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To the self and beyond: Arousal and functional connectivity of the temporo-parietal junction contributes to spontaneous sensations perception

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ABSTRACT

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

1. Introduction

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

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

The focus of this paper is placed deliberately on embodiment and

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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.

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

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

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

In this paper, we present two studies investigating how these factors, as individual traits, affect SPS perception. In the first study, we focused mainly on resting-state TPJ functional connectivity with the AI and EBA, as well as the self-reported propensity to high arousal. As we have an interest in the role of cortical oscillations, we used EEG. In the second study, we investigated the question of arousal further through resting-state electrodermal activity. Specifically, we used skin conductance level (SCL), since it reflects tonic components of autonomic arousal and qualifies as a physiological trait of arousal [60]. We hypothesized that, since arousal relates closely to attention [35,36], the propensity to high arousal would be associated with decreased perceived frequency of SPS. Given that the literature remains inconsistent regarding how functional connections in the brain, arousal, and self-referential processes interrelate, we can formulate the general hypothesis that functional connectivity of the TPJ with both the AI and EBA would be related to the perception of SPS. We might expect this relationship to translate primarily in low oscillations (i.e. delta, theta, and alpha), based on the assumption that those oscillations would reflect attentional processes involved in SPS perception.

2. Experiment 1

2.1. Participants

The study followed the Helsinki Declaration and the protocol was approved by the local ethics committee (reference number IRB 00,009,118). Participants were students at the Lumière University in Lyon, France. During the first steps of the experimental procedure, they completed a form containing questions on sociodemographic and health characteristics. Items included age, gender, height, weight, use of psychotropic medication (and if so, the reason why; antidepressants, anxiolytics, neuroleptics, anticonvulsants, hypnotics, tranquilizers, etc.), regular use of other psychoactive substances (alcohol, marijuana, etc.), and history of cardiovascular diseases or diabetes mellitus. Besides, participants could report any other information they considered to be of importance for the study. Any report of a history of neurological or psychiatric illness or psychoactive substance abuse or any disease that may affect tactile perception, such as diabetes mellitus or cardiovascular disease, led to exclusion. Thirty-eight volunteers participated in the study, ten were excluded based on the above-mentioned criteria, and one because of recording issues compromising the EEG data. Twenty-seven participants (14 female and 13 male), all right-handed, with a mean age of 22.1 ± 2.77 (age range: 19–28), and a mean body mass index of 21.2 ± 1.33 kg/m^2 (range: 19.26–23.89 kg/m^2) were therefore included in the study. All gave their written informed consent to participate before the test.

Power analyses were conducted on the effect size of the proximo-to-distal gradient in the frequency of SPS, which is the most prominent characteristic of these phenomena. Based on published studies [53,61], the weighted average effect size expressed as Cohen's w is 0.52 (i.e., large) and expressed as Cramers's V is 0.26 (i.e., medium to large). Provided a power of 90 % to detect a similar medium effect size and an alpha at 0.05, the number of hand maps needed is 53. Given that, in the present study, two hand maps per participant are collected (one per hand), the sample size needed is 27 participants. With a sample of 27 participants (i.e., 54 hand maps) there is enough power (91 %) to diminish Type II errors.

2.2. Materials

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

To assess a declarative measure, the propensity (trait) to arousal, participants completed a French trait version of the Activation/Deactivation Check-List (ADCL) [62,63]. It measures the activation (i.e. being actively involved in the processing of the environment) and deactivation (i.e. being prone to sleep or rest) states and was chosen because of its test-retest reliability (ranging from rho = .57 to rho = .87) and validity (correlation with psychophysiological measures of arousal ranging from rho = .43 to rho = .68). Participants must determine, for a list of 49 adjective-items, whether or not each one describes their usual functioning. Among the list of items, 27 adjectives are fillers. They had to rate each item on a 5-point Likert Scale (1=Never; 5=Very often) while taking into account the basic instruction "Usually, daily, I am:". Three main components are evaluated: General Activation (example of items: energetic, full-of-pep, active), Calm (example of items: placid, calm, still), and General Deactivation (example of items: leisurely, sleepy, tired). High scores in those components would reflect a higher propensity to General Activation, Calm, and General Deactivation. The internal consistency for our sample, as assessed through the mean inter-item correlation was good since all values exceeded the conventional threshold of |ρ| 0.15 [64]: General Activation 0.61, Calm 0.62, and General Deactivation 0.27.

2.2.2. *Resting-state EEG*

A resting-state EEG recording was performed immediately after the completion of the questionnaire. Participants were seated comfortably in front of a computer monitor in a recording booth, fitted with the electroencephalographical equipment. An EEG ACTi Champ with active electrodes was used for this experiment. A total of 64 channel electrodes, arranged based on the revised 10/20 system [65], and 5 EOGs were used. Two EOGs were placed horizontally, on each cheekbone, and two vertically above and under the left eye to monitor blinking or eye movement. A monopolar set-up was chosen, with a reference EOG on the nose bridge. Impedances were kept below 20kΩ. Once the EEG equipment was set up, the signal quality was tested asking participants to move their eyes left to right, to blink, and to clench their jaw muscles. Then, instructions were displayed in white font on a black background. Instructions advised the participants to relax their jaw and shoulders, to try not to move, to fully relax, to close their eyes, and to resist sleepiness. To prevent any external distractions leading to an eye-opening, the light in the room was dimmed, and the screen went off when the resting session was started. The session began once the participants stated that they were ready, and the end was announced by the experimenter. The recording session lasted 3 min. At the end of the recording session, participants were asked whether they had fallen asleep. No participants reported having fallen asleep during the resting session.

2.2.3. *SPS task*

Participants completed the SPS task 45 min after the resting-state EEG recording. In the meantime, participants performed a distractive visuo-spatial task. This delay allowed a clear dissociation between the resting-state recording and the SPS task. Electrodes and EOGs were removed from the participants' heads. They were then seated in a quiet and normally lit room with an ambient temperature of 20−23 °C, in front of a desk. Once they were ready, SPS were introduced as normal phenomena, and to give participants some idea of what they could associate with SPS, a list of 11 sensations most likely to be felt was presented (beat/pulse, itch, tickle, numbness, skin stretch, tingling, warming, cooling, muscle stiffness, flutter, and vibration). The list used in the SPS protocol is based on the one used originally by Macefield and colleagues [66] and Ochoa and Torebjörk [67] to study microstimulation-evoked sensations, and then adapted by Naveteur and colleagues [68] to study SPS. Participants were then instructed to remove any jewelry from their hands and wrists and to roll up their sleeves if they were long enough to cover the wrist. For 15 s, they were instructed to cleanse their hands with an antiseptic gel (Aniosgel® 85 NPC, ≈3 mL per participant), to remove any external surface agents that could interfere with the task, and to ensure a homogenous glabrous skin surface across all participants. A 15 s latency was observed between the cleansing operation and the start of the test. Each participant was given a protocol containing the standardized reduced maps of each hand shown palm up (with a distance of 11.2 cm between the tip of the middle finger and the palm/wrist frontier), and below each map, the list of 11 SPS and two visual analog scales (i.e. two 10 cm continuous horizontal lines without markers at each end) for confidence ratings, along with a pencil and a 25 × 25 cm piece of smooth white fabric. Once participants were familiarized with the material, the start of the test session was announced. The protocol and the pencil were placed away from the participants on the desk to prevent any interference from visual stimuli. Each hand was tested once in a balanced order across participants. They were instructed to sit with their back supported by the backrest of their chair. The leg ipsilateral to the tested hand was turned outward by about 60 degrees from the midline. Participants placed the white fabric cotton fabric on their thigh, with the tested hand resting on it, palm up with fingers spaced slightly apart. Only a dorsal part of the hand was in contact with the fabric, apart from the fingers. The hand not being tested hung down on the outer side of the chair contralateral to the tested hand. When the "start" signal was given verbally by the experimenter, marking the start of each trial, participants gazed at their tested hand for 10 s, focusing their attention on the hand so that they could detect any sensations that might occur. They were informed beforehand that there was a possibility that they would perceive no sensation. A "stop" signal given by the experimenter marked the end of the 10 s period. Participants were immediately asked to report on the protocol whether they had detected any sensations on the tested hand or not and if they had, to (a) map the extent and location of the sensations by shading the areas where they perceived sensations on the map of the tested hands; (b) specify the perceived intensity of each sensation according to a 10 point scale (1 = just perceptible; 10 = very intense but not painful) directly on the map; (c) indicate their degree of confidence in the location and the extent of the perceived sensations according to the two visual analog scales (ranging from "not confident" to "very confident"), and (d) identify the sensations with the list of descriptors. They had the option to choose more than one descriptor and to add descriptors to the list according to what they had detected. The task lasted approximately 15 min.

