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► To cite this version:

Sara Salgues, Gaën Plancher, Laurence Jacquot, Janick Naveteur, Lison Fanuel, et al.. To the self and beyond: Arousal and functional connectivity of the temporo-parietal junction contributes to spontaneous sensations perception. Behavioural Brain Research, 2021, 396, pp.112880. 10.1016/j.bbr.2020.112880 . hal-03463982

HAL Id: hal-03463982

<https://uphf.hal.science/hal-03463982v1>

Submitted on 14 Sep 2022

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2 **To the self and beyond: arousal **and** functional connectivity of the temporo-**
3 **parietal junction contributes to spontaneous sensations perception**

4

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25

26 **Funding:** This work was supported by the Lumière Lyon 2 University doctoral grant (2018-
27 30) awarded to the first author; the LABEX CORTEX of the Lyon University (ANR-11-
28 LABX-0042) through the “Investissements d’Avenir” program run by the French National
29 Research Agency (ANR-11-IDEX-0007).

30

31

32

Abstract

33 The temporoparietal junction (TPJ), along with the anterior insula (AI) and the extrastriate
34 body area (EBA), play a major part in embodiment and self-awareness. However, these con-
35 nections also appear to be frequently engaged in arousal and attentional processing of external
36 events. Considering that these networks may focus attention both toward and away from the
37 self, we set to investigate how they contribute to the perception of spontaneous sensations
38 (SPS), a common phenomenon related to self-awareness and mediated by both interoceptive
39 and attentional processes. In Experiment 1, resting-state EEG was recorded, as well as arousal
40 reported via a questionnaire, followed by an SPS task. Functional TPJ-AI and TPJ-EBA con-
41 nectivity were computed using eLORETA. Spatial correlational analyses showed that less
42 frequent SPS coincided with greater TPJ-AI and TPJ-EBA functional connectivity, especially
43 in the theta and alpha frequency bands. High self-reported arousal predicted low intensity and
44 low confidence in the location of SPS. Resting-state skin conductance level (SCL) was rec-
45 orded in Experiment 2, followed by the SPS task. Less frequent SPS coincided with greater
46 SCL. Findings are interpreted in terms of attention and self-related processes, and a discussion
47 of the TPJ participation in self-awareness through SPS is presented.

48

49 **Keywords:** Spontaneous Sensations; Temporoparietal Junction; Anterior Insula; Extrastriate
50 Body Area; Skin Conductance Level; Arousal

51

52 Abbreviations

ADCL	Activation/Deactivation Checklist
AI	Anterior Insula
BMI	Body Mass Index
EBA	Extrastriate Body Area
EEG	Electroencephalography
eLORETA	Exact Low-Resolution Tomography
SCL	Skin Conductance Level
SPS	Spontaneous Sensations
TPJ	Temporoparietal Junction

53

54 1. Introduction

55 Being aware of oneself means having access to many aspects of the self, ranging from body
56 sensations to thoughts and emotions. Awareness requires attentional processes, allowing one
57 to focus on the body and thus to apprehend the information it conveys, from sensory inputs to
58 body representations [1]. Conversely, diverted attention would weaken access to body aware-
59 ness.

60 The temporoparietal junction (TPJ) **would** play a key role in self-awareness. Referring
61 to an area situated at the intersection of the inferior parietal lobule, the superior temporal sul-
62 cus, and the lateral occipital cortex [2], and comprising the supramarginal and angular gyri
63 [3], the TPJ is a multimodal cortical region, receiving inputs from thalamic, limbic, soma-
64 tosensory, visual and auditory areas [2], [4]. Interest in the TPJ persists with the lack of un-
65 derstanding of its precise function since it **is** involved in attentional processes and arousal [5]–
66 [7], as well as in social cognition [8], [9], or memory retrieval [9]. Besides, the TPJ is a great
67 candidate for self-awareness, since it **was** associated with self-referential processes such as
68 theory-of-mind [9], self-other discrimination [10]–[13], self-location [14], [15], agency [16],
69 [17], and embodiment [18], [19].

70 **The focus of this paper is placed deliberately** on embodiment and self-location. As
71 both **involve** the feeling of being present at a certain location, their failure **results** in autoscop-
72 ic experiences, such as out-of-body experiences and heautoscopy, where one **can** see oneself
73 from another location in space [20]. **Temporoparietal junction dysfunction would lead to these**
74 **bodily illusions, as would** two other cortical areas. The first, the extrastriate body area (EBA),
75 located in the lateral occipitotemporal cortex, **intervenes** primarily in the integration of bodily
76 inputs [18], [21]–[25], in body-oriented attention [26], and illusory limb ownership [27]. The
77 second, the anterior insula (AI), located in the ventrolateral prefrontal cortex, within the Syl-
78 vian fissure, **operates *inter alia*** in interoception [28]–[31], i.e. the perception of the physiolog-
79 ical condition of the body, but also in the looking down perspective illusion [14], [15], **i.e. a**
80 **manipulation of the first-person perspective resulting in the feeling of looking down at the**
81 **own body while being in a supine position.** The TPJ shares connections with both the AI [2]–
82 [4], [7], [32], [33], and the EBA [8], [15]. **The** TPJ connections with both the EBA and the AI
83 **appear to** play a critical role in self-awareness.

84 Previously, we mentioned that the TPJ might **participate** in attentional processes and
85 arousal, but activations of both EBA and AI **were** also frequently associated with high arousal

86 [6], [34], [35]. Arousal **refers to** the level of autonomic activation sometimes due to cognitive
87 processing frequently assumed to be attentional processing [34]–[40]. From a functional point
88 of view, attentional processes **seem to translate into** low-frequency cortical oscillations, such
89 as delta (0.5-3.5hz) [41], [42], theta (4-7hz) [41], [43]–[45] and alpha (7.5-12hz) [43], [46]–
90 [49]. Hence, while high arousal is associated with attentional networks mediating capture by
91 salient environmental cues [6], [36], [50], areas processing interoceptive stimuli such as the
92 AI also **stand out** in the generation of arousal. Along with this discrepancy, high arousal
93 would allow attentional focus on the self and access to private information [37], [51], [52].

94 The major influence of attention and self-referential processes in body-awareness was
95 **documented** in a series of studies investigating spontaneous sensations (SPS), i.e. the percep-
96 tion of sensations arising on the body without any external triggers. SPS are quite frequent
97 phenomena that can be easily perceived by almost anyone. Focusing on those events may con-
98 tribute to maintaining the body image in consciousness [53]. While attention taken away from
99 the body dampens the experience of SPS [54], [55], attention directed inwards enhances the
100 perception of SPS [56], [57]. These findings indicate that attention to external events and at-
101 tention to thoughts and internal sensations are two competing states. As Morin [58] suggested,
102 there is evidence that self-awareness rises through a state of focus toward the self, versus a
103 focus toward the environment. When considering the involvement of TPJ connections with
104 the AI and EBA in self-awareness, a discrepancy remains between self-referential processes
105 and attention/arousal implication. There seems to be an anticorrelation between two cognitive
106 states of focus, either toward the inner world (i.e. self-processing) or toward the outer world
107 (i.e. salience and attentional capture). This distinction between the two states of focus **can be**
108 observed in brain imaging [59] and has also been suggested within the context of SPS [56].
109 Many questions arise from this gathering. First, if **SPS relate to** self-awareness, how would
110 SPS **associate with the** functional connections **TPJ-EBA and TPJ-AI**? Second, could arousal
111 be negatively associated with SPS perception, even when affiliated with self-referential pro-
112 cesses? And third, could **the functional connections TPJ-EBA and TPJ-AI correlate** in the
113 same way that arousal **does** with SPS, or could they be dissociated?

114 In this paper, we present two studies investigating how these factors, as individual
115 traits, **affect** SPS perception. In the first study, we focused mainly on resting-state TPJ func-
116 tional connectivity with the AI and EBA, **as well as the self-reported** propensity to high
117 arousal. As we have an interest in the role of cortical oscillations, we used EEG. In the second
118 study, we investigated the question of arousal further through resting-state electrodermal ac-

119 tivity. Specifically, **we used** skin conductance level (SCL), since it reflects tonic components
120 of autonomic arousal and **qualifies** as a physiological trait of arousal [60]. We hypothesized
121 that, since arousal **relates** closely to attention [35], [36], **the** propensity to high arousal would
122 be associated with decreased perceived frequency of SPS. Given that the literature remains
123 inconsistent regarding how functional connections in the brain, arousal, and self-referential
124 processes interrelate, we can formulate the general hypothesis that functional connectivity of
125 the TPJ with both the AI and EBA would be related to the perception of SPS. We might ex-
126 pect this relationship to **translate** primarily in low oscillations (i.e. delta, theta, and alpha),
127 based on the assumption that those oscillations would reflect attentional processes involved in
128 SPS perception.

