rubinov and Sporns, 2010) to describe  
384 their network topologies. Across proportional thresholds (5-40%) graph metrics were  
385 calculated and normalized with the average graph metrics of 100 random networks with  
386 the same degree distribution (see BCT function `randmio_und.m` on  
387 <https://sites.google.com/site/bctnet/Home/functions>). In order to compare our results with  
388 the report for visual awareness (Godwin et al., 2015), we chose the same metrics for (a)

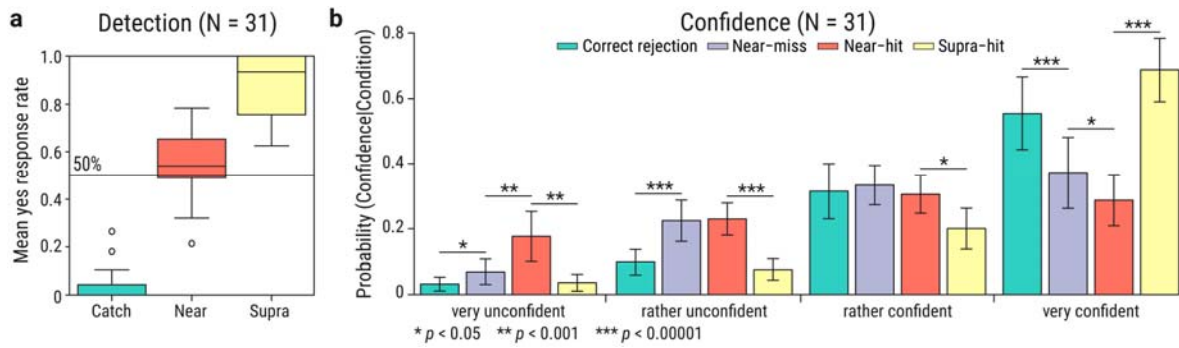


389 segregation, (b) integration, and (c) centrality: (a) weighted undirected modularity (BCT  
390 function `modularity_und.m`; Newman, 2004) and weighted undirected clustering coefficient  
391 averaged over all nodes (BCT function `clustering_coef_wu.m`; Onnela et al., 2005), (b)  
392 weighted characteristic path length (BCT function `charpath.m`), and (c) weighted  
393 participation coefficient averaged over all nodes (BCT function `participation_coef.m`;  
394 Guimerà and Nunes Amaral, 2005). The participants' graph metrics were compared  
395 between each condition with the Wilcoxon's signed-rank test because the distributions of  
396 the graph metrics are unknown. The resulting 24  $p$ -values for each graph metric (8  
397 network threshold times 3 comparisons: hit vs. miss, hit vs. correct rejection, and miss vs.  
398 correct rejection) were FDR-corrected with a false discovery rate of 5% (Benjamini and  
399 Hochberg, 1995). Furthermore, we calculated the Bayes factors based on  $t$ -tests with a  
400 JZS prior ( $r = \sqrt{2}/2$ ) to assess the evidence for the null hypothesis (Rouder et al., 2012).

## 401 **Results**

### 402 **Behavioral data**

403 Participants ( $N = 31$ ) detected on average 55% of the near-threshold pulses ( $SD = 13\%$ ),  
404 88% of the supra-threshold pulses ( $SD = 12\%$ ), and correctly rejected 97% of the catch  
405 trials without stimulation ( $SD = 6.0\%$ ; Figure 2a). Participants reported on average to be  
406 “rather confident” or “very confident” for 87% of the correct rejections ( $SD = 13\%$ ), 70% of  
407 the near-threshold misses ( $SD = 23\%$ ), 59% of the near-threshold hits ( $SD = 27\%$ ) and  
408 89% of the supra-threshold hits ( $SD = 13\%$ ). Participants reported significantly more often  
409 “very confident” for near-threshold misses ( $M = 37.2\%$ ) than hits ( $M = 28.7\%$ , FDR-  
410 corrected  $p = 0.037$ ) and less often “very unconfident” for misses ( $M = 6.9\%$ ) than hits ( $M$   
411  $= 17.7\%$ , FDR-corrected  $p = 0.023$ ; Figure 2b). The conditional probabilities for “rather  
412 unconfident” and “rather confident” did not differ between near-threshold hits and misses.  
413 Near-threshold misses and correct rejections differed in their conditional probabilities for  
414 “very unconfident”, “rather unconfident” and “very confident” (Figure 2b) indicating higher  
415 confidence for correct rejections. Also, participants were on average more confident for  
416 supra-threshold hits than near-threshold hits. Additionally, we assessed the stability of  
417 near-threshold detection and false alarms across the experiment. We used linear mixed-  
418 effects models with maximum likelihood estimation (lmer function in R) to investigate the  
419 effect of block on near-threshold hit rate (near\_yes) and false alarm rate (null\_yes). Model  
420 comparison of the model “near\_yes ~ block + (1|ID)” with the null model “near\_yes ~ 1 +  
421 (1|ID)” resulted in no significant difference ( $\chi^2 = 1.40$ ,  $p = 0.24$ ), indicating no effect of  
422 block on near-threshold hit rate. Also, for false alarms, the linear mixed-effects model  
423 “null\_yes ~ block + (1|ID)” was not significantly different compared to the null model  
424 “null\_yes ~ 1 + (1|ID)” ( $\chi^2 = 1.41$ ,  $p = 0.23$ ). Therefore, we conclude that the behavioral  
425 performance is not affected by acclimatization or mental fatigue.



426

427

**Figure 2.** Mean detection rate and decision confidence across participants. **(a)** Detection rates for each trial

428

condition: without stimulation (catch trials) and with near- and supra-threshold stimulation. The central line

429

indicates the median in each box. The whiskers indicate 1.5 times the interquartile range or the maximum

430

value if smaller. Circles indicate values beyond this whisker range. **(b)** Mean conditional probabilities for

431

each confidence rating given a stimulus-response condition: correct rejection (green), near-threshold misses

432

(purple), near-threshold hits (red), and supra-threshold hits (yellow). Error bars indicate within-participants

433

95% confidence intervals (Morey, 2008). Horizontal lines indicate significant paired  $t$ -tests with FDR-

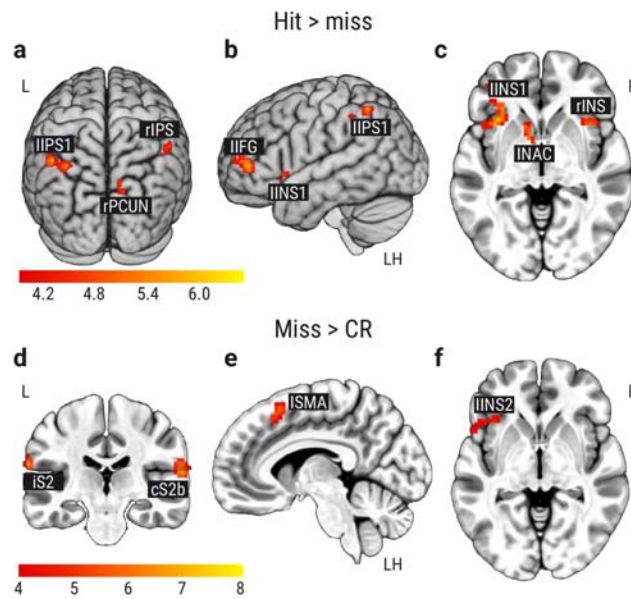
434

corrected  $p$ -values between neighboring conditions (Benjamini and Hochberg, 1995).

## 435 **BOLD amplitude contrasts**

436 First, we modeled the BOLD contrast between hits and misses (Figure 3a-c), as well as  
437 misses and correct rejections independent of the confidence rating (Figure 3d-f). Second,  
438 we compared only confident hits and misses (Figure 4a-c), as well as confident misses  
439 and correct rejections (Figure 4d-f). Third, we modeled the contrast between near-  
440 threshold stimuli and trials without stimulation for the whole brain (Figure 5) and the  
441 primary somatosensory cortex only (Figure 6). The preprocessing for this contrast  
442 excluded smoothing, scaling or nuisance regression. For all group-level comparisons, we  
443 used the detection rate as a covariate to account for the interindividual variance (Figure  
444 2a).