2.3. *Data processing*

2.3.1. *EEG preprocessing*

The EEG data preprocessing was conducted with BrainVision Analyzer 2.1. To ensure a quality signal was processed, a passband of 0.2−120 Hz was first applied, with a 50 Hz notch, and bad electrode signals removed and replaced by the mean signal of the three nearest electrodes. On average, 2.37 ± 0.47 electrodes signals were replaced (up to 8 electrodes) and those most removed from the signal were FP1, FP2 (11 participants), FT9, TP10 (9 participants), FT10 (8 participants), and TP9 (7 participants). Those least removed were F2, POz, T8 (only one participant per electrode), and T7 (4 participants). An ocular correction with the Gratton & Coles algorithm [69], based on the left horizontal EOG and the below-eye vertical EOG, was applied, subtracting the ocular movement from the signal. For each participant, the 3-minute recording was divided into 90 epochs of 2 s, according to the processing used by Chen and colleagues [70] when studying resting-state EEG data. To ensure no evoked response was triggered by the instruction to close the eye, the first 5 epochs were removed [71]. An artifact rejection, with a maximum amplitude of 80μV [70] was carried out on these epochs, resulting in a rejection rate of 12.5 % epochs. A mean of 74.41 ± 12.45 epochs, ranging from 38 to 85 per participant, was obtained.

2.3.2. *Functional connectivity analysis*

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

The artifact-free epochs were analyzed to estimate the current density for five frequency bands: delta (0.5–3.5hz), theta (4−7hz), alpha (7.5−12hz), beta (13−34hz), and gamma (35−45hz). We seeded three areas forming two connections: the TPJ and EBA connectivity, and the TPJ and AI connectivity, considering only ipsilateral connectivity for both hemispheres. Regions of interest (ROI) in both left and right hemispheres were constructed with the eLORETA given MNI coordinates for the TPJ (54, -48, 7) [18], the EBA (48, -67, 3) [18] and the AI (32, 12, 20) [77]. A voxel-wise approach was applied and lagged phase synchronization, indexing the physiological lagged connectivity [72] was used to measure the functional connectivity between the TPJ and EBA first, followed by the TPJ and AI. These analyses resulted in connectivity indices for each frequency band, the value of which ranged from 0 to 1 (the greater the value, the stronger the connection; Table 1), and this was performed independently for the TPJ-EBA connection and the TPJ-AI connection in each hemisphere. Considering no hypothesis regarding the hemispheric location has been presented in this study, we used only mean indices of the right and left hemisphere functional connectivity. Due to scale differences between the connectivities of each frequency band, the indices were z-transformed for homogenization purposes. The z-transform also allowed a mean to be computed across all frequency bands for the TPJ-EBA connection and TPJ-AI connection separately.

2.4. Results and discussion

2.4.1. The topography of SPS frequency

This analysis was carried out to detect any significant effects in the spatial distribution of SPS as a function of TPJ-EBA and TPJ-AI functional connectivity. Maps filled by participants with shaded areas were projected on a 140 × 140 mm grid, with a 1mm^2 resolution, and converted to binary code (0=nil, 1=shaded cell). As a result, two binary maps per participant (i.e. right and left hand) were generated. A frequency map was obtained by superimposing these maps, in which each cell value represented the percentage of participants having shaded it (Fig. 1). SPS were reported for the whole hand but were not distributed uniformly: Fig. 1 shows the presence of a distal-to-proximal gradient in the frequency map [53,54]. Computation of the relative spatial extent of sensations, i.e. the percentage of shaded cells within a segment (distal phalanx, intermediate phalanx, proximal phalanx, and palm) in comparison to the surface of the whole hand was carried out [54]. This analysis is based on the receptor density dispersion on the glabrous surface of the hand [78]. Relative surfaces were entered into an analysis specific to proportions [79] with the anatomical segments as the unique factor. A significant segment effect was found ($Q'(3) = 468.2$, $p < .000001$; Cramer's $V = .09$), with a greater SPS surface in the distal phalanx (11.68 %) than in the intermediate (11.03 %) and in the proximal (8.15 %) phalanges, as well as in the palm (7.96 %). This specific distribution is consistent with previous studies investigating SPS [53,54,56,57,61], presumably reflecting the distribution of peripheral receptive units and/or their trace within the somatosensory cortex. This gradient suggests that the task was carried out successfully.

Table 1
Mean (SD) indices for each frequency band, for TPJ – EBA and TPJ – AI functional 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)

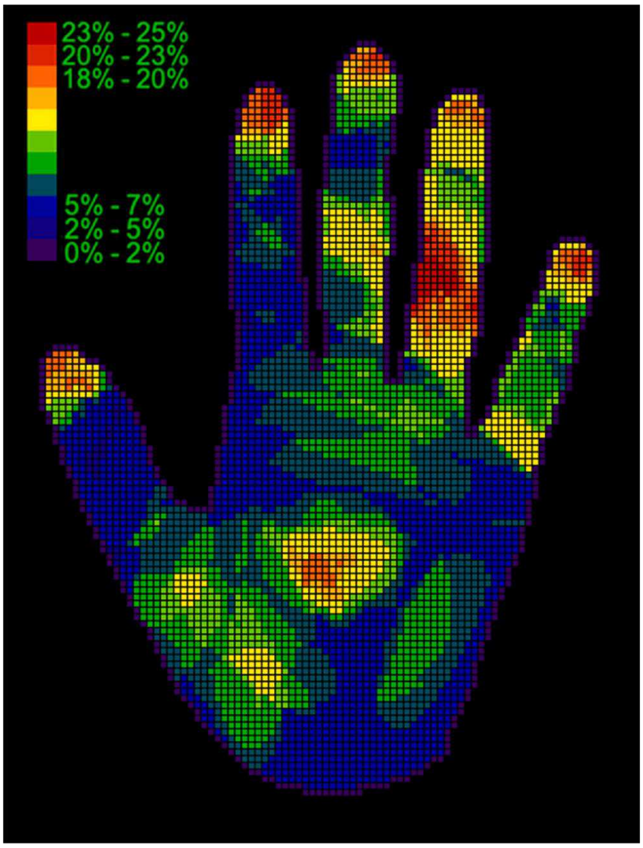

Fig. 1. Topographic map of SPS frequency (% of participants having shaded a cell) using a color scale: cool/blue colors reflect the least frequently shaded areas and hot/red colors the most frequently shaded areas.

2.4.2. Relationship between SPS frequency topography and functional connectivity

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

2.4.3. SPS frequency and TPJ-EBA connectivity

Reliability analysis performed on the indices of TPJ-EBA functional connectivity suggest good to very good reliability, through a Cronbach's α at 0.83, a McDonald's ϖ at 0.80 and an average interitem correlation