129

130 **2. Experiment 1**

131 *2.1. Participants*

132 The study **followed** the Helsinki Declaration **and the protocol was approved by the local eth-**
133 **ics committee (reference number IRB 00009118)**. Participants were students at the Lumière
134 University in Lyon, France. During the first steps of the experimental procedure, they **com-**
135 **pleted** a form containing questions on sociodemographic and health characteristics. Items in-
136 cluded age, gender, height, weight, use of psychotropic medication (and if so, the reason why;
137 antidepressants, anxiolytics, neuroleptics, anticonvulsants, hypnotics, tranquilizers, etc.),
138 regular use of other psychoactive substances (alcohol, marijuana, etc.), and history of cardio-
139 vascular diseases or diabetes mellitus. **Besides**, participants could report any other information
140 they considered to be of importance for the study. **Any report of a** history of neurological or
141 psychiatric **illness or** psychoactive substance abuse or any disease that **may** affect tactile per-
142 ception, such as diabetes mellitus or cardiovascular disease, **led to exclusion**. Thirty-eight
143 volunteers participated in the study, ten were excluded **based** on the above-mentioned criteria,
144 and one because of recording issues compromising the EEG data. Twenty-seven participants
145 (14 female and 13 male), all right-handed, with a mean age of 22.1 ± 2.77 (age range: 19 to
146 28), and a mean body mass index of $21.2 \pm 1.33\text{kg/m}^2$ (range: 19.26 to 23.89kg/m^2) were
147 therefore included in the study. All gave their written informed consent to participate **before**
148 the test.

149 **Power analyses were conducted on the effect size of the proximo-to-distal gradient in**
150 **the frequency of SPS, which is the most prominent characteristic of these phenomena. Based**

151 on published studies [53], [61], the weighted average effect size expressed as Cohen's w is .52
152 (i.e., large) and expressed as Cramers's V is .26 (i.e., medium to large). Provided a power of
153 90% to detect a similar medium effect size and an alpha at .05, the number of hand maps
154 needed is 53. Given that, in the present study, two hand maps per participant are collected
155 (one per hand), the sample size needed is 27 participants. With a sample of 27 participants
156 (i.e., 54 hand maps) there is enough power (91%) to diminish Type II errors.

157

158 2.2. Materials

159 2.2.1. Activation/Deactivation Check-List (ADCL; Thayer, 1967)

160 To assess a declarative measure, the propensity (trait) to arousal, participants completed a
161 French trait version of the Activation/Deactivation Check-List (ADCL) [62], [63]. It measures
162 the activation (i.e. being actively involved in the processing of the environment) and deactiva-
163 tion (i.e. being prone to sleep or rest) states and was chosen because of its test-retest reliability
164 (ranging from $\rho = .57$ to $\rho = .87$) and validity (correlation with psychophysiological
165 measures of arousal ranging from $\rho = .43$ to $\rho = .68$). Participants must determine, for a
166 list of 49 adjective-items, whether or not each one describes their usual functioning. Among
167 the list of items, 27 adjectives are fillers. They had to rate each item on a 5-point Likert Scale
168 (1=Never; 5=Very often) while taking into account the basic instruction "Usually, daily, I
169 am:". Three main components are evaluated: General Activation (example of items: energetic,
170 full-of-pep, active), Calm (example of items: placid, calm, still), and General Deactivation
171 (example of items: leisurely, sleepy, tired). High scores in those components would reflect a
172 higher propensity to General Activation, Calm, and General Deactivation. The internal con-
173 sistency for our sample, as assessed through the mean inter-item correlation was good since
174 all values exceeded the conventional threshold of $|\rho|.15$ [64]: General Activation .61, Calm
175 .62, and General Deactivation .27.

176

177 2.2.2. Resting-State EEG

178 A resting-state EEG recording was performed immediately after the completion of the ques-
179 tionnaire. Participants were seated comfortably in front of a computer monitor in a recording
180 booth, fitted with the electroencephalographical equipment. An EEG ACTi Champ with ac-
181 tive electrodes was used for this experiment. A total of 64 channel electrodes, arranged based

182 on the revised 10/20 system [65], and 5 EOGs were used. Two EOGs were placed horizontal-
183 ly, on each cheekbone, and two vertically above and under the left eye to monitor blinking or
184 eye movement. A monopolar set-up was chosen, with a reference EOG on the nose bridge.
185 Impedances were kept below 20k Ω . Once the EEG equipment was set up, the signal quality
186 was tested asking participants to move their eyes left to right, to blink, and to clench their jaw
187 muscles. Then, instructions were displayed in white font on a black background. Instructions
188 advised the participants to relax their jaw and shoulders, to try not to move, to fully relax, to
189 close their eyes, and to resist sleepiness. To prevent any external distractions leading to an
190 eye-opening, the light in the room was dimmed, and the screen went off when the resting ses-
191 sion was started. The session began once the participants stated that they were ready, and the
192 end was announced by the experimenter. The recording session lasted 3 minutes. At the end
193 of the recording session, participants were asked whether they had fallen asleep. No partici-
194 pants reported having fallen asleep during the resting session.

195

196 2.2.3. SPS task

197 Participants completed the SPS task 45 minutes after the resting-state EEG recording. In the
198 meantime, participants performed a distractive visuo-spatial task. This delay allowed a clear
199 dissociation between the resting-state recording and the SPS task. Electrodes and EOGs were
200 removed from the participants' heads. They were then seated in a quiet and normally lit room
201 with an ambient temperature of 20-23°C, in front of a desk. Once they were ready, SPS were
202 introduced as normal phenomena, and to give participants some idea of what they could asso-
203 ciate with SPS, a list of 11 sensations most likely to be felt was presented (beat/pulse, itch,
204 tickle, numbness, skin stretch, tingling, warming, cooling, muscle stiffness, flutter, and vibra-
205 tion). The list used in the SPS protocol is based on the one used originally by Macefield and
206 colleagues [66] and Ochoa and Torebjörk [67] to study microstimulation-evoked sensations,
207 and then adapted by Naveteur and colleagues [68] to study SPS. Participants were then in-
208 structed to remove any jewelry from their hands and wrists and to roll up their sleeves if they
209 were long enough to cover the wrist. For 15s, they were instructed to cleanse their hands with
210 an antiseptic gel (Aniosgel® 85 NPC, \approx 3ml per participant), to remove any external surface
211 agents that could interfere with the task, and to ensure a homogenous glabrous skin surface
212 across all participants. A 15s latency was observed between the cleansing operation and the
213 start of the test. Each participant was given a protocol containing the standardized reduced
214 maps of each hand shown palm up (with a distance of 11.2cm between the tip of the middle

215 finger and the palm/wrist frontier), and below each map, the list of 11 SPS and two visual
216 **analog** scales (i.e. two 10cm continuous horizontal lines without markers at each **end**) for con-
217 fidence ratings, along with a pencil and a 25 × 25cm piece of smooth white fabric. Once par-
218 ticipants were familiarized with the material, the start of the test session was announced. The
219 protocol and the pencil were placed away from the participants on the desk to prevent any
220 interference from visual stimuli. Each hand was tested once in a balanced order across partici-
221 pants. They were instructed to sit with their back supported by the backrest of their chair. The
222 leg ipsilateral to the tested hand was turned outward by about 60 degrees from the midline.
223 Participants placed the white fabric cotton fabric on their thigh, with the tested hand resting
224 on it, palm up with fingers spaced slightly apart. Only a dorsal part of the hand was in contact
225 with the fabric, apart from the fingers. The hand not being tested hung down on the outer side
226 of the chair contralateral to the tested hand. When the “start” signal was given verbally by the
227 experimenter, marking the start of each trial, participants gazed at their tested hand for 10s,
228 focusing their attention on the hand so that they could detect any sensations that might occur.
229 They were informed beforehand that there was a possibility that they would perceive no sen-
230 sation. A “stop” signal given by the experimenter marked the end of the 10s period. Partici-
231 pants were immediately asked to report on the protocol whether they had detected any sensa-
232 tions on the tested hand or not and if they had, to (a) map the extent and location of the sensa-
233 tions by shading the areas where they perceived sensations on the map of the tested hands; (b)
234 specify the perceived intensity of each sensation according to a 10 point scale (1 = just per-
235 ceptible; 10 = very intense but not painful) directly on the map; (c) indicate their degree of
236 confidence in the location and the extent of the perceived sensations according to the two vis-
237 ual **analog** scales (ranging from "not confident" to "very confident"), and (d) identify the sen-
238 sations with the list of descriptors. They had the option to choose more than one descriptor
239 and to add descriptors to the list according to what they had detected. The task lasted approx-
240 imately 15 min.

241

242 *2.3.Data Processing*

243 *2.3.1. EEG Preprocessing*

244 The EEG data preprocessing was conducted with BrainVision Analyzer 2.1. To ensure a qual-
245 ity signal was processed, a passband of 0.2-120Hz was first applied, with a 50Hz notch, and
246 bad electrode signals removed and replaced by the mean signal of the three nearest electrodes.
247 On average, 2.37 ± 0.47 electrodes signals were replaced (up to 8 electrodes) and those most

248 removed from the signal were FP1, FP2 (11 participants), FT9, TP10 (9 participants), FT10 (8
249 participants), and TP9 (7 participants). Those least removed were F2, POz, T8 (only one par-
250 ticipant per electrode), and T7 (4 participants). An ocular correction with the Gratton & Coles
251 algorithm [69], based on the left horizontal EOG and the below-eye vertical EOG, was ap-
252 plied, subtracting the ocular movement from the signal. For each participant, the 3-minute
253 recording was divided into 90 epochs of 2s, according to the processing used by Chen and
254 colleagues [70] when studying resting-state EEG data. To ensure no evoked response was
255 triggered by the instruction to close the eye, the first 5 epochs were removed [71]. An artifact
256 rejection, with a maximum amplitude of $80\mu\text{V}$ [70] was carried out on these epochs, resulting
257 in a rejection rate of 12.5% epochs. A mean of 74.41 ± 12.45 epochs, ranging from 38 to 85
258 per participant, was obtained.