445 Contrasting near-threshold hits and misses (stimulus awareness) showed a fronto-  
446 parietal network including the left inferior frontal gyrus (IIFG), the left nucleus accumbens  
447 (INAC), the left and right anterior insula (lINS1; rINS), the left and right intraparietal sulcus  
448 (lIPS1; lIPS2; rIPS) and the right precuneus (rPCUN; Figure 3a-c, Table 1). When the  
449 statistical threshold for the family-wise error was set to  $p_{\text{cluster}} \leq 0.06$ , resulting in a  
450 decreased cluster size  $k \geq 28$ , two additional clusters were observed for hits compared to  
451 misses in the contralateral secondary somatosensory cortex (cS2) and the left precuneus  
452 (lPCUN). When comparing missed near-threshold trials with correctly rejected null trials  
453 (somatosensory processing of undetected stimuli), the contra- and ipsilateral S2 (cS2b;  
454 iS2), the left anterior insula (lINS2) and the left supplementary motor area (lSMA) showed  
455 statistically significant activations (Figure 3d-f).



456

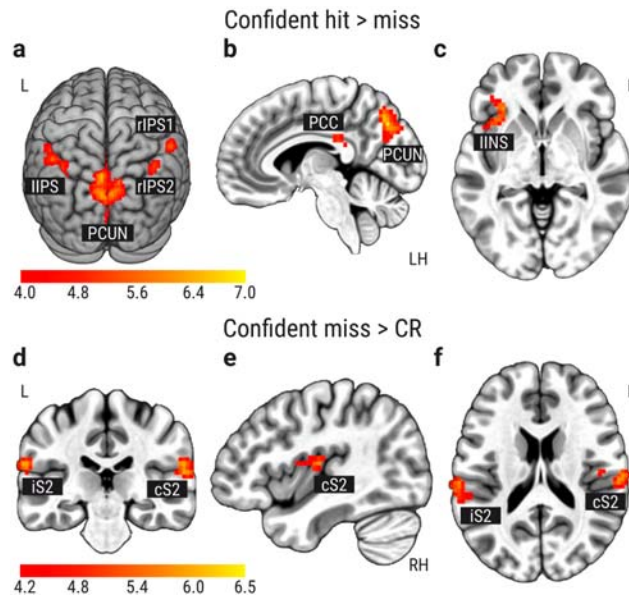
457 **Figure 3.** BOLD amplitude contrasts for awareness and stimulation effect. (a-c) Contrast between near-  
458 threshold hits and misses with focus on (a) the right precuneus (rPCUN) and the left and right intraparietal  
459 sulcus (IIPS1, rIPS1), (b) the left inferior frontal gyrus (IIFG) and (c) the left nucleus accumbens (INAC) and  
460 the left and right anterior insula (IINS1, rINS;  $z = -3$ ). Correction for multiple comparison with  $t_{\text{voxel}}(30) \geq 3.92$ ,  
461  $p_{\text{voxel}} \leq 0.0005$  and cluster size  $k \geq 31$  ( $p_{\text{cluster}} \leq 0.05$ ). (d-f) Contrast between near-threshold misses and  
462 correct rejections (CR) of trials without stimulation. (d) Coronal view ( $y = -29$ ) with the contralateral and  
463 ipsilateral secondary somatosensory cortices (cS2, iS2). (e) Sagittal view ( $x = -7$ ) on the supplementary  
464 motor area (SMA). (f) Axial view ( $z = -3$ ) on the left anterior insula (INS). Correction for multiple comparison  
465 with  $t_{\text{voxel}}(30) \geq 3.92$ ,  $p_{\text{voxel}} \leq 0.0005$  and cluster size  $k \geq 27$  ( $p_{\text{cluster}} \leq 0.05$ ). Left (L), right (R), and the left  
466 hemisphere (LH) are indicated.

467 **Table 1.** MNI coordinates for significant BOLD contrast clusters “hit > miss” and “miss > correct rejection  
 468 (CR)” in Figure 3. Correction for multiple comparisons with  $t_{\text{voxel}}(30) \geq 3.92$ ,  $p_{\text{voxel}} \leq 0.0005$  and  $p_{\text{cluster}} \leq 0.05$ ,  
 469 resulting in a cluster size  $k \geq 31$  for “hit > miss” and a cluster size  $k \geq 27$  for “miss > CR”. Clusters are  
 470 ordered by volume (number of voxels). MNI coordinates of the maximum  $t$  value (peak) are reported in  
 471 millimeters (mm) on the left-right (LR), posterior-anterior (PA) and inferior-superior (IS) axes. The mean  $t$   
 472 value is the average across all voxels of one cluster.

Contrast	Area	Label	Volume	LR	PA	IS	Mean
Hit > miss	Left anterior insula	lINS1	84	-35	19	-3	4.56
$p_{\text{cluster}} \leq 0.05 \mid k \geq 31$ $N = 31$	Left intraparietal sulcus	lIPS1	74	-32	-62	50	4.50
	Right precuneus	rPCUN	64	13	-71	39	4.50
	Left nucleus accumbens	lNAC	62	-14	10	-10	4.47
	Left inferior frontal gyrus	lIFG	57	-44	46	4	4.54
	Right anterior insula	rINS	54	40	19	-7	4.56
	Right intraparietal sulcus	rIPS	42	52	-35	46	4.56
	Left intraparietal sulcus	lIPS2	37	-50	-41	46	4.21
	$p_{\text{cluster}} \leq 0.06 \mid k \geq 28$	Right/contralateral S2	cS2a	30	58	-20	22
Left precuneus		lPCUN	29	-11	-71	39	4.48
Miss > CR	Right/contralateral S2	cS2b	101	64	-20	14	4.78
$p_{\text{cluster}} \leq 0.05 \mid k \geq 27$ $N = 31$	Left anterior insula	lINS2	75	-56	10	0	4.32
	Left/ipsilateral S2	iS2	52	-68	-26	22	4.73
	Left supplementary motor area	lSMA	32	-8	16	57	4.73

473  
 474

475 Second, we contrasted only confident hits, misses, and correct rejections. Trials were  
476 classified as confident when rated with 3 or 4 (“rather confident” or “very confident”). Since  
477 the first trial of each block was not considered for the fMRI analysis, the participants ( $N =$   
478 31) had on average 28 confident hits ( $SD = 14$ ), 28 confident misses ( $SD = 15$ ), and 29  
479 confident correct rejections ( $SD = 7$ ). For confident hits and misses, the precuneus  
480 bilaterally (PCUN), the left and the right intraparietal sulcus (lIPS, rIPS1, rIPS2), the  
481 posterior cingulate cortex (PCC) and the left anterior insula (lINS) had significant activation  
482 clusters with conscious tactile perception (Figure 4a-c). The contralateral secondary  
483 somatosensory cortex (cS2) showed activation again with the statistical threshold  $p_{\text{cluster}} \leq$   
484 0.06 (Table 2). Confident misses showed a higher activation than confident correct  
485 rejections in the ipsilateral and contralateral secondary somatosensory cortices (iS2, cS2).  
486 The cS2 cluster was reaching into the posterior insular cortex (Figure 4d-f).