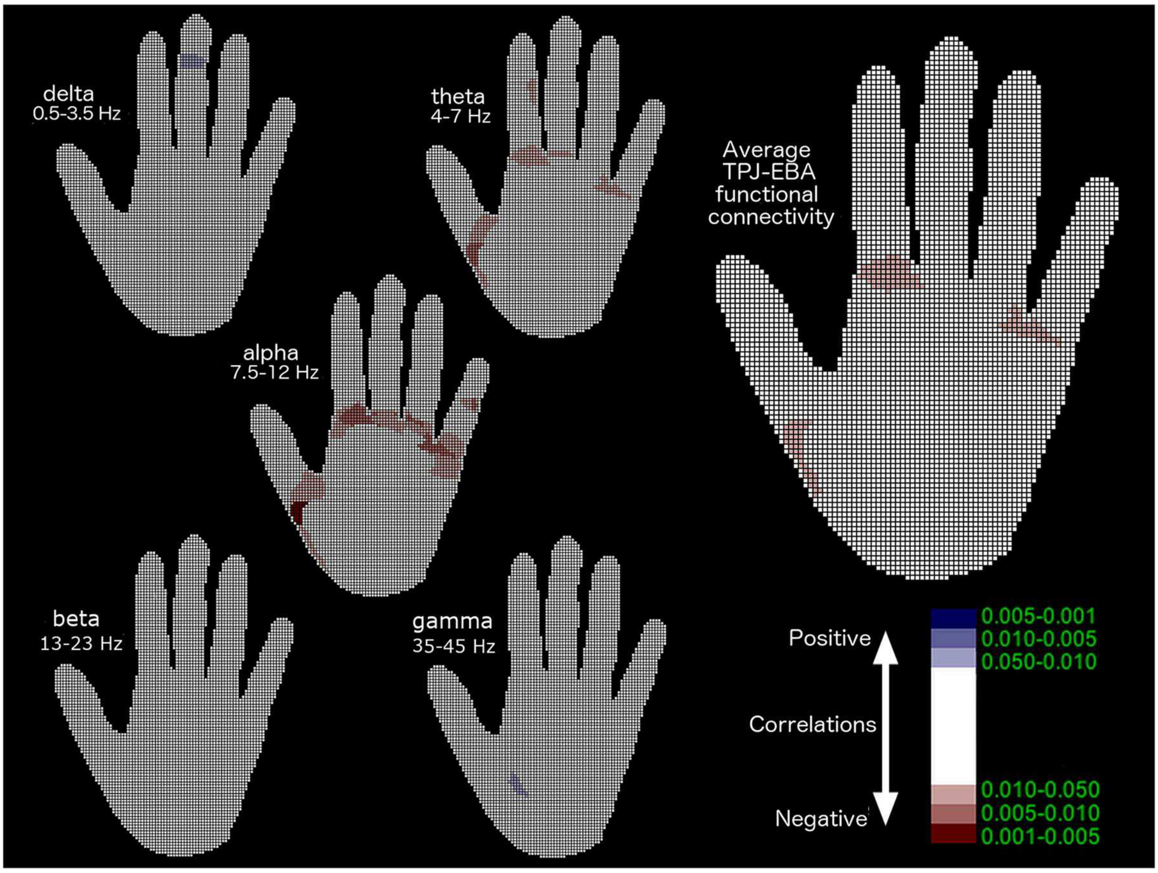

Fig. 2. Topographic probability maps of the correlations between SPS frequency and connectivity index in the delta, theta, alpha, beta, and gamma bands for TPJ-EBA connectivity. Bluish colors represent significant positive correlations and reddish colors represent significant negative correlations. The color intensity denotes the significance level.

|ρ| at 0.43.

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

2.4.4. SPS frequency and TPJ-AI connectivity

Reliability analysis performed on the indices of TPJ-AI functional connectivity suggest as well good to very good reliability, through a Cronbach's α at 0.77, a McDonald's ϖ at 0.80 and an average interitem correlation |ρ| at 0.39.

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

2.4.5. TPJ-EBA and TPJ-AI correlations

Surface percentages of significant correlations were analyzed using a Q' test (Fig. 4) [79] with the connectivity (TPJ-EBA vs TPJ-AI) and the frequency bands (delta, theta, alpha, beta, and gamma) as factors. The main effect of connectivity was highly significant ($Q'(1) = 259$, $p < .001$; Cramer's $V = .31$), with surfaces being overall larger for TPJ-AI connectivity than for TPJ-EBA connectivity. The connectivity x frequency band interaction was also significant ($Q'(4) = 816$, $p < .001$; Cramer's $V = .28$). Multiple corrected comparisons carried out with the Q' test [79] revealed that surfaces were reliably larger in the TPJ-AI than in the TPJ-EBA connectivity in the delta ($q' = 20.15$, $p < .001$), theta ($q' = 19.51$, $p < .001$), and beta ($q' = 14.07$, $p < .001$) bands, but an opposite pattern was observed in the alpha band where surfaces were larger for TPJ-EBA connectivity than for TPJ-AI connectivity ($q' = 9.05$, $p < .001$). Finally, no differences were found in the gamma band ($q' = 1.82$, $p = .51$). The larger correlated surfaces for TPJ-AI connectivity were observed in the theta band, forming a kind of peak, whilst the larger correlated surfaces for TPJ-EBA connectivity were observed in the alpha band. It is in the latter case that TPJ-EBA connectivity surfaces were larger than for TPJ-AI connectivity.

2.4.6. Other parameters

Based on previous studies [56], other parameters of SPS, i.e. spatial extent, mean perceived intensity of SPS, confidence in location and in extent, number of areas, spatial extent per area and variety of SPS

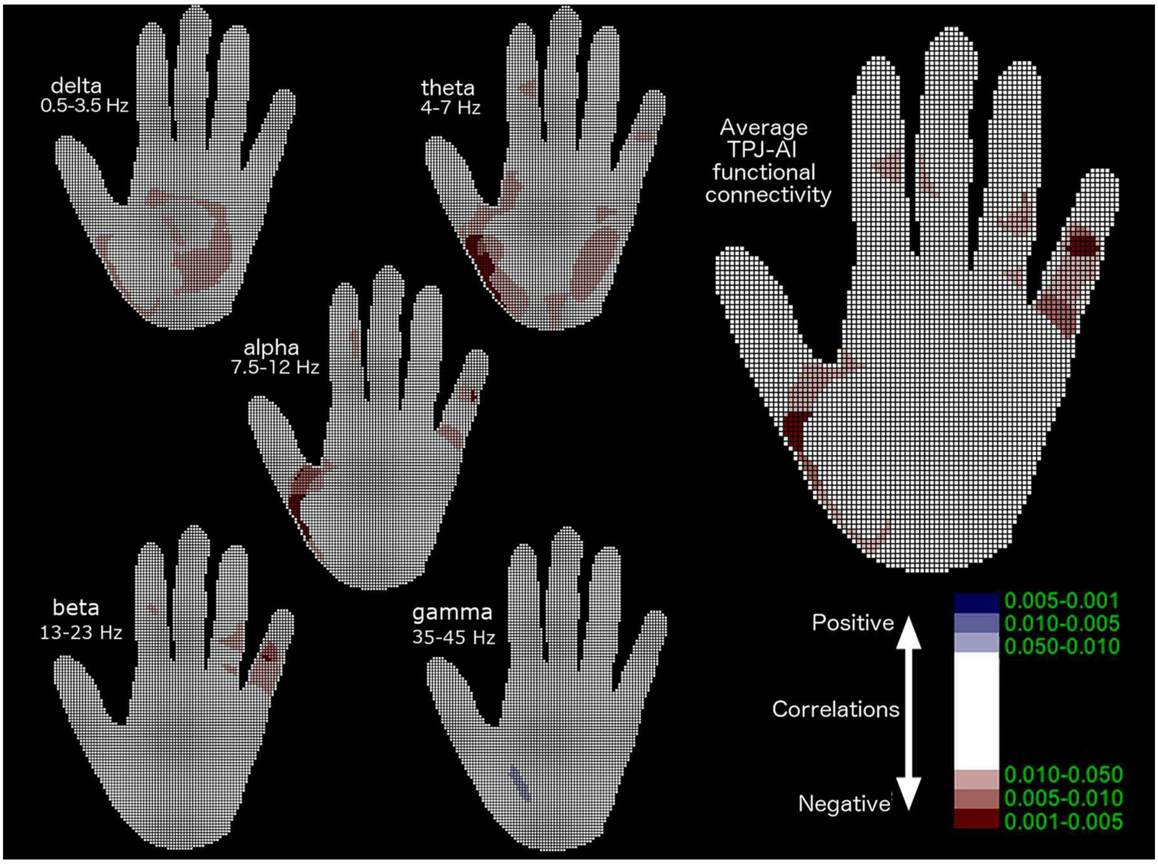

Fig. 3. Topographic probability maps of the correlations between SPS frequency and connectivity index in the delta, theta, alpha, beta, and gamma bands for TPJ-AI connectivity. Bluish colors represent significant positive correlations and reddish colors represent significant negative correlations. The color intensity denotes the significance level.