259

260 2.3.2. *Functional Connectivity Analysis*

261 Further analyses of the EEG data were carried out using exact Low-Resolution Electromag-
262 netic Tomography (eLORETA; [72]). **The eLORETA method is a discrete, three-dimensional**
263 **distributed, linear, and weighted minimal norm inverse solution. Its validity was convincingly**
264 **demonstrated by Pascual-Marqui [72]: the special weights used in eLORETA give tomogra-**
265 **phy the exact localization property to test point sources, resulting in images of the current**
266 **density with exact localization but with low spatial resolution; the eLORETA has no localiza-**
267 **tion bias in the presence of structures noise and multiple source situations; in addition, due to**
268 **the implementation of "lagged phase synchronization" that models the instantaneous and**
269 **lagged components of functional connectivity, the eLORETA can robustly identify true phys-**
270 **iological connectivity.** The choice of method was further supported by the credibility provided
271 by an array of studies investigating functional connectivity [72]–[75] **and was influenced as**
272 **well by the possibility to apply the eLORETA algorithm on filtered data to operate a frequen-**
273 **cy decomposition of the functional connectivity [72].** The cost of electrophysiological record-
274 ing compared to the quality versus **the** amount of information gathered considered, the
275 eLORETA was regarded as an effective analysis method and a good fit for the study. Thus,
276 instructions from Pascual-Marqui and colleagues were followed strictly [73], [75], [76].

277 The artifact-free epochs were analyzed to estimate the current density for five frequen-
278 cy bands: delta (0.5-3.5hz), theta (4-7hz), alpha (7.5-12hz), beta (13-34hz), and gamma (35-
279 45hz). We seeded three areas forming two connections: the TPJ and EBA connectivity, and

280 the TPJ and AI connectivity, considering only ipsilateral connectivity for both hemispheres.
 281 Regions of interest (ROI) in both left and right hemispheres were constructed with the
 282 eLORETA given MNI coordinates for the TPJ (54, -48, 7) [18], the EBA (48, -67, 3) [18] and
 283 the AI (32, 12, 20) [77]. A voxel-wise approach was applied and lagged phase synchroniza-
 284 tion, indexing the physiological lagged connectivity [72] was used to measure the functional
 285 connectivity between the TPJ and EBA first, followed by the TPJ and AI. These analyses re-
 286 sulted in connectivity indices for each frequency band, the value of which ranged from 0 to 1
 287 (the greater the value, the stronger the connection; Table 1), and this was performed inde-
 288 pendently for the TPJ-EBA connection and the TPJ-AI connection in each hemisphere. Con-
 289 sidering no hypothesis regarding the hemispheric location has been presented in this study, we
 290 used only mean indices of the right and left hemisphere functional connectivity. Due to scale
 291 differences between the connectivities of each frequency band, the indices were z-transformed
 292 for homogenization purposes. The z-transform also allowed a mean to be computed across all
 293 frequency bands for the TPJ-EBA connection and TPJ-AI connection separately.

294 Table 1: Mean (SD) indices for each frequency band, for TPJ – EBA and TPJ – AI functional
 295 connectivity.

	Functional Connectivity	
	TPJ – EBA	TPJ – AI
Delta	.08 (.06)	.14 (.05)
Theta	.031 (.14)	.35 (.09)
Alpha	.40 (.16)	.56 (.11)
Beta	.06 (.02)	.09 (.02)
Gamma	.06 (.07)	.05 (.06)

296

297 *2.4. Results and discussion*

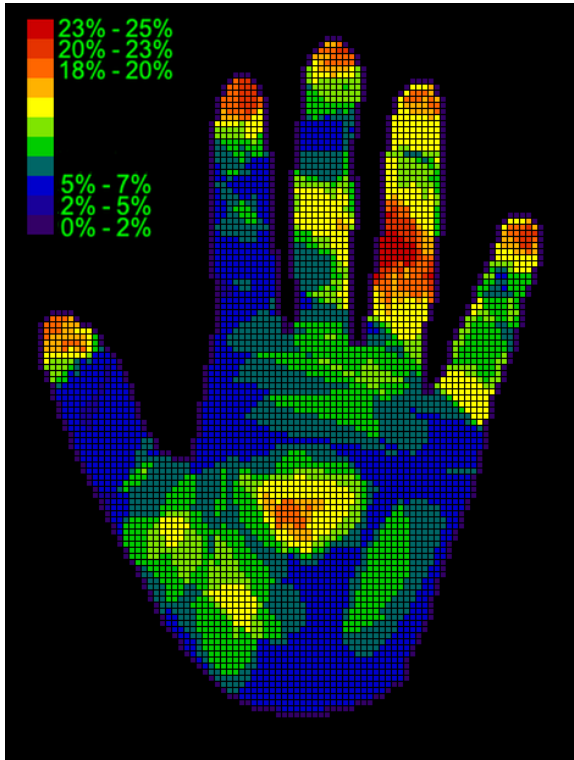
298 *2.4.1. The topography of SPS frequency*

299 This analysis was carried out to detect any significant effects in the spatial distribution of SPS
 300 as a function of TPJ-EBA and TPJ-AI functional connectivity. Maps filled by participants
 301 with shaded areas were projected on a 140 × 140mm grid, with a 1mm² resolution, and con-
 302 verted to binary code (0=nil, 1=shaded cell). As a result, two binary maps per participant (i.e.

303 right and left hand) were generated. A frequency map was obtained by superimposing these
304 maps, in which each cell value represented the percentage of participants having shaded it
305 (Figure 1). SPS were reported for the whole hand but were not distributed uniformly: Figure 1
306 shows the presence of a distal-to-proximal gradient in the frequency map [53], [54]. Computa-
307 tion of the relative spatial extent of sensations, i.e. the percentage of shaded cells within a
308 segment (distal phalanx, intermediate phalanx, proximal phalanx, and palm) in comparison to
309 the surface of the whole hand was carried out [54]. This analysis is based on the receptor den-
310 sity dispersion on the glabrous surface of the hand [78]. Relative surfaces were entered into an
311 analysis specific to proportions [79] with the anatomical segments as the unique factor. A
312 significant segment effect was found ($Q'(3) = 468.2$, $p < .000001$; Cramer's $V = .09$), with a
313 greater SPS surface in the distal phalanx (11.68%) than in the intermediate (11.03%) and in
314 the proximal (8.15%) phalanges, as well as in the palm (7.96%). This specific distribution is
315 consistent with previous studies investigating SPS [53], [54], [56], [57], [61], presumably
316 reflecting the distribution of peripheral receptive units and/or their trace within the soma-
317 tosensory cortex. This gradient suggests that the task was carried out successfully.

318

319 Figure 1: Topographic map of SPS frequency (% of participants having shaded a cell) using a
320 color scale: cool/blue colors reflect the least frequently shaded areas and hot/red colors the
321 most frequently shaded areas



322

323

324 2.4.2. Relationship between SPS frequency topography and functional connectivity

325 For each participant and each hand, a 140 x 140 mm grid identical to that used in the frequen-
 326 cy processing was completed with connectivity indices. This was carried out to achieve a cell-
 327 by-cell analysis between the SPS topography and the functional connectivity. Individual con-
 328 nectivity indexes of the left hemisphere of each participant were used to complete the map of
 329 the right hand and individual connectivity indexes of the right hemisphere of each participant
 330 were used to complete the map of the left hand. This way, 54 individual maps reflecting the
 331 SPS frequency were correlated with 54 individual maps completed with connectivity indices,
 332 using a point biserial cell-wise correlation. This was performed separately for TPJ-EBA and
 333 then TPJ-AI connection and was performed separately for each frequency band. The correla-
 334 tion maps obtained were then converted into binary maps (0=non-significant, 1=significant),
 335 for the application of a spatial scan procedure for binary data [80] consisting of a circular
 336 window that scans, detects, and localizes significant clusters in a step-wise fashion. This also
 337 makes it possible to reduce Type 1 errors. A maximum radius of 6 cells was chosen based on
 338 previous studies [54], [56]. After 999 runs of the Bernoulli (binomial) model, all detected and
 339 localized clusters were significant at least at the $p < .001$ level bicaudal. Figures 2 and 3 dis-
 340 play only those significant clusters for each connection.