487

488 **Figure 4.** BOLD amplitude contrasts for only confident trials. Correction for multiple comparison with  $t_{\text{voxel}}(30)$   
489  $\geq 3.92$ ,  $p_{\text{voxel}} \leq 0.0005$  and cluster size  $k \geq 28$  ( $p_{\text{cluster}} \leq 0.05$ ). (a-c) Contrast between confident near-threshold  
490 hits and misses with focus on (a) the precuneus (PCUN) and the intraparietal sulcus (IPS), (b) the posterior  
491 cingulate cortex (PCC;  $x = -7$ ), and (c) the left anterior insula (IIINS;  $z = -3$ ). (d-f) Contrast between near-  
492 threshold misses and correct rejections (CR) of trials without stimulation. (d) Coronal view ( $y = -26$ ) with the  
493 contralateral and ipsilateral secondary somatosensory cortices (cS2; iS2). (e) Sagittal view ( $x = 41$ ) on the  
494 cS2 cluster reaching into insular cortex. (f) Axial view on cS2 and iS2 ( $z = 18$ ). Left (L), right (R), the left  
495 hemisphere (LH), and the right hemisphere (RH) are indicated.

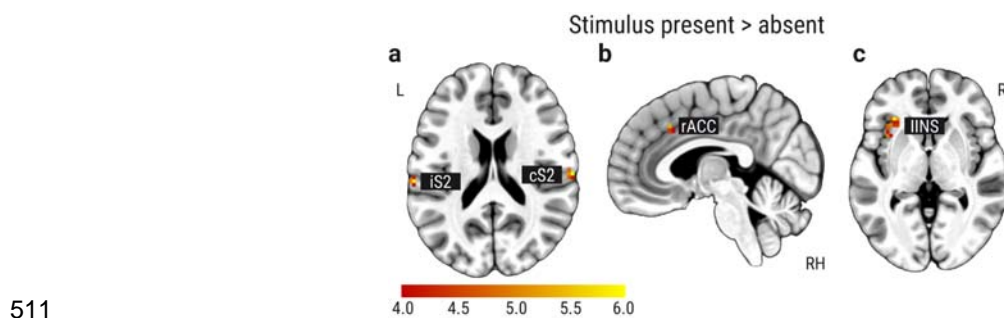


496 **Table 2.** MNI coordinates for significant BOLD contrast clusters “confident hit > miss” and “confident miss >  
 497 correct rejection (CR)” in Figure 4. Correction for multiple comparisons with  $t_{\text{voxel}}(30) \geq 3.92$ ,  $p_{\text{voxel}} \leq 0.0005$   
 498 and  $p_{\text{cluster}} \leq 0.05$ , resulting in a cluster size  $k \geq 28$ . Clusters are ordered by volume (number of voxels). MNI  
 499 coordinates of the maximum  $t$  value (peak) are reported in millimeters (mm) on the left-right (LR), posterior-  
 500 anterior (PA) and inferior-superior (IS) axes. The mean  $t$  value is the average across all voxels of one  
 501 cluster.

Contrast	Area	Label	Volume	LR	PA	IS	Mean
Confident hit > miss	Left/right precuneus	PCUN	387	-8	-74	39	4.66
$p_{\text{cluster}} \leq 0.05 \mid k \geq 28$	Left intraparietal sulcus	lIPS	137	-47	-53	50	4.43
$N = 31$	Left anterior insula	lINS	57	-32	28	-3	4.68
	Right intraparietal sulcus	rIPS1	42	55	-38	50	4.46
	Posterior cingulate cortex	PCC	39	4	-35	22	4.45
	Right intraparietal sulcus	rIPS2	34	40	-62	53	4.33
$p_{\text{cluster}} \leq 0.06 \mid k \geq 26$	Right/contralateral S2	cS2	26	61	-20	22	4.36
Confident miss > CR	Right/contralateral S2	cS2	141	64	-20	14	4.56
$p_{\text{cluster}} \leq 0.05 \mid k \geq 28$	Left/ipsilateral S2	iS2	85	-65	-26	22	4.60

502

503 Third, we contrasted all near-threshold and catch trials independent of their behavioral  
504 response to investigate the stimulation effect in the whole brain. In contrast to the BOLD  
505 contrast analysis above, the preprocessing excluded smoothing, scaling or nuisance  
506 regression to align it with the preprocessing of the functional connectivity analysis. For the  
507 near-threshold stimulation compared to no stimulation, the ipsilateral and contralateral  
508 secondary somatosensory (iS2, cS2), the left anterior insula (lINS) and the right anterior  
509 cingulate cortex (rACC) showed significant clusters with a larger activation (Figure 5, Table  
510 3).



511

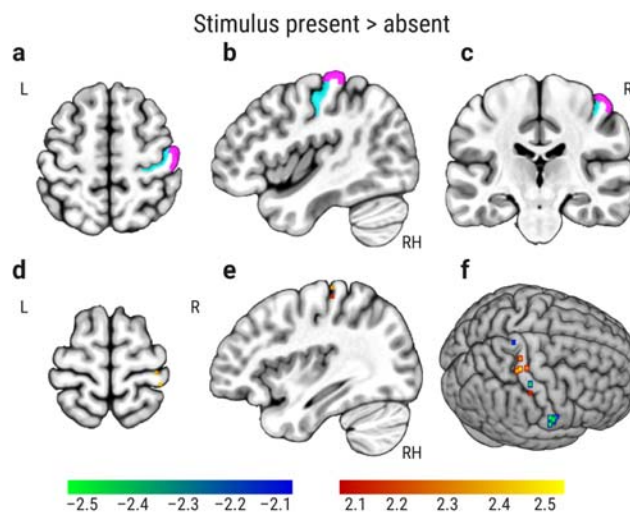
512 **Figure 5.** BOLD amplitude contrast for near-threshold stimulation. Correction for multiple comparison with  
513  $t_{\text{voxel}}(30) \geq 3.92$ ,  $p_{\text{voxel}} \leq 0.0005$  and cluster size  $k \geq 5$  ( $p_{\text{cluster}} \leq 0.05$ ). (a-c) Contrast between near-threshold  
514 stimulation trials and trials without stimulation with significant clusters in (a) the ipsilateral and contralateral  
515 secondary somatosensory cortex (iS2, cS2;  $z = 19$ ), (b) the right anterior cingulate cortex (rACC;  $x = 4$ ), and  
516 (c) the left anterior insula (lINS;  $z = 0$ ). Left (L), right (R), and the right hemisphere (RH) are indicated.

517 **Table 3.** MNI coordinates for significant BOLD contrast clusters “near-threshold stimulation > trials without  
518 stimulation (catch trials)” in Figure 5. Correction for multiple comparisons with  $t_{\text{voxel}}(30) \geq 3.92$ ,  $p_{\text{voxel}} \leq 0.0005$   
519 and  $p_{\text{cluster}} \leq 0.05$ , resulting in a cluster size  $k \geq 5$ . Clusters are ordered by volume (number of voxels). MNI  
520 coordinates of the maximum  $t$  value (peak) are reported in millimeters (mm) on the left-right (LR), posterior-  
521 anterior (PA) and inferior-superior (IS) axes. The mean  $t$  value is the average across all voxels of one  
522 cluster.

Contrast	Area	Label	Volume	LR	PA	IS	Mean
Near > catch trials	Left anterior insula	lINS	35	-35	13	4	4.64
$p_{\text{cluster}} \leq 0.05 \mid k \geq 5$	Right anterior cingulate cortex	rACC	15	4	22	39	4.37
$N = 31$	Right/contralateral S2	cS2	13	64	-20	18	5.07
	Left/ipsilateral S2	iS2	6	-65	-26	18	4.62

523

524 Fourth, we contrasted all near-threshold and catch trials independent of their behavioral  
525 response only within the right primary somatosensory cortex (Area 3b and Area 1). The  
526 region of interest was defined by a multi-modal brain atlas (Glasser et al., 2016).  
527 Furthermore, the preprocessing did not include smoothing, scaling, or nuisance  
528 regression. We found positive and negative significant voxels for uncorrected  $p_{\text{voxel}} \leq 0.05$   
529 in Area 3b and Area 1. A positive voxel in the latter ( $x = 38, y = -38, z = 67$ ; Figure 6) was  
530 close to previously reported peak coordinates in Area 1 ( $x = 38, y = -40, z = 66$ ) for  
531 electrical stimulation of the median nerve (Schröder et al., 2019). Yet, these voxels did not  
532 meet the criteria by a correction for multiple comparisons (FDR-corrected  $p \leq 0.05$  or a  
533 cluster size  $k \geq 12$  for  $p_{\text{cluster}} \leq 0.05$ ; Table 4). Additionally, a contrast of supra-threshold  
534 hits and correct rejections corrected for multiple comparisons in the whole brain ( $p_{\text{voxel}} <$   
535  $0.0005$  and cluster size  $k \geq 5, p_{\text{cluster}} \leq 0.05$ ) revealed a cluster in the contralateral primary  
536 somatosensory cortex ( $k = 6$  voxels, mean  $t = 4.27$ ) whose peak coordinates ( $x = 52, y = -$   
537  $32, z = 53$ ) were in Area 1 according to the Eickhoff-Zilles atlas (Eickhoff et al., 2005).