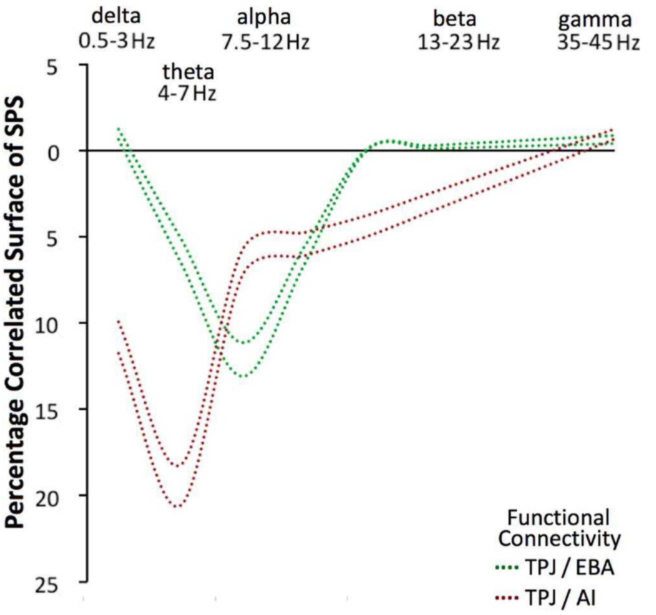

Fig. 4. Percentages of significant SPS surfaces correlated with each of the frequency bands, for TPJ-EBA and TPJ-AI connectivity, respectively. Values below 0 on the Y-axis represent percentages of negative correlations and above 0 represent percentages of positive correlations. The widths of the bands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

(Table 2), were considered for analysis. Analysis revealed good to very good reliability as suggested through the Cronbach's α at 0.78, the McDonald's ϖ at 0.83 and the average interitem correlation |ρ| at 0.34. 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 (β = -1.03, SEM = .36, $t(18)$ = -2.83, p = .01, R^2 = .22) and the spatial extent per area (β = -.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 (β = -.54, SEM = .21, $t(18)$ = -2.58, p = .02, R^2 = .24) and participants' confidence in the location of SPS (β = -.51, SEM = .22, $t(18)$ = -2.30, p = .03, R^2 = .13). Finally, body mass

Table 2
Mean (SD) of the parameters collected in the SPS task in both Experiments, other 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)

Table 3

Standardized β coefficients (1 SEM) and adjusted R^2 coefficient from the multiple regression analysis carried out on each of the 7 collected dependent variables with age, gender, body mass index, mean *z*-transformed connectivity index for TPJ-EBA and TPJ-AI connections, and scores for the General Activation, Calm and General Deactivation items of the ADCL as independent variables. Significant predictors at least at $p < .05$ are marked with an 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)◦	.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

index (BMI) negatively predicted the spatial extent per area ($\beta = .47$, SEM = .19, $t(18) = -2.50$, $p = .02$, $R^2 = .19$).

2.4.7. Types of sensations

All SPS types were reported at least once and some participants even reported other types of sensations, such as pins and needles, weightiness, and compression. Types of reported SPS were clustered in five categories based on previous studies [83,84]: thermal (warming and cooling), deep (beat/pulse and muscle tension), paresis-like (numbness and weightiness), surface (tickle, stretch, tingling, flatter, vibration, and compression), and pain-like (pins and needles and itch). SPS types were not clustered uniformly among these five categories ($\chi^2(4) = 84.95$, $p < .001$, Cramer's $V = .42$). Surface types of SPS were most likely to be perceived and reported (51.72 %), followed by deep (20.69 %), thermal (14.66 %), paresis-like (12.07 %), and then pain-like sensations (0.86 %). Each of the five categories of sensations as well as the sum of SPS reported were submitted to multiple regression analyses (not Bonferroni-corrected [81,82]) with the same predictors as before. No significant effect was observed.

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

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

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

Nonetheless, the arousal indices chosen in this experiment were declarative and direct, i.e. the list of adjectives was explicitly related to arousal, and this may have led to desirability bias. This may constitute a methodological flaw. The possibility of regression results stemming from desirability bias and common methodology variance needs to be ruled out. For this reason, we propose the use of a direct physiological index of arousal, i.e. skin conductance level (SCL). To our knowledge, only a single study investigated the association between SPS perception and arousal through physiological parameters and found no link between them [87]. However, Tihanyi and Köteles [87] used a different method to investigate the perception of SPS, in which SPS topography was not explored. We further propose to use an indirect and non-explicit declarative measure of arousal, through reporting of inner speech presence. According to Alderson-Day and Fernyhough [88], inner speech or self-talk is "a subjective experience of language in the absence of overt and audible articulation" (p.931). It is a demanding sustained cognitive activity, and as such, it increases stress and autonomic arousal as demonstrated through changes in breathing patterns and electromyography [89,90]. The general hypothesis is that SCL and inner speech, as parameters of arousal, would be negatively associated with SPS perception.

3. Experiment 2

3.1. Participants

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

3.2. Materials

3.2.1. Electrodermal recording at rest

Participants were seated in a comfortable armchair in a quiet room (room temperature ranged from 20 to 22 °C). Electrodermal activity was recorded using the BIOPAC System MP150 module and a GSR100C Amplifier with a sampling rate of 1000 Hz. Disposable Ag/AgCl electrodes (EL509) were attached to the palmar surface of the medial phalanges of the index and middle fingers of the non-dominant hand (all BIOPAC Systems, Inc., CA). Once the electrodes had been fitted, a 15-minute rest period was observed before the recordings began to allow the electrode gel to diffuse and to establish good baseline conductivity. Participants were then required to put on headphones and a sleep mask to minimize any sensory input interference. Participants then were asked to relax during the recording session and to avoid any movements and any irregular or deep breaths. The at-rest electrodermal activity recording started and lasted 5 min. An experimenter was present in the room at a distance from the participant to record any movements and deep breaths of the participant liable to produce unwanted electrodermal responses. Data were analyzed offline using AcqKnowledge 4.2 software (BIOPAC Systems, Inc., CA). A low-pass filter with a cut-off frequency of 0.05 Hz was applied. The SCL (μS) was computed as the mean value of skin conductance measured during the 5-minute resting phase.

3.2.2. *Inner speech*

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

3.2.3. *SPS task*

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

3.3. *Results*

3.3.1. *Skin conductance level*

The SCL level ranged from 2.06 to 31.1 μS, and the mean was 15.9 ± 7.77 μS. No reliable difference was found between men (14.8 ± 6.7 μS) and women (16.3 ± 8.3 μS, $t(24) = .43$, $p > .67$).

3.3.2. *Inner speech*

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

3.3.3. *SPS*

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

3.3.3.2. Other parameters. Regression analyses were carried out in order to understand whether the mean SCL predicted SPS parameters, i.e. overall spatial extent, spatial extent per area, intensity, variety, number of areas, confidence in location, and confidence in extent (Table 2). Once again, analysis revealed good to very good reliability as suggested through a Cronbach's α at 0.85, the McDonald's ϖ at 0.85 and the average interitem correlation $|\rho|$ at 0.39. Age, gender, body mass index, average and scores in the inner speech question (Mean = 2.65 ± 1.49, Min = 0, Max = 5) were also included in the analyses as independent variables. The results (not Bonferroni-corrected [81,82]) are presented in Table 4. We found that the average SCL significantly and negatively predicted the variety of SPS ($\beta = -.43$, SEM = .19, $t(20) = -2.25$, $p = .04$, $R^2 = .30$) as well as participants' confidence in location ($\beta = -.46$, SEM = .22, $t(20) = -2.09$, $p = .05$, $R^2 = .06$). Meanwhile, inner speech significantly and positively predicted the variety of SPS ($\beta = .55$, SEM = .20, $t(20) = 2.83$, $p = .01$, $R^2 = .30$). The gender of our participants also predicted significantly but negatively the variety of SPS ($\beta =$