341

342 *2.4.3. SPS frequency and TPJ-EBA connectivity*

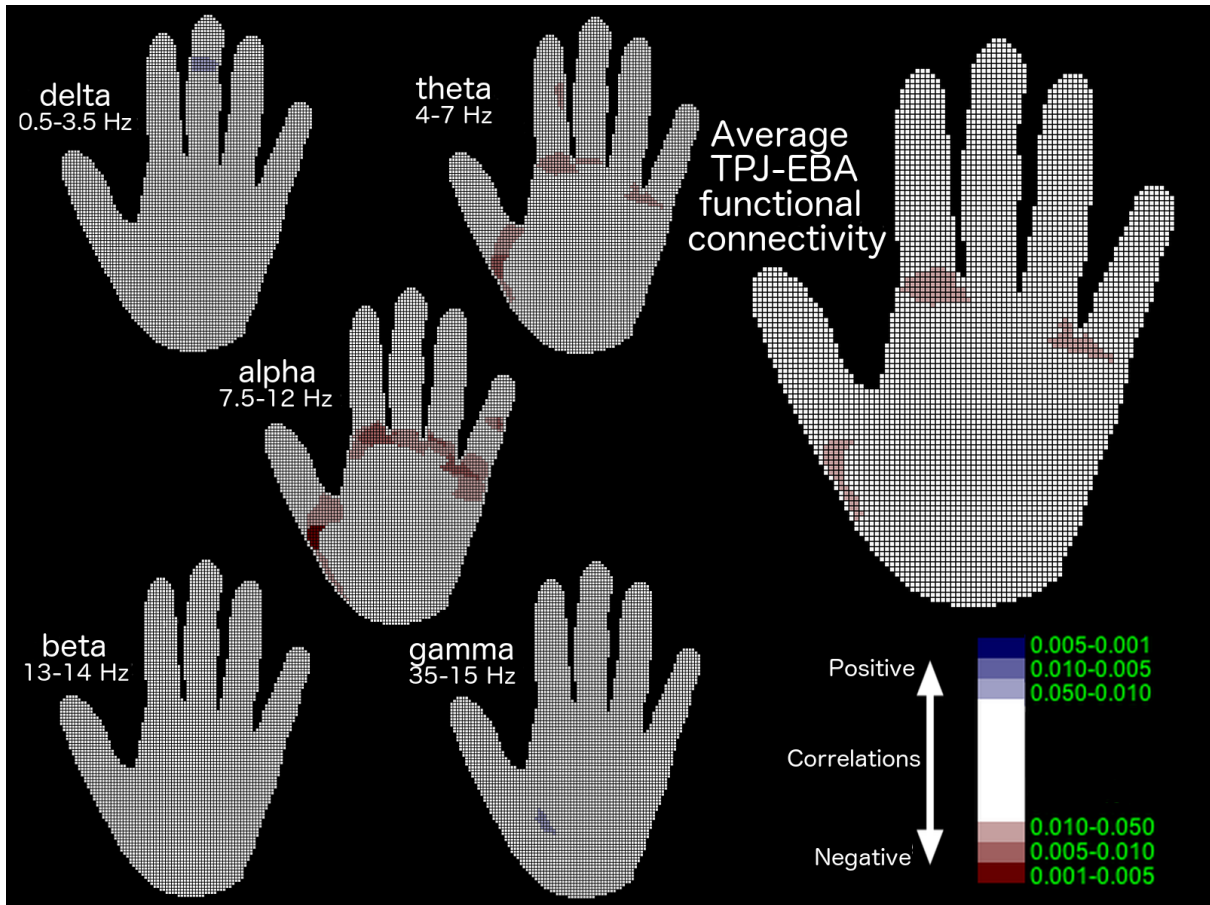
343 Reliability analysis performed on the indices of TPJ-EBA functional connectivity suggest
344 good to very good reliability, through a Cronbach's α at .83, a McDonald's ω at .80 and an
345 average interitem correlation $|\rho|$ at .43.

346 For the relationship between SPS frequency and TPJ-EBA connectivity (Figure 2),
347 positive significant correlations (bluish cells) were found covering a surface of 0.9% (95%
348 Wilson Confidence Interval [0.66%, 0.01%]) in the delta band and of 0.6% (95% CI [0.39%,
349 0.85%]) in the gamma band, and negative significant correlations (reddish cells) were found
350 covering a surface of 5.7% (95% CI [5.05%, 0.43%]) in the theta band and of 12.1% (95% CI
351 [11.16%, 13.10%]) in the alpha band. To process the relationship between the SPS frequency
352 and the functional connectivity for the average TPJ-EBA connectivity, i.e. independently of
353 frequency band influence, SPS frequency maps were correlated with the mean z -transformed
354 index of functional connectivity for TPJ-EBA connection in the manner described above. On-
355 ly negative correlations were found in an area covering 3.5% (95% CI [3.00%, 4.10%]) of the
356 hand.

357

358 Figure 2: Topographic probability maps of the correlations between SPS frequency and con-
359 nectivity index in the delta, theta, alpha, beta, and gamma bands for TPJ-EBA connectivity.
360 Bluish colors represent significant positive correlations and reddish colors represent signifi-
361 cant negative correlations. The color intensity denotes the significance level.

362



363

364

365 *2.4.4. SPS frequency and TPJ-AI connectivity*

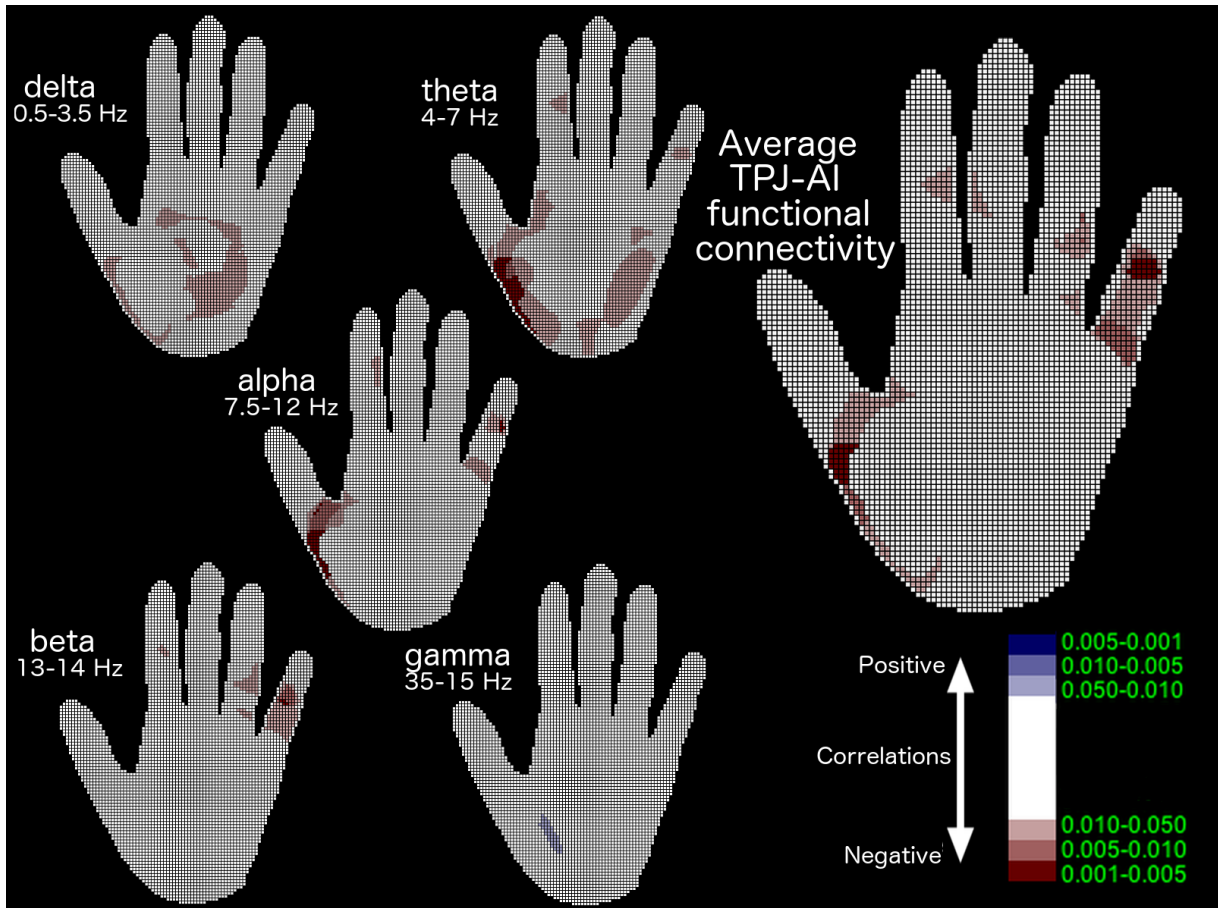
366 Reliability analysis performed on the indices of TPJ-AI functional connectivity suggest as
 367 well good to very good reliability, through a Cronbach's α at .77, a McDonald's ω at .80 and
 368 an average interitem correlation $|\rho|$ at .39.

369 For the relationship between SPS frequency and TPJ-AI connectivity (Figure 3), nega-
 370 tive correlations were mainly found in all frequencies, covering 10.8% (95% CI [9.91%,
 371 11.76%]) of the hand in the delta band, 19.4% (95% CI [18.24%, 20.59%]) in the theta band,
 372 6.5% (95% CI [5.81%, 7.28%]) in the alpha band, and 4.4% (95% CI [3.84%, 5.06%]) in the
 373 beta band. Positive correlations were observed only in the gamma band, covering a surface of
 374 0.9% (95% CI [0.66%, 1.23%]). To process the relationship between the SPS frequency and
 375 the functional connectivity for TPJ-AI connection independently of frequency band influence,
 376 SPS frequency maps were correlated with the mean z-transformed index of functional connec-
 377 tivity for TPJ-AI connection in the manner described above. Only negative correlations were
 378 found in an area covering 9.6% (95% CI [8.76%, 10.52%]) of the hand.