538  
539 **Figure 6.** BOLD amplitude contrast for near-threshold stimulation in the primary somatosensory cortex (Area  
540 3b and Area 1). (a-c) Region of interest Area 3b (cyan) and Area 1 (violet,  $z = 56, x = 43, y = -22$ ). (d-f) Only  
541 voxels with  $t_{\text{voxel}}(30) \leq -2.045$  and  $t_{\text{voxel}}(30) \geq 2.045, p_{\text{voxel}} \leq 0.05$  ( $z = 68, x = 36$ ). Left (L), right (R), and the  
542 right hemisphere (RH) are indicated.

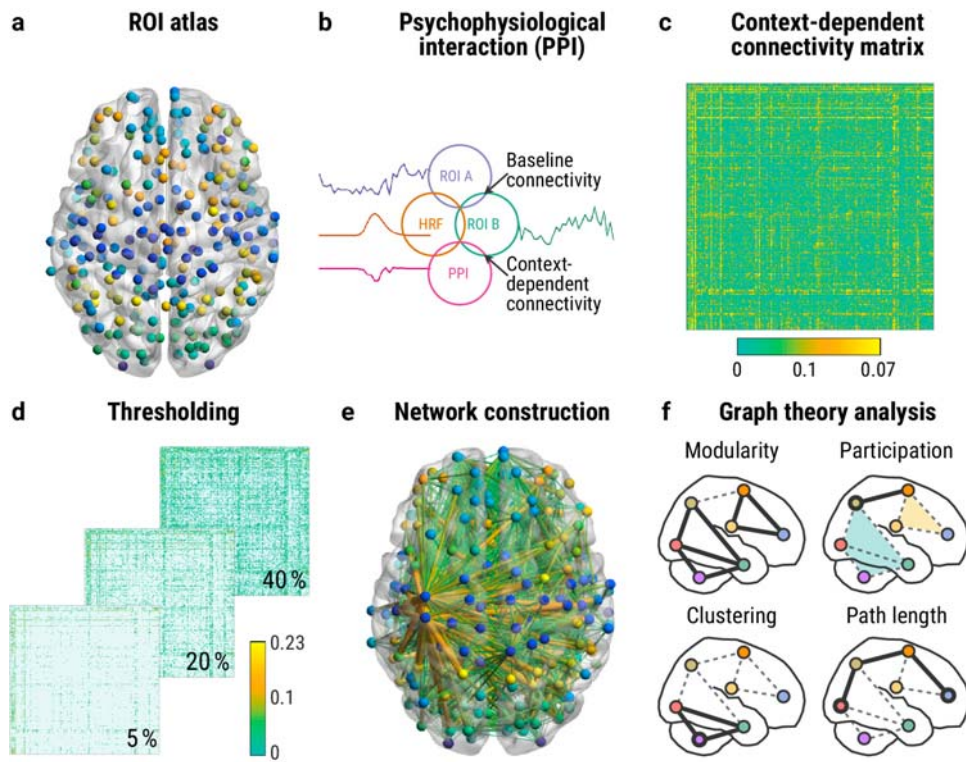
543 **Table 4.** MNI coordinates for BOLD contrast clusters in the primary somatosensory cortex (Area 3b and Area  
544 1) for “near-threshold stimulation > trials without stimulation (catch trials)” in Figure 6. Voxel threshold  
545  $t_{\text{voxel}}(30) \geq 2.045$  and  $t_{\text{voxel}}(30) \leq -2.045$ ,  $p_{\text{voxel}} \leq 0.05$  and cluster size  $k \geq 2$ . Clusters are ordered by displaying  
546 first the positive cluster and then the negative cluster. MNI coordinates of the maximum  $t$  value (peak) are  
547 reported in millimeters (mm) on the left-right (LR), posterior-anterior (PA) and inferior-superior (IS) axes. The  
548 mean  $t$  value is the average across all voxels of one cluster.

Contrast	Area	Label	Volume	LR	PA	IS	Mean
Near > catch trials	Right/contralateral Area 3b	A3b	2	31	-29	60	2.25
Near < catch trials	Right/contralateral Area 1	A1	7	67	-8	22	-2.63

549

## 550 **Context-Dependent Graph Measures**

551 We assessed whether tactile conscious perception is accompanied by alterations of the  
552 brain's functional network topology. An atlas of 264 nodes (Power et al., 2011) was used  
553 to capture the whole-brain network as in (Godwin et al., 2015), who reported decreased  
554 modularity and increased participation with visual awareness. Whole-brain functional  
555 networks were modeled for each condition with the generalized psychophysiological  
556 interaction (gPPI; McLaren et al., 2012) without the deconvolution step (O'Reilly et al.,  
557 2012); see Methods Functional Connectivity Analysis for details). The gPPI has the  
558 advantage of controlling the context-dependent functional connectivity estimates for (a) the  
559 stimulation-related BOLD response and (b) the baseline functional connectivity across the  
560 experiment (Figure 7b). The graph-theoretical analysis of the context-dependent functional  
561 connectivity matrices was performed with the Brain Connectivity Toolbox (Rubinov and  
562 Sporns, 2010) to test for changes in the same measures of integration and segregation as  
563 in (Godwin et al., 2015). We thresholded the context-dependent connectivity matrices  
564 across a range of proportional thresholds from 5% to 40% in steps of 5% (Garrison et al.,  
565 2015) and separately calculated their normalized modularity, mean clustering coefficient,  
566 mean participation coefficient and characteristic path length (Figure 7c-f). Since Godwin et  
567 al. (2015) analyzed the graph-theoretical metrics only for confident hits and misses, we  
568 first ran the analysis for confident trials only (Figure 8). Trials were classified as confident  
569 when the yes/no-decision was rated with 3 or 4 ("rather confident" or "very confident").  
570 Additionally, we repeated the analysis for all trials independent of their confidence rating  
571 (Figure 10) and with an extended preprocessing including a nuisance regression (Figure  
572 11, 12).