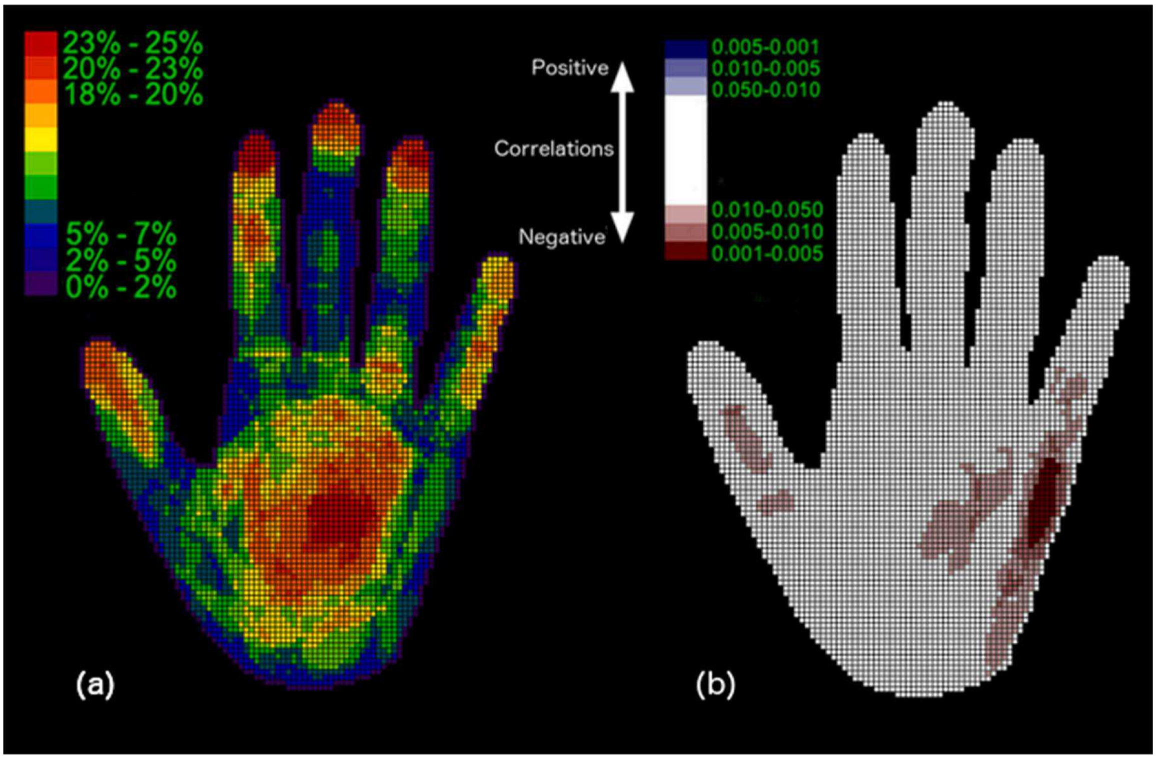

Fig. 5. Topographic maps. Left. Frequency map of SPS frequency (%) through a heat scale, cool/blue colors reflecting least frequently reported areas, and hot/red colors most frequently reported areas. Right. Probability map representing the correlations between SPS frequency and SCL. Bluish colors represent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

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

-.43, SEM = .17, $t(20) = -2.50$, p = .02, $R^2 = .30$), meaning that women reported a greater variety of SPS than men. Finally, participants' age significantly and positively predicted the SPS intensity ($\beta = .53$, SEM = .20, $t(20) = 2.60$, p = .02, $R^2 = .11$).

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

Experiment 2 was conducted to better acknowledge the association between arousal and the perception of SPS. Experiment 2 focused on a direct parameter of arousal, i.e. average SCL, as well as a self-reported and indirect parameter, i.e. inner speech, which was linked with arousal. This relationship between arousal and inner speech was confirmed here. In line with the first study, we hypothesized that these parameters would be negatively associated with SPS perception.

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

4. Discussion

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

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

4.1. *SPS and arousal*

Arousal has been investigated with the use of three indices: SCL, a self-reported arousal trait measure, and inner speech. We found that SCL correlated negatively with SPS frequency. It also negatively predicted the variety of SPS and participants' confidence in their location. Increased self-reported arousal trait predicted lower intensities of SPS and weaker confidence in their location. Finally, a greater presence of inner speech positively predicted the variety of SPS, but in interaction with gender and SCL. The variety of SPS was greater for women with a greater presence of inner speech and lower SCL. Inner speech is thought to be linked with arousal as shown both in past research [37] and in the present study. Morin and Michaud [92] suggested that inner speech would appear to be involved in the acquisition of self-information, meaning that collecting information through an inner speech about oneself raises the perception of various SPS, especially in women with low levels of arousal. All these data are in agreement with our hypothesis that increased arousal would dampen the perception of SPS. However, they also suggest that multiple other factors may determine the perception of SPS.

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

Another line of evidence suggests that high arousal reliably predicts spontaneous brain activity, in that a subject with high arousal levels would show decreased activation of the brain network involved in self-referential processes [6], i.e. the default mode network. Indeed, previous findings showed that SPS frequency, intensity, and participants' confidence in location, were greater with increased propensity to mind wandering [57], a cognitive activity associated with the default mode network [93,94]. These findings are consistent overall with the suggestion that activity in the default mode network allows better perception of SPS, and therefore increases self-awareness [57]. Also, decreased activity of the default mode network associated with increased attention away from the body dampens perception of SPS and therefore decreases self-awareness. These observations tally well with the idea that attention directed to and maintained on the self is a necessary condition for the development of self-awareness [1,95].

4.2. SPS and brain networks involved in self-awareness

Directing attention away from the self and toward the environment involves a network that anticorrelates with the default mode network [59]. Among the key node structures of this attention network are the TPJ and the AI, which have also been associated with embodiment and self-location [15,18]. Another area, independent of this network, has also been associated with embodiment, the EBA [18]. Both the EBA and the AI are functionally connected to the TPJ [2,7,18]. However, belonging to the attention network or not suggests that these connections might serve different functions, and therefore contribute differently to self-awareness. We found that, independently of frequency bands, increased TPJ-EBA functional connectivity was associated with lower perceived frequency of SPS. In turn, high TPJ-AI functional connectivity was associated with lower SPS frequency, smaller spatial extent, and smaller surfaces per sensitive area. These results are consistent overall with our findings linking high arousal with lowered SPS perception. Indeed, TPJ and AI activation are associated with high arousal [6]. Moreover, the TPJ and AI are part of the ventral attention network, whose activity has been closely linked with arousal through the locus coeruleus noradrenergic system [36,50]. Greater connectivity among areas of this network would dampen the perception of SPS. Attention directed away from the body suppresses SPS [53–55]. Nevertheless, taken altogether, these findings indicate that high connectivity between the TPJ and structures implicated in self-awareness experiences such as the AI or the EBA will impair the perception of SPS. The TPJ is a multisensory integration hub [18], as such abnormal functioning of the TPJ would be associated with imperfect integration, resulting in disturbed self-awareness and embodiment [18,85,96]. This would present as asomatognosia and autoscopic experiences, such as out-of-body experiences, autoscopy, feeling of presence, depersonalization, failure of self-agency, etc. [20,23,97,98]. In our study, high connectivity between the TPJ and AI, and the TPJ and EBA, seems to be associated with a high propensity to altered bodily experiences as SPS.

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

4.3. Limitations and future directions

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

It is noteworthy to mention that, in Experiment 1, the resting-state task and the SPS task were separated by a 45-minute computerized visuospatial task. Separating the resting task and the SPS task by a third task reduces their contamination. However, some influence from the visuospatial task might be observed, such as tiredness.

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

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

5. Conclusion

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

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CRediT authorship contribution statement

Sara Salgues: Conceptualization, Investigation, Formal analysis, Writing - original draft. **Gaën Plancher:** Supervision, Writing - review & editing. **Laurence Jacquot:** Investigation. **Janick Naveteur:** Writing - review & editing. **Lison Fanuel:** Investigation. **Germán Gálvez-García:** Writing - review & editing. **George A. Michael:** Conceptualization,

Supervision, Project administration, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.bbr.2020.112880.

References

[1] M. Kinsbourne, Awareness of one's own body: an attentional theory of its nature, development, and brain basis, in: J. Bermúdez (Ed.), The Body and the Self, The MIT Press, 1998, pp. 205–223.

[2] R.B. Mars, J. Sallet, U. Schüffelgen, S. Jbabdi, I. Toni, M.F.S. Rushworth, Connectivity-based subdivisions of the human right 'temporoparietal junction area': evidence for different areas participating in different cortical networks, Cereb. Cortex 22 (August 8) (2012) 1894–1903, https://doi.org/10.1093/cercor/bhr268.

[3] K.M. Igelström, T.W. Webb, M.S.A. Graziano, Neural processes in the human temporoparietal cortex separated by localized independent component analysis, J. Neurosci. 35 (June 25) (2015) 9432–9445, https://doi.org/10.1523/JNEUROSCI.0551-15.2015.