379

380 Figure 3: Topographic probability maps of the correlations between SPS frequency and con-
381 nectivity index in the delta, theta, alpha, beta, and gamma bands for TPJ-AI connectivity. Blu-
382 ish colors represent significant positive correlations and reddish colors represent significant
383 negative correlations. The color intensity denotes the significance level.

384



385

386

387 2.4.5. TPJ-EBA and TPJ-AI correlations

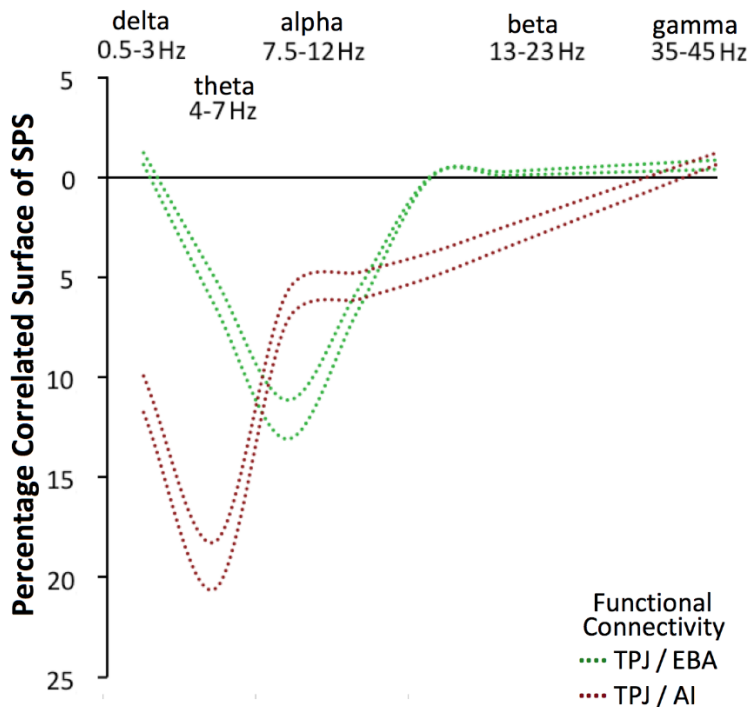
388 Surface percentages of significant correlations were analyzed using a Q' test (Figure 4) [79]
389 with the connectivity (TPJ-EBA vs TPJ-AI) and the frequency bands (delta, theta, alpha, beta,
390 and gamma) as factors. The main effect of connectivity was highly significant ($Q'(1) = 259$, p
391 $< .001$; Cramer's $V = .31$), with surfaces being overall larger for TPJ-AI connectivity than for
392 TPJ-EBA connectivity. The connectivity x frequency band interaction was also significant
393 ($Q'(4) = 816$, $p < .001$; Cramer's $V = .28$). Multiple corrected comparisons carried out with
394 the Q' test [79] revealed that surfaces were reliably larger in the TPJ-AI than in the TPJ-EBA

395 connectivity in the delta ($q' = 20.15$, $p < .001$), theta ($q' = 19.51$, $p < .001$), and beta ($q' =$
 396 14.07 , $p < .001$) bands, but an opposite pattern was observed in the alpha band where surfaces
 397 were larger for TPJ-EBA connectivity than for TPJ-AI connectivity ($q' = 9.05$, $p < .001$). Fi-
 398 nally, no differences were found in the gamma band ($q' = 1.82$, $p = .51$). The larger correlated
 399 surfaces for TPJ-AI connectivity were observed in the theta band, forming a kind of peak,
 400 whilst the larger correlated surfaces for TPJ-EBA connectivity were observed in the alpha
 401 band. It is in the latter case that TPJ-EBA connectivity surfaces were larger than for TPJ-AI
 402 connectivity.

403

404 Figure 4: Percentages of significant SPS surfaces correlated with each of the frequency bands,
 405 for TPJ-EBA and TPJ-AI connectivity, respectively. Values below 0 on the Y-axis represent
 406 percentages of negative correlations and above 0 represent percentages of positive correlations.
 407 The widths of the bands represent 95% confidence intervals. Positive values represent positive
 408 correlations, and negative values represent negative correlations.

409



410

411

412 Table 2: Mean (SD) of the parameters collected in the SPS task in both Experiments, other
 413 than spatial distribution.

	Experiment 1	Experiment 2
Spatial extent (%)	8.94 (10.67)	11.76 (10.53)
Spatial extent per area (%)	5.84 (10.28)	2.91 (3.33)
Intensity	2.76 (1.72)	3.49 (2.28)
Variety	2.41 (1.31)	2.53 (1.47)
Number of areas	4.11 (2.98)	4.65 (3.07)
Confidence in location	6.46 (2.63)	5.26 (2.53)
Confidence in extent	5.43 (2.44)	4.73(2.16)

414

415 2.4.6. Other parameters

416 Based on previous studies [56], other parameters of SPS, i.e. spatial extent, mean perceived
 417 intensity of SPS, confidence in location and in extent, number of areas, spatial extent per area
 418 and variety of SPS, were considered for analysis. **Analysis revealed good to very good reliability as suggested through the Cronbach's α at .78, the McDonald's ω at .83 and the average interitem correlation $|\rho|$ at .34.** The predictive value of the mean z -transformed index of functional connectivity for TPJ-EBA and TPJ-AI connections and of the self-reported ADCL measures (Mean score = 20.15 ± 3.39 , Min = 13, Max = 25) on each of these parameters was examined by mean of multiple regression analyses. Furthermore, age, gender, and BMI were also included as predictors since they are known to influence perception of SPS [54], [55]. The results (not Bonferroni-corrected [81], [82]) are presented in Table 3. We found that the mean z -transformed index of the TPJ-AI functional connectivity negatively predicted the spatial extent of the SPS ($\beta = -1.03$, SEM = .36, $t(18) = -2.83$, $p = .01$, $R^2 = .22$) and the spatial extent per area ($\beta = -.79$, SEM = .37, $t(18) = -2.14$, $p = .05$, $R^2 = .19$). The scores in the General Activation sub-scale of the ADCL negatively predicted the intensity of SPS ($\beta = -.54$, SEM = .21, $t(18) = -2.58$, $p = .02$, $R^2 = .24$) and participants' confidence in the location of SPS ($\beta = -.51$, SEM = .22, $t(18) = -2.30$, $p = .03$, $R^2 = .13$). Finally, body mass index (BMI) negatively predicted the spatial extent per area ($\beta = .47$, SEM = .19, $t(18) = -2.50$, $p = .02$, $R^2 = .19$).

435 Table 3: Standardized β coefficients (1 SEM) and adjusted R^2 coefficient from the multiple
 436 regression analysis carried out on each of the 7 collected dependent variables with age, gen-
 437 der, body mass index, mean z-transformed connectivity index for TPJ-EBA and TPJ-AI con-
 438 nections, and scores for the General Activation, Calm and General Deactivation items of the
 439 ADCL as independent variables. Significant predictors at least at $p < .05$ are marked with an
 440 asterisk.

	Spatial extent	Spatial extent per area	Intensity	Variety	Number of areas	Confidence in location	Confidence in extent
Age	-.09 (.21)	-.13 (.21)	-.32 (.21)	-.18 (.28)	.06 (.24)	.21 (.22)	-.08 (.24)
Gender	-.07 (.23)	-.22 (.24)	.09 (.23)	.04 (.31)	-.18 (.26)	.01 (.25)	.07 (.26)
BMI	.38 (.18) ^o	.47 (.19)*	.00 (.17)	.17 (.24)	-.01 (.20)	.16 (.20)	-.04 (.20)
TPJ-EBA connectivity	.56 (.35)	.35 (.36)	-.01 (.36)	-.17 (.46)	-.26 (.39)	-.24 (.37)	-.29 (.39)
TPJ-AI connectivity	-1.03 (.36)*	-.79 (.37)*	-.24 (.36)	.02 (.47)	.03 (.41)	.15 (.38)	.15 (.40)
General Activation	.02 (.21)	.02 (.21)	-.54 (.21)*	-.15 (.27)	-.48 (.23)	-.51 (.22)*	-.48 (.23)
Calm	.16 (.19)	.14 (.19)	.28 (.19)	.03 (.25)	.29 (.21)	-.06 (.20)	-.24 (.21)
General Deactivation	-.09 (.19)	-.06 (.19)	.00 (.18)	-.09 (.25)	-.18 (.21)	-.01 (.20)	-.26 (.21)
Adj. R^2	.22	.19	.24	-.33	.02	.13	.03

441

442 2.4.7. Types of sensations

443 All SPS types were reported at least once and some participants even reported other types of
 444 sensations, such as pins and needles, weightiness, and compression. Types of reported SPS
 445 were clustered in five categories based on previous studies [83], [84]: thermal (warming and
 446 cooling), deep (beat/pulse and muscle tension), paresis-like (numbness and weightiness), sur-
 447 face (tickle, stretch, tingling, flatter, vibration, and compression), and pain-like (pins and nee-
 448 dles and itch). SPS types were not clustered uniformly among these five categories ($\chi^2(4) =$
 449 84.95 , $p < .001$, **Cramer's $V = .42$**). Surface types of SPS were most likely to be perceived and
 450 reported (51.72%), followed by deep (20.69%), thermal (14.66%), paresis-like (12.07%), and
 451 then pain-like sensations (0.86%). Each of the five categories of sensations as well as the sum

452 of SPS reported were submitted to multiple regression analyses (not Bonferroni-corrected
453 [81], [82]) with the same predictors as before. No significant effect was observed.