573

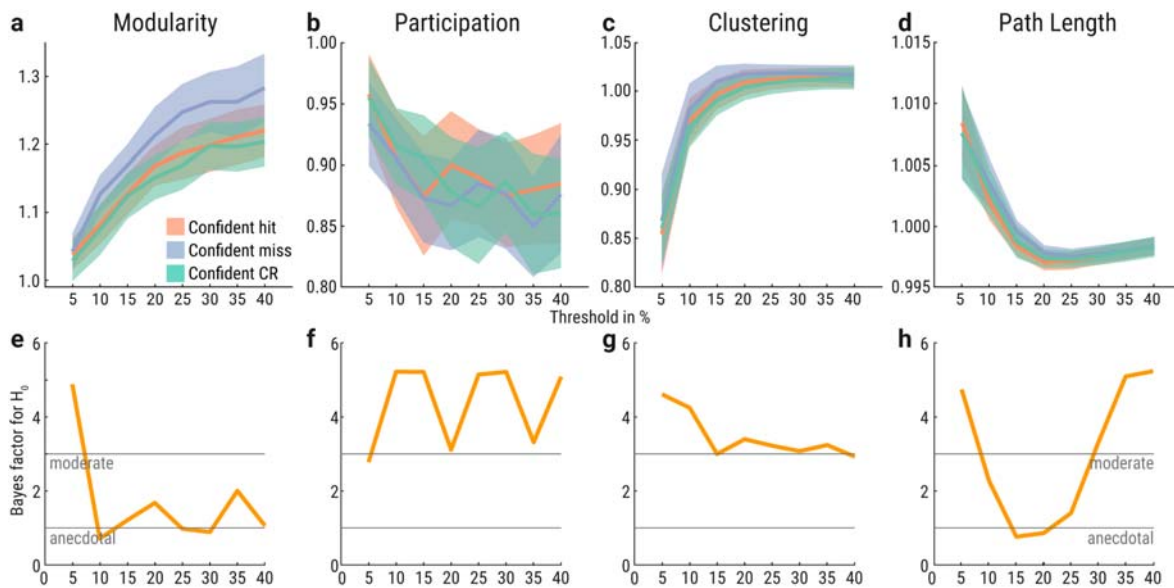
574 **Figure 7.** Context-dependent functional connectivity analysis. (a) Regions of interest (ROIs) were defined as  
575 4-mm radius spheres at the MNI coordinates of a 264-nodes atlas (Power et al., 2011). (b) We used the  
576 generalized psychophysiological interaction (gPPI; McLaren et al., 2012) to calculate the context-dependent  
577 functional connectivity between all pairs of ROIs for each condition separately (hit, miss, and correct  
578 rejection). This measure controls for baseline functional connectivity and the stimulus-evoked hemodynamic  
579 response (HRF). (c) These context-dependent functional connectivity estimates were merged into individual,  
580 normalized, symmetric functional connectivity matrices to evaluate their network topology. For the latter, the  
581 matrices were thresholded to include only the strongest edges (d), and the resulting networks (e) were  
582 analyzed with graph-theoretical measures (f). For visualization, we selected the mean context-dependent  
583 connectivity matrix for hits (c) and thresholded it proportionally with 5-40% (d) and with 5% for the  
584 visualization of the edges (e). Edge color and diameter capture the strength of functional connectivity. Figure  
585 concept was inspired by Figure 2 in (Uehara et al., 2014).

586

587 Confident hits and misses showed no significant differences in measures of global  
588 segregation into distinct networks (modularity), local segregation (clustering), integration  
589 (path length), and centrality (participation) based on paired two-sided Wilcoxon's signed-  
590 rank tests and FDR-correction (Figure 8a-d). Additionally, we calculated the Bayes factors

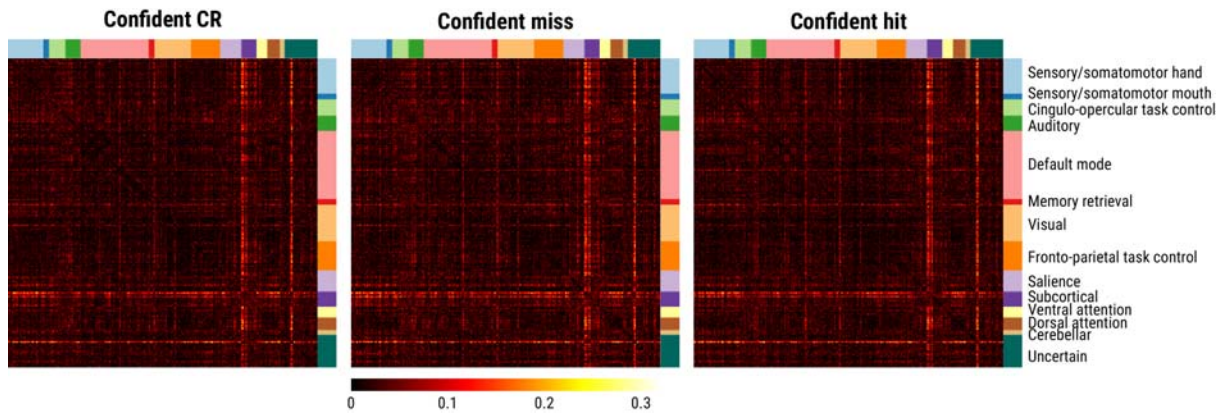


591 based on paired  $t$ -tests with a JZS prior ( $r = \sqrt{2}/2$ ; Rouder et al., 2012) to evaluate the  
592 evidence for the null hypothesis ( $H_0$ : confident hits and misses do not differ). For  
593 modularity, participation, clustering, and path length, the evidence was anecdotal or  
594 moderate for the null hypothesis across the network thresholds (Figure 8e-h). The Bayes  
595 factor for modularity was below 1 at the 10%-, 25%- and 30%-threshold (Figure 8e) and  
596 hence reflecting anecdotal evidence for the alternative hypothesis. Path length had a  
597 Bayes factor below 1 at the 20%-threshold (Figure 8h). Confident correct rejections  
598 showed no significant differences to confident misses or confident hits (Figure 8a-d).  
599 Furthermore, we calculated the mean connectivity matrices of each condition for the 10%-  
600 network threshold to visualize the context-dependent functional connectivity estimates  
601 across all 264 nodes (Figure 9).



602  
603 **Figure 8.** Functional network topology of only confident hits (red), misses (purple), and correct rejections  
604 (green). (a-d) Graph measures for network thresholds from 5-40% in 5% steps (x-axes). Y-axes indicate  
605 normalized graph metric values. Confidence bands reflect within-participant 95% confidence intervals. (e-h)  
606 Bayes factors ( $BF_{01}$ ) based on paired  $t$ -test between confident hits and misses. Bayes factor of 2 indicates  
607 that the evidence for the null hypothesis is twice as likely compared to the alternative hypothesis given the  
608 data. Bayes factors between 1-3 are interpreted as anecdotal and between 3-10 as moderate evidence for  
609 the null hypothesis (Schönbrodt and Wagenmakers, 2018).





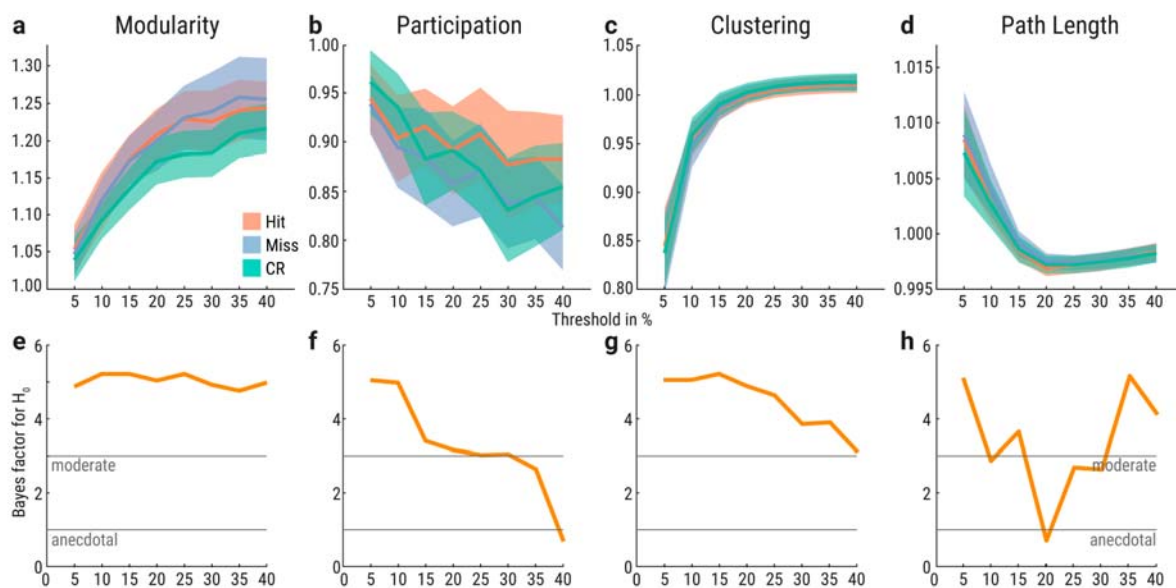
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611 **Figure 9.** Mean connectivity matrices of confident correct rejections (CR), misses and hits for the 10%-  
612 threshold (Figure 8). The values represent the normalized gPPI estimates between the 264 nodes ordered  
613 by subnetworks.