[4] D. Bzdok, et al., Characterization of the temporo-parietal junction by combining data-driven parcellation, complementary connectivity analyses, and functional decoding, Neuroimage 81 (November) (2013) 381–392, https://doi.org/10.1016/j.neuroimage.2013.05.046.

[5] M. Corbetta, G.L. Shulman, Control of goal-directed and stimulus-driven attention in the brain, Nat. Rev. Neurosci. 3 (3) (2002) 201–215, https://doi.org/10.1038/nrn755.

[6] J. Fan, et al., Spontaneous brain activity relates to autonomic arousal, J. Neurosci. 32 (August 33) (2012) 11176–11186, https://doi.org/10.1523/JNEUROSCI.1172-12.2012.

[7] K.M. Igelström, M.S.A. Graziano, The inferior parietal lobule and temporoparietal junction: a network perspective, Neuropsychologia 105 (October) (2017) 70–83, https://doi.org/10.1016/j.neuropsychologia.2017.01.001.

[8] R.M. Carter, S.A. Huettel, A nexus model of the temporal-parietal junction, Trends Cogn. Sci. 17 (July 7) (2013) 328–336, https://doi.org/10.1016/j.tics.2013.05.007.

[9] K.M. Igelström, T.W. Webb, Y.T. Kelly, M.S.A. Graziano, Topographical organization of attentional, social, and memory processes in the human temporoparietal cortex, eNeuro 3 (2) (2016) 1363–1377, https://doi.org/10.1523/ENEURO.0060-16.2016.

[10] C.M. Eddy, The junction between self and other? Temporo-parietal dysfunction in neuropsychiatry, Neuropsychologia 89 (August) (2016) 465–477, https://doi.org/10.1016/j.neuropsychologia.2016.07.030. Elsevier Ltd.

[11] C. Farrer, et al., Neural correlates of action attribution in schizophrenia, Psychiatry Res. - Neuroimaging 131 (1) (2004) 31–44, https://doi.org/10.1016/j.pscychresns.2004.02.004.

[12] A.K. Martin, J. Huang, A. Hunold, M. Meinzer, Dissociable roles within the social brain for self–other processing: a HD-tDCS study, Cereb. Cortex 29 (August 8) (2019) 3642–3654, https://doi.org/10.1093/cercor/bhy238.

[13] H. Wang, E. Callaghan, G. Gooding-Williams, C. McAllister, K. Kessler, Rhythm makes the world go round: an MEG-TMS study on the role of right TPJ theta oscillations in embodied perspective taking, Cortex 75 (February) (2016) 68–81, https://doi.org/10.1016/j.cortex.2015.11.011.

[14] S. Ionta, et al., Multisensory mechanisms in temporo-parietal cortex support self-location and first-person perspective, Neuron 70 (April 2) (2011) 363–374, https://doi.org/10.1016/j.neuron.2011.03.009.

[15] S. Ionta, R. Martuzzi, R. Salomon, O. Blanke, The brain network reflecting bodily self-consciousness: a functional connectivity study, Soc. Cogn. Affect. Neurosci. 9 (12) (2013) 1904–1913, https://doi.org/10.1093/scan/nst185.

[16] M. Jeannerod, E. Pacherie, Agency, Simulation and Self-identification, # Blackwell Publishing Ltd, 2004.

[17] M. Sperduti, P. Delaveau, P. Fossati, J. Nadel, Different brain structures related to self- and external-agency attribution: a brief review and meta-analysis, Brain Struct. Funct. 216 (June 2) (2011) 151–157, https://doi.org/10.1007/s00429-010-0298-1.

[18] S. Arzy, G. Thut, C. Mohr, C.M. Michel, O. Blanke, Neural basis of embodiment: distinct contributions of temporoparietal junction and extrastriate body area, J. Neurosci. 26 (August 31) (2006) 8074–8081, https://doi.org/10.1523/JNEUROSCI.0745-06.2006.

[19] A.K. Martin, K. Kessler, S. Cooke, J. Huang, M. Meinzer, The right temporoparietal junction is causally associated with embodied perspective-taking, J. Neurosci. 40 (April 15) (2020) 3089–3095, https://doi.org/10.1523/JNEUROSCI.2637-19.2020.

[20] C. Lopez, P. Halje, O. Blanke, Body ownership and embodiment: vestibular and multisensory mechanisms, Neurophysiol. Clin. Neurophysiol. 38 (June 3) (2008) 149–161, https://doi.org/10.1016/j.neucli.2007.12.006.

[21] O. Blanke, T. Landis, L. Spinelli, M. Seeck, Out-of-body experience and autoscopy of neurological origin, Brain 127 (2) (2004) 243–258, https://doi.org/10.1093/brain/awh040. Oxford University Press.

[22] O. Blanke, et al., Linking out-of-body experience and self processing to mental own-body imagery at the temporoparietal junction, J. Neurosci. 25 (January 3) (2005) 550–557, https://doi.org/10.1523/JNEUROSCI.2612-04.2005.

[23] O. Blanke, C. Mohr, Out-of-body experience, heautoscopy, and autoscopic hallucination of neurological origin: implications for neurocognitive mechanisms of corporeal awareness and self-consciousness, Brain Res. Rev. 50 (December 1) (2005) 184–199, https://doi.org/10.1016/j.brainresrev.2005.05.008.

[24] S. Lacey, et al., Engagement of the left extrastriate body area during body-part metaphor comprehension, Brain Lang. 166 (March) (2017) 1–18, https://doi.org/10.1016/j.bandl.2016.11.004.

[25] C. Urgesi, G. Berlucchi, S.M. Aglioti, Magnetic stimulation of extrastriate body area impairs visual processing of nonfacial body parts, Curr. Biol. 14 (2004) 2130–2134, https://doi.org/10.1016/j.

[26] D. Perruchoud, L. Michels, M. Piccirelli, R. Gassert, S. Ionta, Differential neural encoding of sensorimotor and visual body representations, Sci. Rep. 6 (November) (2016), https://doi.org/10.1038/srep37259.

[27] J. Limanowski, A. Lutti, F. Blankenburg, The extrastriate body area is involved in illusory limb ownership, Neuroimage 86 (February) (2014) 514–524, https://doi.org/10.1016/j.neuroimage.2013.10.035.

[28] A.D.B. Craig, Interoception: the sense of the physiological condition of the body, Curr. Opin. Neurobiol. 13 (4) (2003) 500–505, https://doi.org/10.1016/S0959-4388(03)00090-4. Elsevier Ltd.

[29] A.D.B. Craig, How do you feel - now? The anterior insula and human awareness, Nat. Rev. Neurosci. 10 (1) (2009) 59–70, https://doi.org/10.1038/nrn2555.

[30] A.D.B. Craig, Significance of the insula for the evolution of human awareness of feelings from the body, Ann. N. Y. Acad. Sci. 1225 (1) (2011) 72–82, https://doi.org/10.1111/j.1749-6632.2011.05990.x.

[31] O. Pollatos, R. Schandry, D.P. Auer, C. Kaufmann, Brain structures mediating cardiovascular arousal and interoceptive awareness, Brain Res. 1141 (April 1) (2007) 178–187, https://doi.org/10.1016/j.brainres.2007.01.026.

[32] A. Kucyi, M. Moayedi, I. Weissman-Fogel, M. Hodaie, K.D. Davis, Hemispheric asymmetry in white matter connectivity of the temporoparietal junction with the insula and prefrontal cortex, PLoS One 7 (April 4) (2012), https://doi.org/10.1371/journal.pone.0035589.

[33] Q. Wu, et al., A critical role of temporoparietal junction in the integration of top-down and bottom-up attentional control, Hum. Brain Mapp. 36 (November 11) (2015) 4317–4333, https://doi.org/10.1002/hbm.22919.

[34] H.D. Critchley, R. Elliott, C.J. Mathias, R.J. Dolan, Neural activity relating to generation and representation of galvanic skin conductance responses: a functional magnetic resonance imaging study, J. Neurosci. 20 (8) (2000) 3033–3040, https://doi.org/10.1523/jneurosci.20-08-03033.2000.