454

455 Based on previous literature, the TPJ, EBA, and AI **would** play a role in the emergence of
456 self-awareness, **by contributing** either in embodiment [19], [85], or **in** the emergence of the
457 "material me" [29]. However, those areas were also associated with high arousal [6] and
458 **would** be strongly connected to attentional networks [7], [86]. For these reasons, SPS were
459 studied in association with at-rest functional connectivity between the TPJ and the AI, and
460 between the TPJ and the EBA, along with a questionnaire investigating self-reported trait
461 arousal.

462 The first finding of this study was that, independently of frequency bands, the func-
463 tional connectivity of the TPJ was negatively associated with the propensity of perceiving
464 SPS. Exhibiting stronger functional connectivity is associated with decreased perception of
465 SPS.

466 The second finding was a distinction between TPJ-AI and TPJ-EBA connectivities.
467 Indeed, TPJ-AI connectivity correlated with larger surfaces than TPJ-EBA connectivity and
468 also predicted the SPS total surface and surface per area. Moreover, a dissociation **appeared**
469 since the TPJ-AI dominated over the theta band whilst TPJ-EBA dominated over the alpha
470 band. The last finding of this experiment was that non-topographic SPS parameters, such as
471 intensity, confidence in location, were negatively predicted by self-reported General Activa-
472 tion. Taken altogether, the results of Experiment 1 intimate that processes reflected in the
473 TPJ-AI and TPJ-EBA connectivities, as well as self-reported trait arousal, would play a rather
474 inhibitory role in **the** perception of SPS.

475 Nonetheless, the arousal indices chosen in this experiment were declarative and direct,
476 i.e. the list of adjectives was explicitly related to arousal, and this may have led to desirability
477 bias. This may constitute a methodological flaw. The possibility of regression results stem-
478 ming from desirability bias and common methodology variance needs to be ruled out. For this
479 reason, we propose the use of a direct physiological index of arousal, i.e. skin conductance
480 level (SCL). To our knowledge, only a single study investigated the association between SPS
481 perception and arousal through physiological parameters and found no link between them
482 [87]. However, Tihanyi and Köteles [87] used a different method to investigate the perception
483 of SPS, in which SPS topography was not explored. We further propose to use an indirect and

484 non-explicit declarative measure of arousal, through reporting of inner speech presence. Ac-
485 cording to Alderson-Day and Fernyhough [88], inner speech or self-talk is "a subjective expe-
486 rience of language in the absence of overt and audible articulation" (p.931). It is a demanding
487 sustained cognitive activity, and as such, it increases stress and autonomic arousal as demon-
488 strated through changes in breathing patterns and electromyography [89], [90]. The general
489 hypothesis is that SCL and inner speech, as parameters of arousal, would be negatively asso-
490 ciated with SPS perception.

491

492 **3. Experiment 2**

493 *3.1. Participants*

494 A different sample from the one used in Experiment 1 was tested here. All participants were
495 students at the University of Franche-Comté (Eastern France) participating in psychology
496 teaching programs. **Based on** the criteria listed in Experiment 1, the study included a total of
497 26 participants (19 female, 7 males; 23 right-handed subjects) with a mean age of 21.9 ± 2.8
498 (age range: 20 to 33), and a mean body mass index of $21.5 \pm 2.7 \text{ kg/m}^2$ (range: 17.5 to 30.1
499 kg/m^2). All gave their informed written consent to participate **before** the test. **With a sample of**
500 **26 participants (i.e., 52 hand maps) there is enough power (90%) to diminish Type II errors.**

501

502 *3.2. Materials*

503 *3.2.1. Electrodermal recording at rest*

504 Participants were seated in a comfortable armchair in a quiet room (room temperature ranged
505 from 20 to 22°C). Electrodermal activity was recorded using the BIOPAC System MP150
506 module and a GSR100C Amplifier with a sampling rate of 1000 Hz. Disposable Ag/AgCl
507 electrodes (EL509) were attached to the palmar surface of the medial phalanges of the index
508 and middle fingers of the non-dominant hand (all BIOPAC Systems, Inc., CA). Once the elec-
509 trodes had been fitted, a 15-minute rest period was observed before the recordings began to
510 allow the electrode gel to diffuse and to establish good baseline conductivity. Participants
511 were then required to put on headphones and a sleep mask to minimize any sensory input in-
512 terference. Participants then were asked to relax during the recording session and to avoid any
513 movements and any irregular or deep breaths. The at-rest electrodermal activity recording
514 started and lasted 5 minutes. An experimenter was present in the room at a distance from the

515 participant to record any movements and deep breaths of the participant liable to produce un-
516 wanted electrodermal responses. Data were analyzed offline using AcqKnowledge 4.2 soft-
517 ware (BIOPAC Systems, Inc., CA). A low-pass filter with a cut-off frequency of 0.05 Hz was
518 applied. The SCL (μS) was computed as the mean value of skin conductance measured during
519 the 5-minute resting phase.

520

521 3.2.2. *Inner speech*

522 At the end of the at-rest electrodermal recording session, participants received a single ques-
523 tion on inner speech, inspired by Nikula [37]: "How present was an inner speech in your
524 thoughts during the recordings?" (French, *À quel degré le langage interne était-il présent*
525 *dans vos pensées pendant les enregistrements ?*). The question was presented on a sheet of
526 paper and participants were required to respond using a 5-point Likert scale (0 = not much; 5
527 = a lot). Even though some full questionnaires on inner speech exist, they are suspected to
528 have limited validity [91]. For this reason, a single straight-forward question on the presence
529 of inner speech was preferred here, which had already been shown to correlate with electro-
530 dermal activity [37].

531

532 3.2.3. *SPS task*

533 The task was strictly identical to that described in 2.2.3. Each participant completed an SPS
534 task 1 to 3 weeks after the electrodermal recording session. This variable delay was mostly
535 due to organizational reasons and separating the two sessions in time would avoid contamina-
536 tion between them. The SPS task was performed in a quiet room with an ambient temperature
537 of 20 to 23°C.

538

539 3.3. *Results*

540 3.3.1. *Skin conductance level*

541 The SCL level ranged from 2.06 to 31.1 μS , and the mean was $15.9 \pm 7.77 \mu\text{S}$. No reliable
542 difference was found between men ($14.8 \pm 6.7 \mu\text{S}$) and women ($16.3 \pm 8.3 \mu\text{S}$, $t(24) = .43$, $p >$
543 $.67$).

544

545 3.3.2. *Inner speech*

546 The mean rating of inner speech was 2.85 (SD = 1.3), ranging from 1 to 5. Interestingly, yet
547 in keeping with the extant literature [37], inner speech correlated positively with the mean
548 SCL ($r(24) = .40, p < .05$), suggesting that the greater the presence of inner speech, the higher
549 the arousal.