614

615 Because graph metrics of the whole brain might be similar between conditions while the  
616 graph metrics of individual nodes and subnetworks differ, we normalized the averaged  
617 participation and clustering coefficients separately for each of the 14 Power et al. (2011)  
618 subnetworks. For this analysis, we chose the networks thresholded for the top 10%  
619 connections (Figure 9). The resulting graph metrics were compared with Wilcoxon's  
620 signed-rank tests between the three conditions while correcting for multiple comparisons  
621 with a false discovery rate of 5%. There was no significant difference in any subnetwork  
622 between confident correct rejections, misses, and hits.

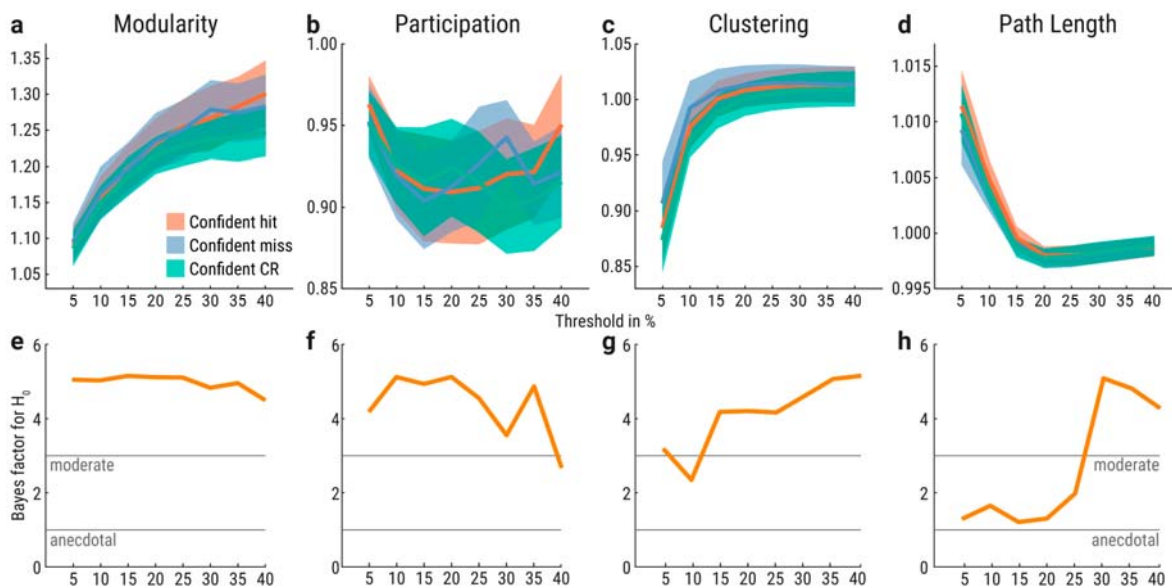
623 We repeated the analysis for all trials independent of the confidence rating to increase the  
624 number of trials and hence the statistical power. As in the preceding analysis (Figure 8),  
625 we observed no significant differences in modularity, participation, clustering, and path  
626 length based on paired two-sided Wilcoxon's signed-rank tests and FDR-correction (Figure  
627 10a-d). There was anecdotal to moderate evidence for the null hypothesis ( $H_0$ : hits and  
628 misses do not differ; Fig 9e-h). Only the Bayes factors for participation at the 40%-  
629 threshold (Figure 10f) and path length at the 20%-threshold (Figure 10h) were below 1 and  
630 hence reflected anecdotal evidence for the alternative hypothesis. Correct rejections  
631 showed no significant differences to misses or hits (Figure 10a-d).



632

633 **Figure 10.** Functional network topology of all hits (red), misses (purple), and correct rejections (green). (a-d)  
634 Graph measures for network thresholds from 5-40% in 5% steps (x-axes). Y-axes indicate normalized graph  
635 metric values. Confidence bands reflect within-participant 95% confidence intervals. (e-h) Bayes factors  
636 ( $BF_{01}$ ) based on paired  $t$ -tests between detected and undetected near-threshold trials. Bayes factor of 2  
637 indicates that the evidence for the null hypothesis is twice as likely compared to the alternative hypothesis  
638 given the data. Bayes factors between 1-3 are interpreted as anecdotal and between 3-10 as moderate  
639 evidence for the null hypothesis (Schönbrodt and Wagenmakers, 2018).

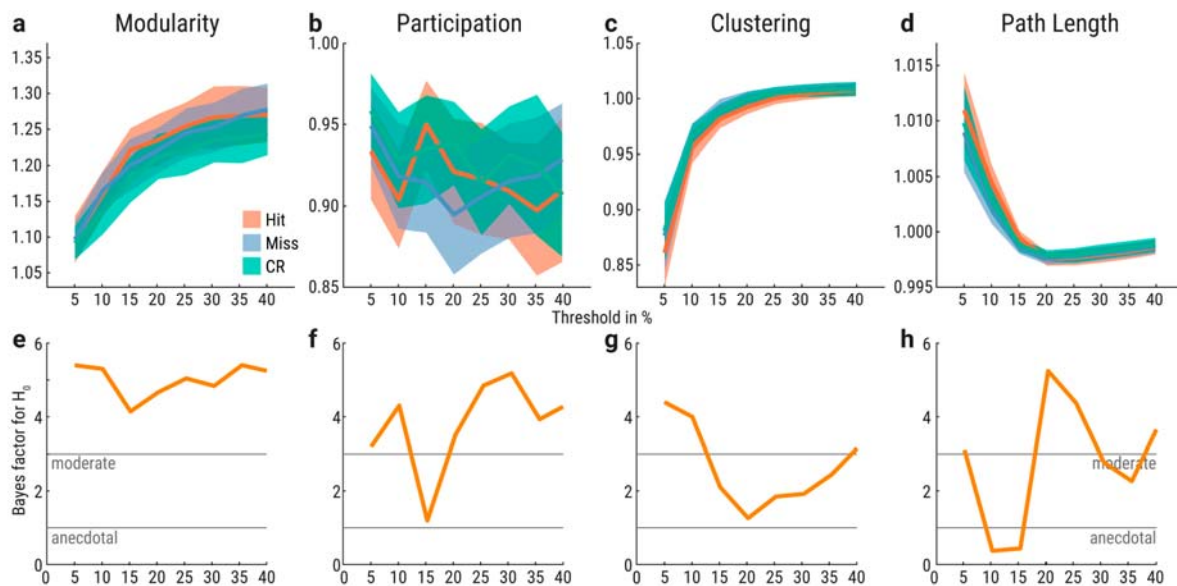
640 In a third step, we extended the preprocessing to include smoothing, scaling and a  
641 nuisance regression as in the whole-brain BOLD contrast analysis (Figure 3, 4). We then  
642 analyzed again the graph metrics for only confident trials (Figure 11) and all trials  
643 independent of the confidence response (Figure 12). For only confident trials, we observed  
644 no significant differences in modularity, participation, clustering, and path length based on  
645 paired two-sided Wilcoxon's signed-rank tests and FDR-correction (Figure 11a-d). There  
646 was anecdotal to moderate evidence for the null hypothesis ( $H_0$ : confident hits and misses  
647 do not differ; Figure 8e-h). Confident correct rejections showed no significant differences to  
648 confident misses or confident hits (Figure 11a-d).