[35] Y. Nagai, H.D. Critchley, E. Featherstone, M.R. Trimble, R.J. Dolan, Activity in ventromedial prefrontal cortex covaries with sympathetic skin conductance level: a physiological account of a 'default mode' of brain function, Neuroimage 22 (May 1) (2004) 243–251, https://doi.org/10.1016/j.neuroimage.2004.01.019.

[36] S.J. Sara, S. Bouret, Orienting and reorienting: the locus coeruleus mediates cognition through arousal, Neuron 76 (October 1) (2012) 130–141, https://doi.org/10.1016/j.neuron.2012.09.011.

[37] R. Nikula, Psychological correlates of nonspecific skin conductance responses, Psychophysiology 28 (1) (1991) 86–90, https://doi.org/10.1111/j.1469-8986.1991.tb03392.x.

[38] H.D. Critchley, Electrodermal responses: what happens in the brain, Neuroscientist 8 (2) (2002) 132–142, https://doi.org/10.1177/107385840200800209.

[39] H.D. Critchley, R.N. Melmed, E. Featherstone, C.J. Mathias, R.J. Dolan, Volitional control of autonomic arousal: a functional magnetic resonance study, Neuroimage 16 (4) (2002) 909–919, https://doi.org/10.1006/nimg.2002.1147.

[40] O. Pollatos, B.M. Herbert, E. Matthias, R. Schandry, Heart rate response after emotional picture presentation is modulated by interoceptive awareness, Int. J. Psychophysiol. 63 (January 1) (2007) 117–124, https://doi.org/10.1016/j.ijpsycho.2006.09.003.

[41] R.J. Barry, A.R. Clarke, M. Hajos, R. McCarthy, M. Selikowitz, F.E. Dupuy, Resting-state EEG gamma activity in children with Attention-Deficit/Hyperactivity Disorder, Clin. Neurophysiol. 121 (November 11) (2010) 1871–1877, https://doi.org/10.1016/j.clinph.2010.04.022.

[42] D. Karamacoska, R.J. Barry, G.Z. Steiner, E.P. Coleman, E.J. Wilson, Intrinsic EEG and task-related changes in EEG affect Go/NoGo task performance, Int. J. Psychophysiol. 125 (March) (2018) 17–28, https://doi.org/10.1016/j.ijpsycho.2018.01.015.

[43] M.S. Clayton, N. Yeung, R. Cohen Kadosh, The roles of cortical oscillations in sustained attention, Trends Cogn. Sci. 19 (April 4) (2015) 188–195, https://doi.org/10.1016/j.tics.2015.02.004. Elsevier Ltd.

[44] K. Van der Hiele, et al., EEG markers of future cognitive performance in the elderly, J. Clin. Neurophysiol. 25 (2) (2008) 83–89 [Online]. Available: http://ovidsp.ovid.com/ovidweb.cgi?T=JS&PAGE=reference&D=emed8&NEWS=N&AN=2008170890.

[45] S. Finnigan, I.H. Robertson, Resting EEG theta power correlates with cognitive performance in healthy older adults, Psychophysiology 48 (August 8) (2011) 1083–1087, https://doi.org/10.1111/j.1469-8986.2010.01173.x.

[46] M. Benedek, R.J. Schickel, E. Jauk, A. Fink, A.C. Neubauer, Alpha power increases in right parietal cortex reflects focused internal attention, Neuropsychologia 56 (1) (2014) 393–400, https://doi.org/10.1016/j.neuropsychologia.2014.02.010.

[47] H. Laufs, et al., Electroencephalographic signatures of attentional and cognitive default modes in spontaneous brain activity fluctuations at rest, Proc. Natl. Acad. Sci. U. S. A. 100 (19) (2003) 11053–11058, https://doi.org/10.1073/pnas.1831638100.

[48] M. Çiçek, E. Nalçac, Interhemispheric asymmetry of EEG alpha activity at rest and during the Wisconsin Card sorting Test: relations with performance, Biol. Psychol. 58 (1) (2001) 75–88, https://doi.org/10.1016/S0301-0511(01)00103-X.

[49] P.M. Keune, et al., Exploring resting-state EEG brain oscillatory activity in relation to cognitive functioning in multiple sclerosis, Clin. Neurophysiol. 128 (September 9) (2017) 1746–1754, https://doi.org/10.1016/j.clinph.2017.06.253.

[50] M. Corbetta, G.H. Patel, G.L. Shulman, The reorienting system of the human brain: from environment to theory of mind, Neuron 58 (May 3) (2008) 306–324, https://doi.org/10.1016/j.neuron.2008.04.017.

[51] M.F. Scheier, C.S. Carver, F.X. Gibbons, Self-directed attention, awareness of bodily states, and suggestibility, J. Pers. Soc. Psychol. 37 (9) (1979) 1576–1588, https://doi.org/10.1037//0022-3514.37.9.1576.

[52] D.M. Wegner, T. Giuliano, Arousal-induced attention to self, J. Pers. Soc. Psychol. 38 (5) (1980) 719–726, https://doi.org/10.1037//0022-3514.38.5.719.

[53] G.A. Michael, J. Naveteur, The tickly homunculus and the origins of spontaneous sensations arising on the hands, Conscious. Cogn. 20 (September 3) (2011) 603–617, https://doi.org/10.1016/j.concog.2010.11.013.

[54] G.A. Michael, M.A. Dupuy, A. Deleuze, M. Humblot, B. Simon, J. Naveteur, Interacting effects of vision and attention in perceiving spontaneous sensations arising on the hands, Exp. Brain Res. 216 (January1) (2012) 21–34, https://doi.org/10.1007/s00221-011-2901-y.

[55] J. Naveteur, M.A. Dupuy, F. Gabrielli, G.A. Michael, How we perceive our own hands: effects of attention, aging, and sex, Somatosens. Mot. Res. 32 (October 4) (2015) 227–235, https://doi.org/10.3109/08990220.2015.1086326.

[56] G.A. Michael, J. Naveteur, M.A. Dupuy, L. Jacquot, My heart is in my hands: the interoceptive nature of the spontaneous sensations felt on the hands, Physiol. Behav. 143 (May) (2015) 113–120, https://doi.org/10.1016/j.physbeh.2015.02.030.

[57] G.A. Michael, I. Tapiero, G. Gálvez-García, L. Jacquot, Thoughts and sensations, twin galaxies of the inner space: the propensity to mind-wander relates to spontaneous sensations arising on the hands, Conscious. Cogn. 55 (October) (2017) 223–231, https://doi.org/10.1016/j.concog.2017.08.007.

[58] A. Morin, Levels of consciousness and self-awareness: a comparison and integration of various neurocognitive views, Conscious. Cogn. 15 (June 2) (2006) 358–371, https://doi.org/10.1016/j.concog.2005.09.006.

[59] M.D. Fox, A.Z. Snyder, J.L. Vincent, M. Corbetta, D.C. Van Essen, M.E. Raichle, The human brain is intrinsically organized into dynamic, anticorrelated functional networks, Proc. Natl. Acad. Sci. U. S. A. 102 (27) (2005) 9673–9678, https://doi.org/10.1073/pnas.0504136102.

[60] A.M. Schell, M.E. Dawson, D.L. Filion, Psychophysiological correlates of electrodermal lability, Psychophysiology 25 (6) (1988) 619–632, https://doi.org/10.1111/j.1469-8986.1988.tb01899.x.

[61] C. Borg, F.C. Emond, D. Colson, B. Laurent, G.A. Michael, Attentional focus on subjective interoceptive experience in patients with fibromyalgia, Brain Cogn. 101 (December) (2015) 35–43, https://doi.org/10.1016/j.bandc.2015.10.002.

[62] R.E. Thayer, Measurement of activation through self-report, Psychol. Rep. 20 (2) (1967) 663–678, https://doi.org/10.2466/pr0.1967.20.2.663.

[63] R.E. Thayer, Activation states as assessed by verbal report and four psychophysiological variables, Psychophysiology 7 (1) (1970) 86–94, https://doi.org/10.1111/j.1469-8986.1970.tb02278.x.

[64] L.A. Clark, D. Watson, Constructing validity: basic issues in objective scale development, Psychol. Assess. 7 (3) (1995) 309–319, https://doi.org/10.1037/1040-3590.7.3.309.

[65] V. Jurcak, D. Tsuzuki, I. Dan, 10/20, 10/10, and 10/5 systems revisited: their validity as relative head-surface-based positioning systems, Neuroimage 34 (February 4) (2007) 1600–1611, https://doi.org/10.1016/j.neuroimage.2006.09.024.