550

551 3.3.3. *SPS*

552 3.3.3.1. *The topography of SPS frequency*

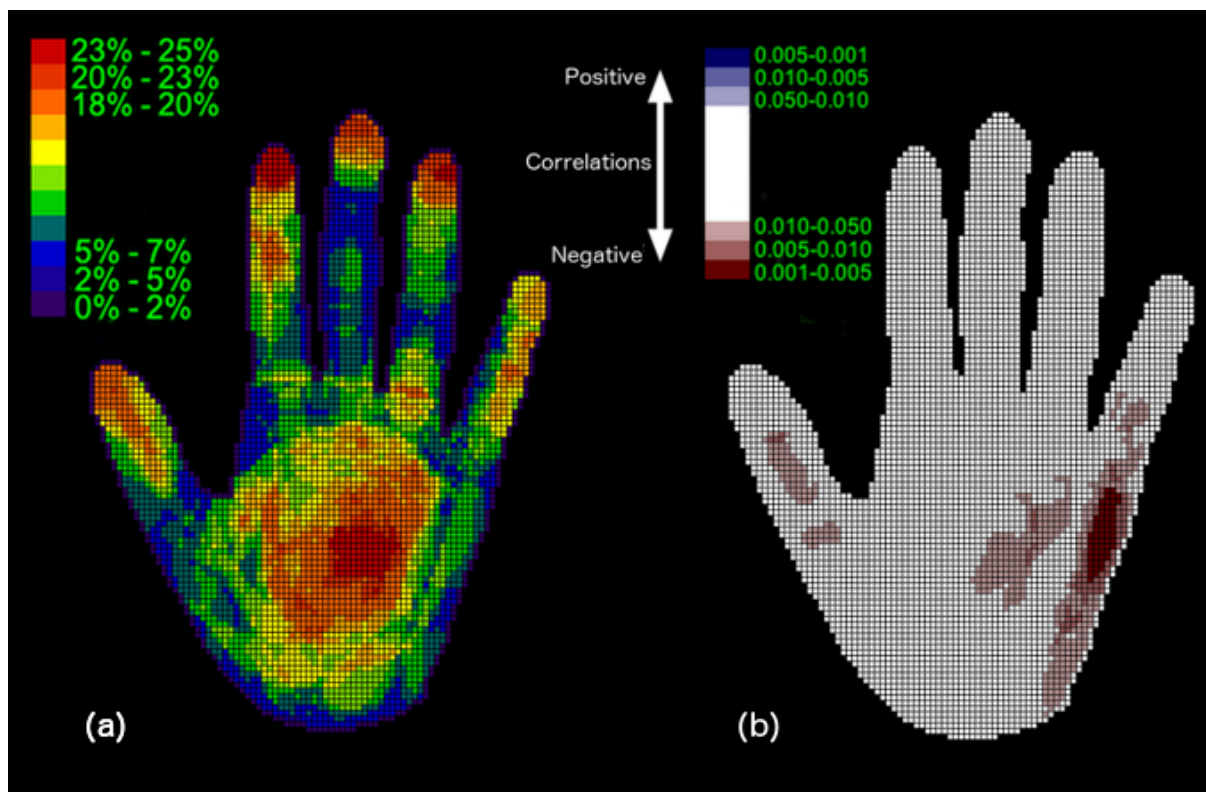
553 The same analyses described in 2.4.1 were conducted. The frequency map (Figure 5) reveals a
554 typical distal-to-proximal distribution of SPS [53], [54] with higher frequencies over the fin-
555 gertips and the center of the palm. Topographical statistics were compiled using point biserial
556 cell-wise correlation between the presence of SPS and the mean z-transformed SCL. The sig-
557 nificance maps were then submitted to the spatial scan procedure for binary data to isolate
558 those clusters that reached the $p < .001$ level. Only negative correlations were found between
559 the mean SCL level and the presence of the SPS. They covered an area of 13.4% (95% CI
560 [11.51%, 13.48%]) of the hand (Figure 5).

561

562 Figure 5: Topographic maps. Left. Frequency map of SPS frequency (%) through a heat scale,
563 cool/blue colors reflecting least frequently reported areas, and hot/red colors most frequently
564 reported areas. Right. Probability map representing the correlations between SPS frequency
565 and SCL. Bluish colors represent positive correlations and reddish colors represent negative
566 correlations. The color intensity depends on the significance level.

567

568



569

570

571 3.3.3.2. Other parameters

572 Regression analyses were carried out in order to understand whether the mean SCL predicted
 573 SPS parameters, i.e. overall spatial extent, spatial extent per area, intensity, variety, number of
 574 areas, confidence in location, and confidence in extent. **Once again, analysis revealed good to**
 575 **very good reliability as suggested through a Cronbach's α at .85, the McDonald's ω at .85**
 576 **and the average interitem correlation $|\rho|$ at .39.** Age, gender, body mass index, average and
 577 scores in the inner speech question (Mean = 2.65 ± 1.49 , Min = 0, Max = 5) were also includ-
 578 ed in the analyses as independent variables. The results (not Bonferroni-corrected [81], [82])
 579 are presented in Table 4. We found that the average SCL significantly and negatively predict-
 580 ed the variety of SPS ($\beta = -.43$, SEM = .19, $t(20) = -2.25$, $p = .04$, $R^2 = .30$) as well as partici-
 581 pants' confidence in location ($\beta = -.46$, SEM = .22, $t(20) = -2.09$, $p = .05$, $R^2 = .06$). Mean-
 582 while, inner speech significantly and positively predicted the variety of SPS ($\beta = .55$, SEM =
 583 .20, $t(20) = 2.83$, $p = .01$, $R^2 = .30$). The gender of our participants also predicted significantly
 584 but negatively the variety of SPS ($\beta = -.43$, SEM = .17, $t(20) = -2.50$, $p = .02$, $R^2 = .30$),
 585 meaning that women reported a greater variety of SPS than men. Finally, participants' age
 586 significantly and positively predicted the SPS intensity ($\beta = .53$, SEM = .20, $t(20) = 2.60$, $p =$
 587 **.02**, $R^2 = .11$).

589 Table 4: Standardized β coefficients (1 SEM) and adjusted R^2 coefficient from the multiple
 590 regression analysis carried out on each of the seven collected dependent variables with age,
 591 gender, body mass index, average skin conductance level, and scores for the inner speech
 592 question as independent variables. Significant predictors at least at $p < .05$ are marked with an
 593 asterisk.

	Spatial extent	Spatial extent per area	Intensity	Variety	Number of areas	Confidence in location	Confidence in extent
Age	.01 (.25)	-.06 (.21)	.53 (.20)*	-.08 (.18)	.06 (.22)	.36 (.21)	.36 (.22)
Gender	-.06 (.22)	-.27 (.20)	.03 (.19)	-.43 (.17)*	.00 (.22)	-.06 (.20)	.01 (.20)
BMI	.05 (.23)	-.13 (.21)	.20 (.20)	.07 (.18)	.23 (.22)	.23 (.21)	.18 (.22)
Average SCL	-.30 (.24)	-.13 (.23)	-.31 (.22)	-.43 (.19)*	-.41 (.23)	-.46 (.22)*	-.30 (.23)
Inner Speech	.01 (.25)	-.22 (.23)	-.11 (.22)	.55 (.20)*	.23 (.23)	.00 (.20)	-.05 (.24)
Adjusted R^2	-.15	.02	.11	.30	-.01	.06	-.05

594

595 3.3.3.3. Types of sensations

596 All 11 sensations were reported at least once, and one participant added pins and needles to
 597 the list. Since they probably reflect different underlying mechanisms, sensations were clus-
 598 tered in the same distinct categories as in Experiment 1. SPS types were not clustered uni-
 599 formly among these five categories ($\chi^2(4) = 51.83$; $p < .001$, **Cramer's $V = .31$**). Surface tac-
 600 tile/mechanical sensations were most frequently reported by participants (38.8%), followed by
 601 thermal (27.34%), deep internal (16.5%), and paresis-like sensations (14.39%). Pain-like sen-
 602 sations were those least reported (2.9%). Each of the five categories of sensations as well as
 603 the sum of SPS reported were submitted to multiple regression analyses (not Bonferroni-
 604 corrected [81], [82]) with the same predictors as before. The mean SCL significantly predict-
 605 ed internal sensations, and this prediction was negative ($\beta = -.49$, $SEM = .23$, $t(20) = -2.17$, **p**
 606 **$= .04$** , $R^2 = .01$).

607

608 Experiment 2 was conducted to better acknowledge the association between arousal and the
 609 perception of SPS. Experiment 2 focused on a direct parameter of arousal, i.e. average SCL,

610 as well as a self-reported and indirect parameter, i.e. inner speech, which **was** linked with
611 arousal. This relationship between arousal and inner speech was confirmed here. In line with
612 the first study, we hypothesized that these parameters would be negatively associated with
613 SPS perception.

614 As a first finding, we observed that SCL correlated negatively with SPS frequency and
615 negatively predicted SPS parameters, such as variety and **participants'** confidence in **the** loca-
616 tion. **The skin** conductance level also negatively predicted deep/internal sensations. These
617 results corroborate the hypothesis formulated earlier that arousal would exert primarily an
618 inhibitory influence on SPS perception. Nevertheless, **the** self-reported inner speech seems to
619 facilitate the perception of SPS variety, but this relationship results only when gender and
620 inhibitory influence of SCL are taken into account simultaneously.

621

622 **4. Discussion**

623 As part of the background of bodily sensations, SPS would allow the experiencing self to
624 come to the fore by focusing attention on body representation [1], [57]. Which factors con-
625 tribute to SPS perception and therefore to the emergence of body awareness? Evidence sug-
626 gests that SPS **depend** on **self-focus** [57]. Also, directing attention away from the body de-
627 creases SPS [53], [54], [56]. In this paper, we proposed to investigate how neuronal networks
628 reflecting attentional focus and self-referential processes, i.e. TPJ functional connectivity with
629 EBA and with AI, were associated with SPS perception. **Besides, because** these two networks
630 were associated with arousal, we investigated further how arousal was associated with SPS
631 perception.

632 For the greatest interest of the reader, to present a clear and comprehensive discussion
633 of the numerous data obtained, we will first focus on the results concerning arousal, and will
634 then develop the results concerning brain networks.

635

636 *4.1.SPS and Arousal*

637 Arousal has been investigated with the use of three indices: SCL, a self-reported arousal trait
638 measure, and inner speech. We found that SCL correlated negatively with SPS frequency. It
639 also negatively predicted the variety of SPS and participants' confidence in their location.
640 Increased self-reported arousal trait predicted lower intensities of SPS and weaker confidence

641 in their location. Finally, a greater presence of inner speech positively predicted the variety of
642 SPS, but in interaction with gender and SCL. **The** variety of SPS was greater for women with
643 a greater presence of inner speech and lower SCL. Inner speech is thought to be linked with
644 arousal as shown both in past research [37] and in the present study. Morin and Michaud [92]
645 suggested that inner speech would appear to be involved in the acquisition of self-
646 information, meaning that collecting information through **an** inner speech about oneself raises
647 the perception of various SPS, especially in women with low levels of arousal. All these data
648 are in agreement with our hypothesis that increased arousal would dampen the perception of
649 SPS. However, they also suggest that multiple other factors may determine the perception of
650 SPS.