649

650 **Figure 11.** Functional network topology of only confident hits (red), misses (purple), and correct rejections  
651 (green) with extended preprocessing. (a-d) Graph measures for network thresholds from 5-40% in 5% steps  
652 (x-axes). Y-axes indicate normalized graph metric values. Confidence bands reflect within-participant 95%  
653 confidence intervals. (e-h) Bayes factors ( $BF_{01}$ ) based on paired  $t$ -tests between confident detected and  
654 undetected near-threshold trials. Bayes factor of 2 indicates that the evidence for the null hypothesis is twice  
655 as likely compared to the alternative hypothesis given the data. Bayes factors between 1-3 are interpreted as  
656 anecdotal and between 3-10 as moderate evidence for the null hypothesis (Schönbrodt and Wagenmakers,  
657 2018).

658 For the extended preprocessing and all trials independent of the confidence response, hits  
659 and misses did not differ significantly in modularity, participation, clustering, and path  
660 length based on paired two-sided Wilcoxon's signed-rank tests and FDR-correction (Figure  
661 12a-d). There was anecdotal or moderate evidence for the null hypothesis ( $H_0$ : hits and  
662 misses do not differ; Figure 12e-h). Only the Bayes factors for path length at the 10%- and  
663 15%-threshold were below 1 (Figure 12h) and hence reflected anecdotal evidence for the  
664 alternative hypothesis. The path length was higher for correct rejections than hits at the  
665 35%-threshold (FDR-corrected  $p = 0.017$ ), and at the 40%-threshold (FDR-corrected  $p =$   
666 0.042).



667

668 **Figure 12.** Functional network topology of all hits (red), misses (purple), and correct rejections (green) with  
669 extended preprocessing. (a-d) Graph measures for network thresholds from 5-40% in 5% steps (x-axes). Y-  
670 axes indicate normalized graph metric values. Confidence bands reflect within-participant 95% confidence  
671 intervals. (e-h) Bayes factors ( $BF_{01}$ ) based on paired  $t$ -tests between detected and undetected near-  
672 threshold trials. Bayes factor of 2 indicates that the evidence for the null hypothesis is twice as likely  
673 compared to the alternative hypothesis given the data. Bayes factors between 1-3 are interpreted as  
674 anecdotal and between 3-10 as moderate evidence for the null hypothesis (Schönbrodt and Wagenmakers,  
675 2018).

676 Furthermore, to investigate whether the atlas-based approach missed functional  
677 connectivity of subnetworks, we performed a seed-based gPPI analysis with the cS2  
678 cluster from the contrast between near-threshold and catch trials (Figure 5;  $x = 64$ ,  $y = -20$ ,  
679  $z = 18$ ). We created a 4-mm radius sphere and extracted the mean BOLD time course, as  
680 in the atlas-based approach. After computing individual gPPI models, we tested the  
681 psychophysiological interaction regressors of the three conditions (confident correct  
682 rejections, misses, and hits) against each other across participants for all voxels and  
683 applied a cluster correction for multiple comparisons ( $p_{\text{voxel}} \leq 0.0005$ , cluster size  $k \geq 4$  for  
684  $p_{\text{cluster}} \leq 0.05$ ). We did not observe any significant cluster for the cS2 functional connectivity  
685 contrast between confident hits and misses, and confident hits and correct rejections. For  
686 the contrast of confident misses and correct rejections, we found one negative significant  
687 cluster at threshold (cluster size  $k = 4$  voxels) in the right cerebellum ( $x = 7$ ,  $y = -41$ ,  $z =$   
688  $17$ ). We repeated the analysis with extended preprocessing (including smoothing, scaling,  
689 and nuisance regression) and with all trials independent of their confidence response  
690 (corresponding to Figure 11). We did not observe any significant cluster for the cS2  
691 functional connectivity contrast between any two of the three conditions (correct rejections,  
692 misses, and hits) for  $p_{\text{voxel}} \leq 0.0005$  and  $p_{\text{cluster}} \leq 0.05$  (cluster size  $k \geq 18$  for hits vs.  
693 misses, and cluster size  $k \geq 19$  for hits vs. correct rejections, and misses vs. correct  
694 rejections). That is why we conclude that the small negative cluster between confident  
695 misses and correct rejections is a spurious finding.

## 696 **Discussion**

697 Using fMRI during a near-threshold somatosensory detection task, we investigated  
698 changes in local brain activity and functional brain network topology associated with  
699 conscious perception. We found that conscious somatosensory perception ('detected'  
700 compared to 'undetected' stimuli) led to higher activation in precuneus, intraparietal sulcus,  
701 insula, inferior frontal gyrus, and nucleus accumbens. The latter two showed higher  
702 activation only when all trials were included (confident and unconfident) but not with  
703 confident trials only. At a slightly looser statistical threshold ( $p = 0.06$ ) bilateral secondary  
704 somatosensory cortex also showed higher activity during conscious perception. Significant  
705 positive voxels in contralateral S1 for near-threshold stimuli were only noted in an ROI-  
706 based analysis. The graph-theoretical analysis of network topology did not provide any  
707 evidence for a difference between aware and unaware trials in modularity, participation,  
708 clustering, nor path length. Finally, when comparing misses with correctly rejected catch  
709 trials, we found activation of S2, insula, and supplementary area; also, in this contrast, no  
710 changes in network properties were observed. Subsequently, we first discuss the  
711 observed BOLD activity patterns and then the absent graph metric changes in comparison  
712 to the findings in the visual system using a masking paradigm by Godwin et al. (2015).

713 It is generally accepted, that primary and secondary somatosensory cortices (S1,  
714 S2) are necessary for somatosensory processing leading to conscious perception  
715 (Hirvonen and Palva, 2016; Moore et al., 2013). It has long been established that lesions  
716 in S1 go along with hypoesthesia (Roland, 1987). Recently, we have shown in stroke  
717 patients, that - despite intact S1 - also lesions in S2 (along with anterior and posterior  
718 insula, putamen, and subcortical white matter connections to prefrontal structures) lead to  
719 impaired tactile conscious experience (Preusser et al., 2015). fMRI studies employing  
720 supra-threshold somatosensory stimulation - in passive or active designs - have  
721 consistently shown activation of S1 and S2 (Ruben et al., 2001). As we have previously



722 shown, S1 and S2 are already affected by subthreshold stimuli (below the absolute  
723 detection threshold), which lead to a deactivation of these areas (Blankenburg et al.,  
724 2003). In the current study, we now show that near-threshold stimuli, which are not  
725 detected, i.e., below the response criterion (in signal detection theory terminology) for  
726 conscious detection, lead to an activation of S2 and insula (when compared to ‘correct  
727 rejections’ of catch trials). This leads to the interesting conclusion that non-detected stimuli  
728 lead to differential involvement of S1 and S2 depending on their intensity. Similarly, in our  
729 recent EEG study, we found that non-detected stimuli lead to a negativity 150 milliseconds  
730 after stimulation (N150) for principally detectable near-threshold stimuli but not for  
731 imperceptible stimuli intensities (Forschack et al., 2020). The N150 has been shown to  
732 originate in area S2 (Aukstulewicz et al., 2012). It will be an interesting issue for future  
733 studies whether an analysis based on objective detection paradigms (e.g., two-alternative  
734 forced-choice tasks, 2AFC) will further help to differentiate the meaning of these signal  
735 changes in S1 and S2, i.e., whether the “transition” from deactivation in S2 (and S1) to an  
736 activation is related to the “objective detection” in a criterion-free 2AFC task and the  
737 emergence of the N150. It should be noted that while others have shown that S1  
738 represents the stimulus properties that get access to consciousness in interaction with S2  
739 (Blankenburg et al., 2006; Moore et al., 2013; Rajaei et al., 2018; Schröder et al., 2019),  
740 we did not observe a strong stimulation effect in S1 for our near-threshold trials. This might  
741 be due to the weak stimulus intensity and stimulation “only” at the index finger in contrast  
742 to the commonly used median nerve stimulation.