[66] G. Macefield, S.C. Gandevia, D. Burke, Perceptual responses to microstimulation of single afferents innervating joints, muscles and skin of the human hand, J. Physiol. 429 (1) (1990) 113–129, https://doi.org/10.1113/jphysiol.1990.sp018247.

[67] J. Ochoa, H.E. Torebjörk, Sensations evoked by intraneural microstimulation of single mechanoreceptor units innervating the human hand, J. Physiol. 342 (1) (1983) 633–654, https://doi.org/10.1113/jphysiol.1983.sp014873.

[68] J. Naveteur, J. Honoré, G.A. Michael, How to detect an electrocutaneous shock which is not delivered? Overt spatial attention influences decision, Behav. Brain Res. 165 (December 2) (2005) 254–261, https://doi.org/10.1016/j.bbr.2005.07.001.

[69] G. Gratton, M.G.H. Coles, E. Donchin, A new method for off-line removal of ocular artifact, Electroencephalogr. Clin. Neurophysiol. 55 (4) (1983) 468–484, https://doi.org/10.1016/0013-4694(83)90135-9.

[70] A.C.N. Chen, W. Feng, H. Zhao, Y. Yin, P. Wang, EEG default mode network in the human brain: spectral regional field powers, Neuroimage 41 (June 2) (2008) 561–574, https://doi.org/10.1016/j.neuroimage.2007.12.064.

[71] R.J. Barry, A.R. Clarke, S.J. Johnstone, Caffeine and opening the eyes have additive effects on resting arousal measures, Clin. Neurophysiol. 122 (October 10) (2011) 2010–2015, https://doi.org/10.1016/j.clinph.2011.02.036.

[72] R.D. Pascual-Marqui, et al., Assessing interactions in the brain with exact low-resolution electromagnetic tomography, Philos. Trans. R. Soc. A Math. Phys. Eng. Sci. 369 (October 1952) (2011) 3768–3784, https://doi.org/10.1098/rsta.2011.0081.

[73] C. Imperatori, et al., Default Mode Network alterations in alexithymia: an EEG power spectra and connectivity study, Sci. Rep. 6 (November) (2016), https://doi.org/10.1038/srep36653.

[74] L. Canuet, et al., Resting-state network disruption and APOE genotype in Alzheimer's disease: a lagged functional connectivity study, PLoS One 7 (September 9) (2012), https://doi.org/10.1371/journal.pone.0046289.

[75] L. Canuet, et al., Resting-state EEG source localization and functional connectivity in schizophrenia-like psychosis of epilepsy, PLoS One 6 (November 11) (2011), https://doi.org/10.1371/journal.pone.0027863.

[76] M. Hata, et al., Functional connectivity assessed by resting state EEG correlates with cognitive decline of Alzheimer's disease - an eLORETA study, Clin. Neurophysiol. 127 (February 2) (2016) 1269–1278, https://doi.org/10.1016/j.clinph.2015.10.030.

[77] A.D.B. Craig, K. Chen, D. Bandy, E.M. Reiman, Thermosensory activation of insular cortex, Nat. Neurosci. 3 (2) (2000) 184–190, https://doi.org/10.1038/72131.

[78] R.S. Johansson, A.B. Vallbo, Detection of tactile stimuli. Thresholds of afferent units related to psychophysical thresholds in the human hand, J. Physiol. 297 (1) (1979) 405–422, https://doi.org/10.1113/jphysiol.1979.sp013048.

[79] G.A. Michael, A significance test of interaction in 2 x K designs with proportions, Tutor. Quant. Methods Psychol. 3 (1) (2007) 1–7, https://doi.org/10.20982/tqmp.03.1.p001.

[80] M. Kulldorff, A spatial scan statistic, Commun. Stat. - Theory Methods 26 (6) (1997) 1481–1496, https://doi.org/10.1080/03610929708831995.

[81] R.J. Cabin, R.J. Mitchell, E. Siemann, D. Wedin, K.S.N. Bio, To bonferroni or not to bonferroni : when and how are the questions, Source Bull. Ecol. Soc. Am. 81 (3) (2000) 246–248.

[82] T.V. Perneger, What's wrong with Bonferroni adjustments, Br. Med. J. 316 (7139) (1998) 1236–1238, https://doi.org/10.1136/bmj.316.7139.1236.

[83] R. Beaudoin, G.A. Michael, Gating of spontaneous somatic sensations by movement, Somatosens. Mot. Res. 31 (3) (2014) 111–121, https://doi.org/10.3109/08990220.2014.888992.

[84] A.B. Vallbo, Sensations evoked from the glabrous skin of the human hand by electrical stimulation of unitary mechanosensitive afferents, Brain Res. 215 (1–2) (1981) 359–363, https://doi.org/10.1016/0006-8993(81)90517-5.

[85] S. Arzy, C. Mohr, C.M. Michel, O. Blanke, Duration and not strength of activation in temporo-parietal cortex positively correlates with schizotypy, Neuroimage 35 (March 1) (2007) 326–333, https://doi.org/10.1016/j.neuroimage.2006.11.027.

[86] L.Q. Uddin, et al., Dissociable connectivity within human angular gyrus and intraparietal sulcus: evidence from functional and structural connectivity, Cereb. Cortex 20 (November 11) (2010) 2636–2646, https://doi.org/10.1093/cercor/bhq011.

[87] B.T. Tihanyi, F. Köteles, Physiological and psychological correlates of attention-related body sensations (tingling and warmth), Physiol. Int. 104 (September 3) (2017) 235–246, https://doi.org/10.1556/2060.104.2017.3.4.

[88] B. Alderson-Day, C. Fernyhough, Relations among questionnaire and experience sampling measures of inner speech: a smartphone app study, Front. Psychol. 6 (April) (2015), https://doi.org/10.3389/fpsyg.2015.00517.

[89] J.T. Cacioppo, R.E. Petty, Electromyographic specificity during covert information processing, Psychophysiology 18 (5) (1981) 518–523, https://doi.org/10.1111/j.1469-8986.1981.tb01819.x.

[90] M.S. Chapell, Inner speech and respiration: toward a possible mechanism of stress reduction, Percept. Mot. Skills 79 (2) (1994) 803–811, https://doi.org/10.2466/pms.1994.79.2.803.

[91] A. Morin, B. Uttl, B. Hamper, Self-reported frequency, content, and functions of inner speech, Procedia - Soc. Behav. Sci. 30 (2011) 1714–1718, https://doi.org/10.1016/j.sbspro.2011.10.331.

[92] A. Morin, J. Michaud, Self-awareness and the left inferior frontal gyrus: Inner speech use during self-related processing, Brain Res. Bull. 74 (November 6) (2007) 387–396, https://doi.org/10.1016/j.brainresbull.2007.06.013.

[93] S. Kajimura, T. Kochiyama, R. Nakai, N. Abe, M. Nomura, Causal relationship between effective connectivity within the default mode network and mind-wandering regulation and facilitation, Neuroimage 133 (June) (2016) 21–30, https://doi.org/10.1016/j.neuroimage.2016.03.009.

[94] M.F. Mason, et al., Wandering minds: stimulus-independent thought, Science (80-.) 315 (January) (2007) 393–395, https://doi.org/10.1126/science.1131295.

[95] D.M. Wolpert, S.J. Goodbody, M. Husain, Maintaining internal representations : the role of the human superior parietal lobe, Nat. Neurosci. 1 (6) (1998) 529–533, https://doi.org/10.1038/2245.

[96] O. Blanke, S. Arzy, The out-of-body experience: disturbed self-processing at the temporo-parietal junction, Neuroscientist 11 (February 1) (2005) 16–24, https://doi.org/10.1177/1073858404270885.

[97] P.H. Donaldson, N.J. Rinehart, P.G. Enticott, Noninvasive stimulation of the temporoparietal junction: a systematic review, Neurosci. Biobehav. Rev. 55 (August) (2015) 547–572, https://doi.org/10.1016/j.neubiorev.2015.05.017. Elsevier Ltd.

[98] S.A. Spence, D.J. Brooks, S.R. Hirsch, P.F. Liddle, J. Meehan, P.M. Grasby, A PET study of voluntary movement in schizophrenic patients experiencing passivity