651 Contrary to Tihanyi and Köteles [87], we found relationships between SPS and arousal
652 through SCL. This concerned the frequency of SPS perceived over the hand, as well as the
653 intensity of SPS through the self-reported arousal trait. This discrepancy might be explained
654 by the many differences identified in our protocol, such as (a) the use of topographical
655 measures that **have** proven to be sensitive to distinct cognitive processes [54], [56]; (b) the
656 lack of restrictions considering SPS variety resulting in a greater quantity of SPS taken into
657 account for our studies and not focusing on specific SPS; (c) the time spent focusing followed
658 by **an** immediate recall of the **participant's** perception ensuring a low impact of visuospatial
659 short-term memory, and enabling participants to perceive and report numerous and detailed
660 SPS [55]. According to the extant literature, arousal indexes readiness to respond to environ-
661 mental stimuli [60]. Attention **to** the environment results in focus away from the body and the
662 self. In this regard, diverted attention may suppress SPS [53]–[55] while self-focused atten-
663 tion increases interoceptive processes and results in **a** heightened perception of SPS [56]. Al-
664 so, abnormally enhanced interoception results in **an** abnormally enhanced perception of SPS
665 [61].

666 Another line of evidence suggests that high arousal reliably predicts spontaneous brain
667 activity, in that a subject with high arousal levels would show decreased activation of the
668 brain network involved in self-referential processes [6], i.e. the default mode network. Indeed,
669 previous findings showed that SPS frequency, intensity, and participants' confidence in loca-
670 tion, were greater with increased propensity to mind wandering [57], a cognitive activity as-
671 sociated with the default mode network [93], [94]. These findings are consistent overall with
672 the suggestion that activity in the default mode network allows better perception of SPS, and
673 therefore increases self-awareness [57]. Also, decreased activity of the default mode network

674 associated with increased attention away from the body dampens perception of SPS and there-
675 fore decreases self-awareness. These observations tally well with the idea that attention di-
676 rected to and maintained on the self is a necessary condition for the development of self-
677 awareness [1], [95].

678

679 *4.2.SPS and brain networks involved in self-awareness*

680 Directing attention away from the self and toward the environment involves a network **that**
681 anticorrelates with the default mode network [59]. Among the key node structures of this at-
682 tention network are the TPJ and the AI, which have also been associated with embodiment
683 and self-location [15], [18]. Another area, independent of this network, has also been associ-
684 ated with embodiment, the EBA [18]. Both the EBA and the AI are functionally connected to
685 the TPJ [2], [7], [18]. However, belonging to the attention network or not suggests that these
686 connections might serve different functions, and therefore contribute differently to self-
687 awareness. We found that, independently of frequency bands, increased TPJ-EBA functional
688 connectivity was associated with lower perceived frequency of SPS. In turn, high TPJ-AI
689 functional connectivity was associated with lower SPS frequency, smaller spatial extent, and
690 smaller surfaces per sensitive area. These results are consistent overall with our findings link-
691 ing high arousal with lowered SPS perception. Indeed, TPJ and AI activation **are** associated
692 with high arousal [6]. Moreover, the TPJ and AI are part of the ventral attention network,
693 whose activity has been closely linked with arousal through the locus coeruleus noradrenergic
694 system [36], [50]. Greater connectivity among areas of this network would dampen the per-
695 ception of SPS. Attention directed away from the body suppresses SPS [53]–[55]. Neverthe-
696 less, taken altogether, these findings indicate that high connectivity between the TPJ and
697 structures implicated in self-awareness experiences such as the AI or the EBA will impair the
698 perception of SPS. The TPJ **is** a multisensory integration hub [18], **as such** abnormal function-
699 ing of the TPJ would be associated with imperfect integration, resulting in disturbed self-
700 awareness and embodiment [18], [85], [96]. This would present as asomatognosia and auto-
701 scopic experiences, such as out-of-body experiences, autoscopia, feeling of presence, deper-
702 sonalization, failure of self-agency, etc. [20], [23], [97], [98]. In our study, high connectivity
703 between the TPJ and AI, and the TPJ and EBA, seems to be associated with a high propensity
704 to altered bodily experiences as SPS.

705 Closer inspection of the correlation patterns between functional connectivity and SPS
706 frequency revealed that the TPJ-AI dominated over the theta band whilst the TPJ-EBA domi-
707 nated over the alpha band. Distinct cognitive processes might be reflected by these two con-
708 nectivities. For instance, in an array of studies investigating neuropsychological performances
709 and EEG frequency bands, the alpha band has been linked to broad cognitive processes such
710 as attention and executive functions [46], [48], [49], [99], [100]. In particular, the alpha band
711 would appear to promote sustained attention by inhibiting irrelevant cognitive and sensory
712 processing [43], [46]. This tallies well with our interpretation of the TPJ-AI connectivity in-
713 fluence on the perception of SPS, and overall with the assumption that SPS are suppressed
714 when attention is directed away from the body. In turn, the theta band has been associated
715 with memory, but also attention and executive functions [41], [43], [45], [99], and would ra-
716 ther appear to reflect a global cognitive efficiency [44], [101], [102]. However, on another
717 line of evidence, the alpha and theta band taken altogether have been observed respectively
718 peaking in occipital and temporal regions with the elicitation of OBE [103]. This pattern of
719 activity would reflect self-altered experience, such as autoscopic illusions in this specific case,
720 and further, reinforce our interpretation of TPJ functional connectivity with the EBA and AI
721 as deleterious for self-awareness processing.

722 *4.3.Limitations and future directions*

723 The findings and interpretations presented in this study are sources of limitations that should
724 be taken into account. The main limitation of this study **lies in the interpretation of attentional**
725 **and self-related** cognitive processes related to TPJ functional connectivity **that would have an**
726 **impact on the perception of SPS**. Hence the lack of consensus in the literature regarding its
727 involvement in self-awareness and the evidence of functional dissociation within the same
728 area results in multiple possible interpretations. Nevertheless, these two studies provide a set
729 of quite consistent findings regarding arousal and bring new data considering the duality be-
730 tween attentional processes focusing **on** outwards and towards oneself [54]–[57]. Our inter-
731 pretation, considering the state of the literature, appears to be the most consistent to date. The
732 authors admit they did not directly investigate inward vs outward attention in the experiments
733 presented here, however, they do believe these studies, along with the literature concerning
734 SPS, contribute to a better understanding of this quite broad topic.

735 It is noteworthy to mention that, in Experiment 1, the resting-state task and the SPS
736 task were separated by a 45-minute computerized visuospatial task. **Separating** the resting task

737 and the SPS task by a third task reduces their contamination. However, some influence from
738 the visuospatial task might be observed, such as tiredness.

739 Concerning Experiment 2, the use of an inner speech questionnaire may be debated.
740 Inner speech is a solely subjective experience that cannot be assessed using measures other
741 than declarative ones. The question used here required participants to decide how, according
742 to their own experience of inner speech, it was present during the rest period, as there is no
743 example provided to determine what is "not much" or "a lot". This can be considered as unu-
744 usual since there is no external guideline to ensure an identical baseline across participants. Yet
745 this is also the way a wide variety of subjective measures are made within other contexts (i.e.,
746 perception of pain, perception of intensity, etc). It is a very common method that does not
747 invalidate the use of the questionnaire as inner speech. Inner speech is a matter of subjective
748 judgment and we set to investigate the relationship between self-referential processes and
749 their subtracts, which, by definition, depend on the perception of the self.

750 Finally, the association between arousal and SPS could only reflect superficial activity
751 limited to limbs and spontaneous receptor activity. Although it is not possible to exclude this
752 interpretation completely, the use of declarative indices shows the involvement of high-level
753 processes through arousal in the perception of SPS. The methodology used in these two stud-
754 ies allows a better grasp of the processes underpinning the perception of SPS. There is still
755 scope to investigate which neuronal connectivity is found during the perception of SPS, open-
756 ing a window to a better understanding of cognitive processing found within the background
757 of bodily sensation experience [1] and the emergence of the "material me" [28].

758

759 5. Conclusion

760 Our study aimed to investigate the links between self-awareness and brain networks divided
761 into body-awareness and attention processing. We indeed found that TPJ functional connec-
762 tivity with respectively the AI and the EBA, as well as arousal, was associated with decre-
763 menting SPS, a window to self-awareness. These findings indicate that the propensity to focus
764 attention outward would affect how self-aware we tend to be.

765

766 Acknowledgment

767 We would like to thank Marc Hoonakker for his precious help with the functional connectivi-
768 ty analysis. This research benefited from a Lumière Lyon 2 University doctoral grant (2018-
769 30) and funding support from the LABEX CORTEX of the Lyon University (ANR-11-
770 LABX-0042) under the "Investissements d'Avenir" program run by the French National Re-
771 search Agency (ANR-11-IDEX-0007).

772

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