743 For theories of consciousness, the difference between perceived versus non-  
744 perceived stimuli is most relevant. In our study, contralateral secondary somatosensory  
745 cortex (cS2) was found for both contrasts “hit > miss” and “confident hit > miss” when the  
746 statistical cluster threshold was set to  $p = 0.06$ . This finding is consistent with previous  
747 suggestions that there is additional activity in S2 with conscious detection. For example, a

748 previous fMRI study on vibrotactile detection reported ipsilateral and contralateral S2 as  
749 the best correlate for detection success (Moore et al., 2013), and in another recent study  
750 bilateral S2 activity was best explained by a psychometric (detection) function (Schröder et  
751 al., 2019). One reason for detection-associated S2 activity might be recurrent processing  
752 (Lamme, 2006; van Gaal and Lamme, 2012). For example, in an EEG study, the detection  
753 of near-threshold electrical pulses to the finger was best explained by the recurrent  
754 processing between contralateral S1 and S2, as well as contralateral and ipsilateral S2  
755 (Aukstulewicz et al., 2012). Another explanation might be that separate parts of the  
756 secondary somatosensory cortex might serve different functions. E.g., in a recent study,  
757 more inferior and superior parts of cS2 correlated with a binary detection function, and  
758 more posterior and anterior parts of cS2 correlated with a linear intensity function  
759 (Schröder et al., 2019).

760 While our data overall agree with the necessity of S1 and S2 activation for  
761 conscious perception, it is less clear whether activation of these areas is sufficient for  
762 conscious somatosensory perception: The fact that certain areas “best explain” detection  
763 in an fMRI study (Schröder et al., 2019), does not rule out that the activity of other areas is  
764 also involved in the conscious experience. Like several previous studies on conscious  
765 perception in other sensory domains (Bisenius et al., 2015; Dehaene and Changeux,  
766 2011; Naghavi and Nyberg, 2005; Rees et al., 2002), we find fronto-parietal areas more  
767 active in the ‘detected versus missed’ contrast. Among these, the activations in left and  
768 right intraparietal sulcus, the bilateral posterior cingulate cortices, and the bilateral  
769 precuneus are consistent with the notion of a “posterior hot zone” for conscious  
770 experience as suggested by Koch and colleagues (Koch et al., 2016). Koch et al. (2016)  
771 argue that the increased activity that is seen with conscious perception in additional (e.g.,  
772 frontal) brain areas is related to response preparation, and/or other task-related activations  
773 (confidence, etc.) as they have not been found activated in a no-response paradigm



774 (Frässle et al., 2014). For example, in our study, the nine-second period between  
775 stimulation and response most likely leads to increased activity in areas involved in  
776 working memory (see, e.g., tactospatial sketchpad, Schmidt and Blankenburg, 2018).  
777 Recent literature has pointed out this interrelation: the default mode network (e.g.,  
778 posterior cingulate cortex) supports a stronger global workspace configuration, which  
779 improves working memory performance (Vatansever et al., 2015) and might be beneficial  
780 for conscious perception. On the other hand, even if one assumes that a “pure sensory  
781 conscious experience” could arise from a “posterior hot zone” only, the increased activity  
782 in other brain areas with conscious perception - still leaves the possibility of conscious  
783 experience related to action, confidence, working memory etc. to be dependent on e.g.,  
784 frontal brain areas (Frith, 2019). In this view, the “integrated conscious experience” during  
785 a task would then be related to the entire fronto-parietal network. Obviously, this notion is  
786 close to the global workspace theory (Dehaene et al., 2006; Dehaene and Changeux,  
787 2011; Mashour et al., 2020). While our data do not allow to definitely differentiate between  
788 these major theories of consciousness, we provide new information for somatosensory  
789 conscious perception, which is consistent with the idea that domain-general areas  
790 (interacting with domain-specific areas for example via recurrent processing (Lamme,  
791 2006; van Gaal and Lamme, 2012) play a role for conscious perception.

792 A major hypothesis underlying our study was that conscious perception goes along  
793 with widespread changes in graph metrics as it has recently been reported by Godwin et  
794 al. (2015) for the visual system. However, we did not observe such context-dependent  
795 functional connectivity changes that result in network topology alterations through  
796 modularity, participation, clustering and path length between hits, misses or correct  
797 rejections. This does not change when the number of trials is increased by considering all  
798 trials independent of their confidence response (Figure 10). Also, improving the  
799 preprocessing with a nuisance regression that controls for motion and noise components

800 derived from white matter and ventricles, does not affect this result (Figure 11, 12). The  
801 isolated network topology differences between correct rejections and hits at the 35-40%  
802 threshold for path length with the improved preprocessing (Figure 12d) were not consistent  
803 across thresholds and not present in the analysis of only confident trials (Figure 11), as  
804 well as in the analyses with the basic preprocessing (Figure 8, 10). That is why we do not  
805 interpret these differences as a valid and reliable effect. Thus, there was neither a  
806 functional network alteration by stimulus awareness (hit > miss) nor by the detected (hit >  
807 CR) or undetected stimulation (miss > CR).

808         Two apparent differences between the study of Godwin et al. (2015) and our study  
809 are the somatosensory versus visual modality and the use of a masking paradigm (Godwin  
810 et al.) as opposed to near-threshold stimuli. However, assuming that the connectivity  
811 changes observed by Godwin et al. are related to the conscious experience, it is difficult to  
812 see why those differences should explain the different results. One possible reason why  
813 Godwin et al. observed whole-brain network topology alterations for visual awareness  
814 might be the unbalanced physical similarity between aware and unaware trials. Hits and  
815 misses originated from two different masking conditions: backward masking generated  
816 83% of all hits and forward masking 84% of all misses. Additionally, their total number of  
817 trials for 24 participants was not balanced (276 confident misses vs. 486 confident hits). In  
818 contrast, our study did not rely on masking the target stimulus and resulted in a balanced  
819 total amount of 882 confident misses and 870 confident hits for 31 participants (Figure 8,  
820 10). Furthermore, we also present the results of 1507 hits, and 1190 misses independent  
821 of the confidence rating (Figure 10, 11). Future studies investigating visual awareness may  
822 be able to distill conscious percepts for present stimuli without confounding masking  
823 conditions, for instance taking advantage of sub-millisecond precision of modern  
824 tachistoscopes (Sperdin et al., 2013). Awaiting such studies as well as further studies on  
825 the somatosensory system and acknowledging – of course – that “absence of proof” is not

826 “proof of absence” – our study cannot provide support for changes in graph metrics with  
827 awareness.

828 In summary (integrating our previous findings on the effect of subthreshold  
829 stimulation (Blankenburg et al., 2003; Taskin et al., 2008), there seem to be three  
830 discernable stages of fMRI-BOLD signal changes with increasing somatosensory stimulus  
831 intensity: (i) A deactivation of S1, S2 following (trains of) subthreshold (never-detected)  
832 stimuli, (ii) activation of S1, S2, and insula following near-threshold not-detected stimuli,  
833 (iii) additional activation of S1, S2 accompanied by activation of a fronto-parietal (likely to  
834 be domain-general) network when stimuli are consciously perceived. The potentially  
835 differential contribution of the involved brain areas to the conscious experience should be  
836 subject to future investigations in which modulations of different aspects of the tasks (e.g.,  
837 varying delay, way of report, design e.g., 2AFC versus yes/no task) may be employed. Our  
838 study could not confirm changes in graph metrics with awareness for the somatosensory  
839 system. Whether this is related to the specific somatosensory modality (electrical nerve  
840 stimulation) or the weak stimulation should be investigated by future studies. We think that  
841 the data of electrical finger nerve stimulation - despite its limited spatial extent - is a useful  
842 model for a range of somatosensory receptors in the fingers, because the nerve  
843 integrating the receptor signals is directly stimulated. This view is also supported by similar  
844 topographical activation patterns for passive proprioceptive stimulation compared with  
845 tactile stimulation (Nasrallah et al., 2019). The potentially differential contribution of the  
846 involved brain areas to the conscious experience of electrical stimuli is in line with global  
847 broadcasting of individual content of consciousness across the brain without substantial  
848 reconfiguration of the brain's network topology resulting in an integrative conscious  
849 experience - at least for the observed somatosensory submodality.

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